Transactions of the Wisconsin Academy of Sciences, Arts and Letters. volume 86 1998

Madison, Wis.: Wisconsin Academy of Sciences, Arts and Letters, 1998

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TRANSACTIONS

of the Wisconsin Academy of Sciences, Arts and Letters

Volume 86 • 1998

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Transactions welcomes articles that explore features of the State of Wisconsin and its people. Articles written by Wisconsin authors on topics other than Wisconsin sciences, arts and letters are occasionally published. Manuscripts and queries should be addressed to the editor.

Submission requirements: Submit three copies of the manuscript, double-spaced, to the editor. Abstracts are suggested for science/technical articles. The style of the text and references may follow that of scholarly writing in the author's field. Please prepare figures with reduction in mind.

ISSN 0084-0505

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II. Wisconsin Sesquicentennial Feature Articles

Wisconsin's early writers made literary history in a variety of forms, but following careful scrutiny, several "firsts" in various genres cannot retain their particular distinction.

Though the 1875 book, *Bachelor Ben* by Ella Giles Ruddy, traditionally has been considered Wisconsin's first novel, there are a handful of earlier candidates. Difficulties in determining identities of authors and residency in the state abound, but a novel by Juliette Magill Kinzie seems the best choice for the honor.

III. Wisconsin Fauna

Deer reproductive performance was documented at a time when regional populations were close to prescribed density goals.

Sixty-eight foods eaten by black bears varied with each month of summer and availability in various forest communities.

After 19 years of no harvest, heavy harvest of beaver (3.9/colony) caused a subsequent increase in production insufficient to maintain the population size.

From the Editor

Charles Darwin's *The Voyage of the Beagle,* which chronicles his nearly five-year journey of discovery around the world in 1831–1836, is a classic both as natural history and as literature. A section I return to often is Chapter XVII, which records his amazing observations on the volcanic islands of the Galapagos Archipelago in September and October 1835. Here, for example, is his description of Chatham Island:

> Nothing could be less inviting than the first appearance. A broken field of black basaltic lava, thrown into the most rugged waves, and crossed by great fissures, is every where covered by stunted, sunburnt brushwood, which shows little signs of life . . . . The brushwood appears, from a short distance, as leafless as our trees during winter; and it was some time before I discovered that not only almost every plant was now in full leaf, but that the greater number were in flower. The commonest bush is one of the Euphorbiaceae: an acacia and a great odd-looking cactus are the only trees which afford any shade.

A few days later, after visiting Albemarle and Narborough Islands, the first of which Darwin characterizes as "miserably sterile" in large stretches and both of which he pictures as "covered with immense deluges of black naked lava," Darwin seemed almost relieved to finally note the presence of real trees, "several being two feet and some even two feet nine inches in diameter" on James Island.

How different are these scenes from typical September and October landscapes in Wisconsin, where trees reign supreme in their resplendent Fall costume!

As I write this editor's column in early October, I feel the lingering cold of today's brisk wind on my nose and cheeks. Inside my head I hear echoes of the fallen leaves crunched beneath my steps as I walked from home to my office. Traces of squashed fruit, fallen from the flowering crabapples, rub off the soles of my shoes to leave their tracemarks on floor tiles. Glancing through my window, I am delighted to see clouds dappling a bright blue sky. As they flee across the face of the sun, they alternately brighten and shadow the palette of colors displayed by the deepening hardwoods: cascades of crimsons and purples; bursts of red and orange wreathed by browns, greens, and pale yellows; and, here and there, the stippling of silver and gold.

I admit it. I'm a sucker for trees. They carry a nearly mystical quality for me. Outside our campus day care center stands a great American elm, an unbowed survivor of the devastating Dutch elm disease infestation of some years back. On any given day I, like a hobbit in a Tolkien novel, fully expect it to lean down and solemnly inform me in ancient Ent language that it has observed my comings and goings for the past 26 years. Then I will ask if it has heard the many whispered one-way conversations I have addressed to it and whether I was correct to assume that, just as I have prayed for its continued flourishing year after year, it, too, has been interceding for our campus community in its own inscrutable way.

And then there is the Cameron oak, one of the proudest trees in Oshkosh, entwined by legends and rumored to have shaded great native American council meetings in past centuries. This genuine wonder, whose wide-spreading lower boughs reached out so many yards that they had to be propped up to keep them from bowing all the way to the ground, succumbed a few years ago to a storm. Hundreds of Oshkoshians came to see the last hours of the fallen giant, driving past in funereal procession, silently stopping to take farewell snapshots and ship off branches as mementos, and gravely conversing on the sidewalks about the common loss. In my home I now have a prized relic from this grand oak, a wooden bowl turned from one of its limbs by a local artist. One day, as I rub its burnished surface, a genie is bound to leap out!

This issue of *Transactions* celebrates oak trees and their habitat, specifically, the great oak savannas and woodlands that once were dominant ecosystem types over much of central and southern Wisconsin prior to European settlement. Now, due to agricultural development and fire suppression, these oak habitats are becoming very rare.

The Memorial Union at the University Wisconsin Madison was the site of the 1997 Midwest Oak Savanna and Woodland Conference, part of a series held every other year, rotating among Midwestern states. The meeting was organized by a committee chaired by Alan Haney (UW Stevens Point) and including Mark Boyce (current Vice-President Letters of the Wisconsin Academy), Nancy Braker, Gary Eldred, John Harrington, Rich Henderson, Mark Leach, Evelyn Merrill, and Bob Wernerehl. Featured at the conference were plenary sessions, paper presentations, roundtable discussions, and field trips, all devoted to sharing information about the ecology, management, and restoration of oak savannas and woodlands in Wisconsin and the Midwest.

We are pleased to include in *Transactions* eighteen articles arising from this conference. All represent papers first presented at the meeting, subsequently revised and peer-reviewed for publication. Special thanks are due to Mark Boyce, who solicited the article submissions and helped in identifying suitable reviewers for the manuscripts. In addition, I know that all the authors join me in expressing gratitude and appreciation to the many reviewers who, by their incisive critiques and helpful comments, contributed substantially to the final shape of these articles.

Other articles grace this issue of *Transactions* as well. Three deal with Wisconsin fauna, namely, white-tailed deer, beaver, and black bears. The remaining two, which centered on literary "firsts" in Wisconsin, represent our special farewell to Wisconsin's Sesquicentennial celebrations.

We trust that you, the readers of the 1998 *Transactions,* will find within its covers a landscape not at all resembling those "miserably sterile" reaches Darwin visited in the Galapagos. Rather, we hope you will find a colorful array of informative, challenging, and sometimes entertaining articles on these pages. Like the trees putting on their autumn displays in Wisconsin, may they also carry seeds of new growth!

Bill Urbrock

The Wisconsin Academy of Sciences, Arts and Letters was chartered by the State Legislature on March 16, 1870, as a membership organization serving the people of Wisconsin. Its mission is to encourage investigation in the sciences, arts and letters and to disseminate information and share knowledge.

Roger C. Anderson

Overview of Midwestern Oak Savanna

Abstract *The eastern prairie-forest transition extended as a broad arc along the eastern edge of the mixed and tallgrass prairies from the Canadian provinces of Alberta, Saskatchewan, and Manitoba southward into Texas and was a mosaic of prairie, savanna, and forest. The three communities were not distinct, forming a continuum of vegetation that ranged from prairies to forest through the transitional savanna that shared species with forest and prairies. Savannas had scattered to low densities of trees with an understory that had a high component of species associated with tallgrass prairie. A majority of the plant diversity occurred in the ground cover. Savannas required landscape-scale disturbance (repeated fires) for maintenance of diversity and stability. The origin of the Midwestern savanna is recent. Savannas and prairies replaced mesic forests 3,500 to 8,000 years before present during the Hypsithermal, a warm, dry period associated with an increased frequency of fires. Following the Hypsithermal the climate became cool and moist. Stabilization of vegetation is credited to fires set by native Americans and occasional lightning strikes under a climatic regime that could support prairie, savanna, or forest. The mosaic of vegetation types including prairie, forest, and savanna that characterized the vegetation of the Midwest resulted from the interaction of climate, topography, and fire. Nearly all historic tallgrass savanna was lost as a result of agriculture, urban development, and fire suppression at the time of European settlement, which allowed conversion of many remaining savannas to closed hardwood forests.*

During the past ten years, there has been a growing interest in savannas expressed by scientists, persons working with private and publicly supported conservation organizations, as well as interested members of the general public. In many instances, non-scientists were unaware of the extensive literature available on savanna communities, including their origins, distribution, and ecology. This has resulted in misunderstandings of what savannas are and how they should be managed. In this paper, I summarize some of the literature that considers the natural history and ecology of Midwestern savannas. This summary is intended to increase understanding of savannas and aid in their management and preservation.

Distribution of Midwest Savanna

Midwestern savannas occurred on the eastern edge of a large triangular-shaped grassland that extended from the shortgrass prairies east of the Rocky Mountains into the Midwest where tallgrass prairie was the dominant grassland type (Risser et al. 1981). At its eastern edge, the grassland became increasingly fragmented and interspersed with forest and savanna, forming a broad transition zone to the eastern deciduous forests and conifer forest in the north. This eastern prairie-forest transition (Figure 1) extended as a broad arc along the eastern edge of the mixed and tallgrass prairies from the Canadian Provinces of Alberta, Saskatchewan, and Manitoba southward into Texas (Anderson 1983). Within the transition zone, prairies decreased in importance from west to east, whereas the importance of forests increased along the same gradient primarily in response to changing climatic conditions. From west to east, the climate becomes progressively less suitable for the growth of C4 prairie grasses and more favorable for trees, as periodic drought and low humidity during summer decrease and annual precipitation and its reliability increase (Borchert 1950, Risser et al. 1981). Savannas are a

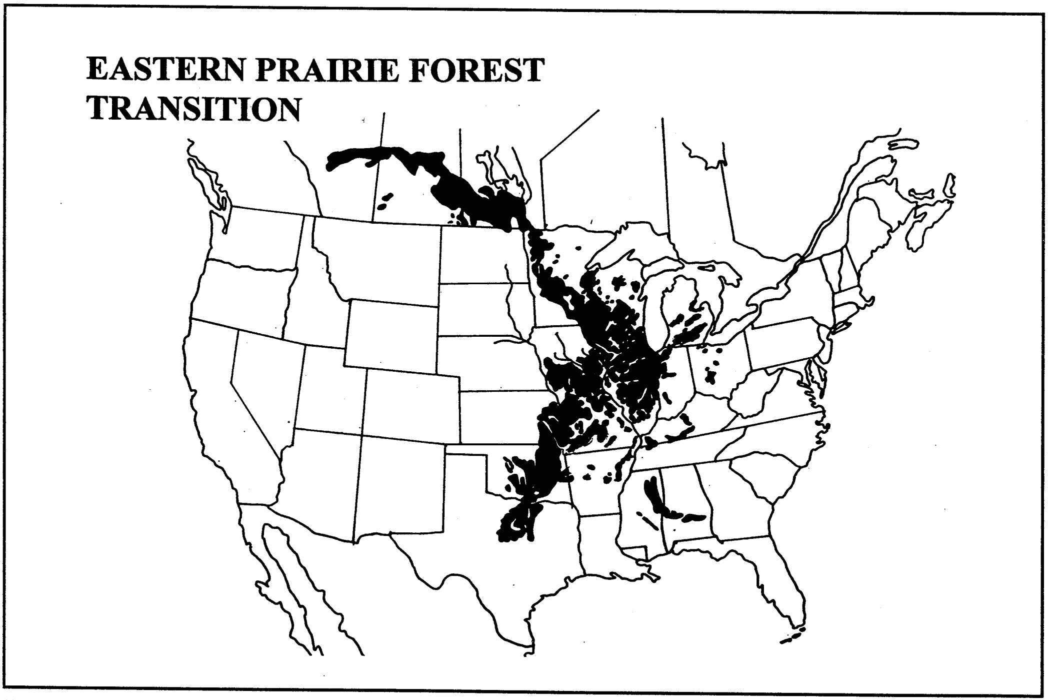

Figure 1. The eastern-prairie-forest transition extended as a broad arc along the eastern edge of the tallgrass prairie and was a mosaic of prairie, forest, and savanna (adapted from Anderson 1983 and Nuzzo 1986).

transitional vegetation, sharing species with the western grasslands and the eastern forested communities. The transition zone also varies along its north-south axis as illustrated by a continual change in savanna tree species composition and abundance. This change is reflected in the dominance of white, bur, and black oaks *(Quercus alba, Q. macrocarpa, Q. velutina)* in the northern and central regions, whereas post oak, blackjack oak, and Texas hickory *(Q. stellata, Q. marilandica, and Carya texana)* are prominent in the cross timbers savanna of Kansas, Oklahoma, and Texas (Curtis 1959, Rice and Penfound 1959, Anderson 1983, Hogland et al. in press).

Eastward through the prairie-forest transition, forest increasingly dominated the landscape, and savanna and prairie occupied less area. For example, in Wisconsin historic oak savannas covered about 3,889,640 ha or about 27.5% of the state, but they were concentrated in southern Wisconsin where savannas covered about 75% of the landscape (about 2.3 million ha) (Curtis 1959, Leach 1996). Eastward from Wisconsin the occurrence of savannas decreased, and only about 3.7% of the townships in Indiana had some oak savanna at the time of the Government Land Office Surveys (between 1799 and 1846). Oak savanna declined rapidly from west to east in Indiana, with oak savanna only occurring in the western third of the state (Potzger et al. 1956). In Ohio, oak savanna encompassed about 0.4% of the landscape prior to European settlement (Gordon 1966). All of this savanna occurred on sands in northwest Ohio (Fulton, Lucas, and Wood Counties). However, Whitney and Steiger (1985) reported that the Sandusky Plain, to the south and east (Marion, Wyandot, and Crawford Counties) of the savannas mapped by Gordon (1966), historically was 48.2% savanna. Adding the Sandusky Plains savannas, with fine textured lacustrine soils, to that reported by Gordon (1966) brings the total area of historic savanna in Ohio to about 0.8% of the state.

Defining Savanna

Recently, there has been discussion about the kind of vegetation that is described by the word savanna. Some ecologists have defined savanna as being grassland with trees (Packard and Mutel 1997). Nevertheless, there is no single definition for the word savanna that would be accepted by a majority of ecologists. The term is used to describe a variety of vegetation types. Vegetation described as savanna in one locality can be called by different names in others. According to Kline (1997), savanna is derived from the Spanish word *saban.* Spanish colonists adopted the word from a native Caribbean Island language in the sixteenth century. They used it to describe flat, grassy, treeless areas found on the Caribbean Islands. By the end of the nineteenth century, savanna became a name widely used for tropical grasslands of many types, with or without trees (Kline 1997). In Illinois in the 1700s and 1800s, savanna referred to grasslands with few or no trees. Immigrants from Great Britain used the word as a substitute for prairie (White 1994).

Several authors used savanna tree canopy coverage as a criterion to separate savannas from other vegetation types. Curtis (1959) defined savannas to have more than one mature tree per acre (2.5 trees/ha), but less than 50% tree canopy cover. Prairies had less than one mature tree per acre (0.4 trees/ha), and vegetation with more than 50% tree cover was classified as forest. By comparison, the Illinois Natural Areas Inventory considered savanna to have more than 10% cover, but less than 80% canopy cover (White 1978), while The Nature Conservancy

(TNC) classified savanna as having 10–30% tree canopy cover. In its classification scheme, TNC also recognized prairie (less than 10% cover), woodland (30–80% cover) and forest, which had more than 80% tree canopy cover (Taft 1997). Elsewhere, savannas were defined to have tree canopy cover ranging from 10 to 50% in Missouri (Nelson 1985) to complete canopy closure in Ohio (Nuzzo 1986).

Nature of the Savanna Community

Prairie-Savanna-Forest Continuum

Prairie, savanna, and forest vegetation are not distinctive vegetation types, but rather they blend into one another, forming what is termed a vegetation continuum (Figure 2) (Anderson 1991*a*). Savanna is the transitional vegetation type between the prairie and forest. Open savannas, that is those with low tree canopy cover, have a high component of species associated with prairies. Along a gradient of increasing tree canopy cover, the importance of the species with high affiliation with prairie decreases, while species associated with open forest increase in prominence (Figure 3). Several studies have demonstrated a gradual change in species composition across the environmental gradient from open prairie to savannas with increasing amounts of tree canopy cover to closed canopy forests (Bray 1958, 1960; Curtis 1959; Pruka 1994*a*, 1994*b*; Leach 1994, 1996). Some species of plants and animals reach their highest abundance in savanna and are adapted to the heterogeneous environment of savannas, with scattered trees or clumps of trees interspersed with open areas. Nevertheless, there are apparently few if any organisms that are restricted solely to savanna (Curtis 1959, Leach 1996).

The varied definitions of savanna likely result from the dynamic relationships occurring between forest, savanna, and prairie and reflect the difficulty of separating a vegetation continuum into discrete classification units. In addition, regional variation affects vernacular usage of terms to describe this transitional vegetation. Barrens, oak openings, glades, or savannas are all terms that have been used to describe the transitional vegetation types containing elements of prairies and forests (Heikens and Robertson 1994). Barrens also included brush prairies, sand barrens (that are similar to sand prairies in terms of herbaceous species composition), and the Hill's oak *(Quercus ellipsoidalis)* and jack pine *(Pinus banksiana)* barrens that occupied sandy soils in the central and northern portions of Michigan, Minnesota, and Wisconsin.

Savanna Common Features

Despite the lack of a common usage for the word savanna, vegetation described as savanna in the Midwest share features in common. They had open canopies, and the dominant trees were a few species of oak. The ground cover often had a high component of species associated with tallgrass prairie, and a majority of the plant diversity occurred in the ground cover. Savannas required landscape-scale disturbance (repeated fires) for maintenance of diversity and stability (Taft 1997). Trees in savannas have a characteristic open-grown form with broad spreading crowns and large branch scars along their trunks. Large branch scars result from the lower branches remaining on the trees for an extended period of time before they are self-pruned. In contrast, lower branches of forest-grown trees are shaded by adjacent trees and contribute little energy to the tree through photosynthesis. Consequently, these branches are soon pruned, leaving small branch scars that are incorporated in the bole

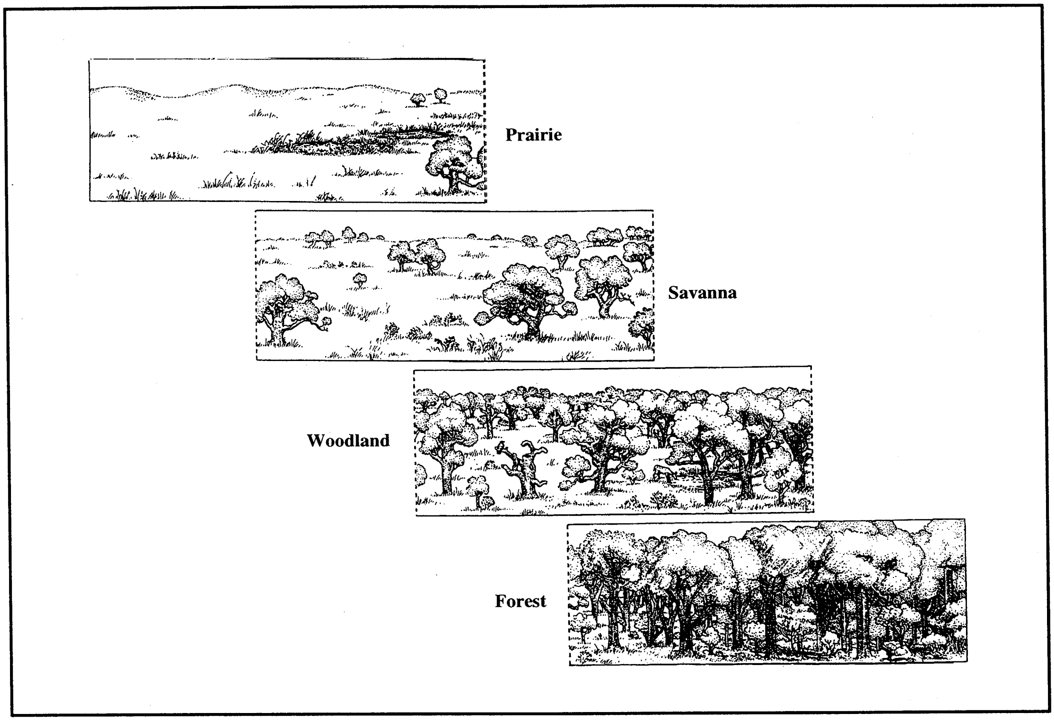

Figure 2. The prairie-forest continuum is characterized by continuous change in tree density and canopy closure from the nearly treeless prairie through the transitional savanna to closed-canopied forest. (Adapted from Packard and Mutel 1997 and granted with permission from *The Tallgrass Restoration Handbook,* Stephen Packard and Cornelia Mutel, eds., © 1997 The Society for Ecological Restoration. Published by Island Press, Washington, D.C. and Covelo, CA.)

as the tree grows. Forest-grown trees have narrow crowns with "clean boles," because of shading from adjacent tree crowns.

Oak grubs, a characteristic feature of some savannas, were oaks with tops one to a few years old but with root systems up to centuries old. Because of nearly annual fires, the tops of these trees would be killed to the ground, but shoots would sprout from the root system. Over a period of years, a massive root system, often with a large surface root crown (basal plate), developed that supported a shoot that would survive until the next fire. The term "grub" is derived from a German word *gruben,* which means to dig. European settlers laboriously dug these massive root systems from their agricultural fields, hence the name oak grub (Curtis 1959).

Black oak is less fire resistant than bur oak and was top killed by intense fire and converted to oak grubs, whereas the shoots of bur oaks develop thicker bark at an early age that more effectively prevents fire damage to the vascular cambium. In some historic savannas, a few bur oaks per acre occurred as scattered open-grown trees in a matrix of prairie grasses and forbs. In addition, there might have been a scattering of oak grubs, often black oaks, which were mostly hidden from view by herbaceous vegetation. These

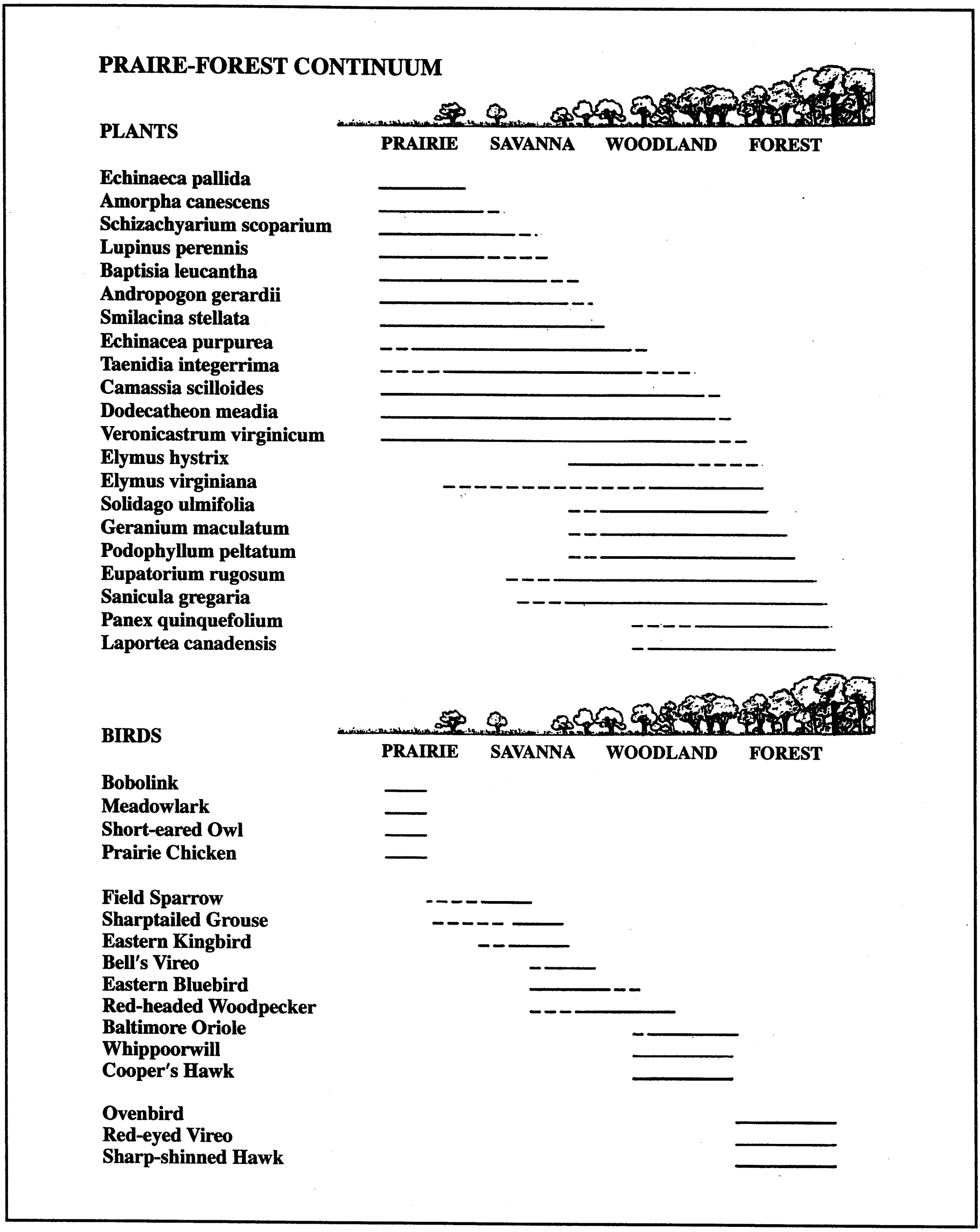

Figure 3. The continual change in species composition across the prairie-forest continuum illustrated for selected plant and bird species. Lines for each species indicate the portion of the continuum in which the species occurs. The species distributions were generalized from the author's field experience with plants. Bird distributions were determined in consultation with Dr. Angelo Capparella (Department of Biology, Illinois State University).

savannas, often called oak openings, had an orchard appearance with scattered bur oaks dotting the landscape (Anderson and Bowles in press). Muir (1965) described oak opening with oak grubs as a feature of historic oak openings in Colombia County, southern Wisconsin. Because "oak grubs" could be very numerous, conversion from savanna to closed forest occurred rapidly as the extensive root systems gave rise to rapidly developing shoots. The often massive open-grown bur oaks would be surrounded by the younger, narrow-crowned black oak shoots as the forest developed (Cottam 1949, Curtis 1959).

Savanna Modal Species

Comparing studies that use different definitions of savanna potentially can create misunderstandings and confusion. For example, Packard (1993) expressed some concern over the paucity of modal species (nine) that Curtis (1959) found in one type of savanna in Wisconsin, the oak opening. Modal species for a community have their highest percent presence in a given community based on quantitative data (Curtis 1959). The low number of modal species in oak openings indicates that few species of plants are more frequently found in oak openings compared with other communities and, as such, can be used to characterize savanna vegetation. However, Curtis (1959) categorized oak openings, oak barrens, pine barrens, and cedar glades as types of savanna vegetation. When these other savanna types are considered there are considerably more modal species. Nineteen species were listed as modal for oak barrens, pine barrens had 5 modal species, and 24 modal species were recognized in cedar glades, so collectively savannas had 57 modal species. This does not mean that these species occurred only in savanna, but rather they occurred in savanna more often than other types of plant communities sampled by Curtis. Furthermore, the number of species that occur predominantly in a community type is a function of the portion of the prairie-savanna-forest continuum that the community encompasses. If Curtis's definition of savanna was broadened to include areas with as much as 80–90% tree canopy cover, as with some definitions, the number of modal species would have been larger. Consequently, conflicting perceptions of the number of modal species found in savannas appear more related to definitions and semantics than to ecology. In addition, Leach (1996) noted that savanna vegetation was converted to woodlands and closed oak forests following cessation of frequent fires at the time of European settlement. Thus, some of the species that were prominent in historic savanna may have been considered to be forest specialists by Curtis (1959).

Origin of Midwest Savanna

Holocene Chronology

The savannas of the Midwest are of recent origin developing following the Wisconsinan glaciation. Analysis of Holocene fossil pollen deposits provides a record of vegetation change during the last 10–12,000 years and documents the origin of savannas during this time. Savannas leave pollen profiles that are different from those of prairies or forests. Savanna pollen profiles have a smaller proportion of hardwood pollen and a larger percentage of herbaceous pollen than forests, but a higher percentage of oak pollen and a lower percentage of herbaceous pollen than prairies (Griffin 1994).

Immediately following the Wisconsinan glaciation, conifer forests occupied much of the Midwest. Mesic hardwood forests replaced conifer forests 9,000–10,000 years before present (BP). On mesic sites, shade-intolerant oaks could not compete with the shade-tolerant mesophytic trees (beech [*Fagus grandifolia*], sugar maple [*Acer saccharum*], elms [*Ulmus* spp.] and basswood [*Tilia americana*]). Many species of oak probably were restricted to sites with low nutrient and moisture availability where they would receive less competition from more mesophytic species. Midwest savannas originated during a relatively warm and dry postglacial period known as the Hypsithermal (Altithermal or Xerothermic in older literature) that peaked about 3,500 to 8,000 BP. The actual time of the Hypsithermal apparently varied within the Midwest (McAndrews 1966; King 1981; Baker et al. 1992; Griffin 1994; Winkler 1995, 1997). In Illinois, the drying trend of the Hypsithermal began about 8,700–7,900 BP. Prairie influx into central Illinois occurred a few hundred years later (about 8,300 BP) with a concomitant displacement of mesic forests by oak forests in northern Illinois. During the hottest and driest part of the Hypsithermal in Illinois (about 8,000–6,000 BP) prairies occupied most of the state (King 1981).

According to Griffin (1994), oak openings appeared in northern Illinois and southern Wisconsin about 5,500 BP. Pollen record and charcoal deposits from Lake Mendota sediments in southern Wisconsin indicate that the climate was drier and hotter and fire frequency higher between 6,500 to 3,500 BP than it was in the early Holocene (Winkler et al. 1986; Winkler 1995, 1997). Oak savannas were associated with the warm dry period during the Holocene, but after 3,500 BP the climate became cooler and more moist, and closed *Quercus* forest dominated the landscape (Winkler et al. 1986; Winkler 1995, 1997). This appears to be in conflict with the generally held view that oak savanna dominated southern Wisconsin immediately prior to extensive European settlement (Curtis 1959, Leach 1996). However, this may reflect the patchy nature of vegetation distribution. The vegetation influencing Lake Mendota pollen records could have been locally dominated by closed forest in a landscape in which savanna predominated.

In northeastern Iowa, pollen records indicate that forest dominated from about 8,000 to 5,100 BP, and then it was replaced by prairie (Baker et al. 1996). Replacement of forest by prairie probably resulted from a climatic shift that increased flow of arid Pacific air and increased frequency of fires. Oak savanna appeared in northeast Iowa about 3,000 BP. These records would support those from other regions in the Midwest with replacement of forest by vegetation (prairie) adapted to a hotter and drier climate and increased fire frequency after 5,100 BP. Invasion of oak savanna after 3,000 BP in a prairie-dominated landscape would suggest that the climate was becoming cooler and more moist, consistent with the results of other studies (Winkler et al. 1986; Winkler 1995, 1997).

Landscape Level Changes

To explain the historic distribution of nearly treeless mesic tallgrass prairies on level to rolling landscapes, Curtis (1959) proposed that during the early part of the Holocene these sites supported mesic forest. The tree species dominating these forests—sugar maples, beech, basswood, ironwood *(Ostrya virginiana)*, and others—were shade tolerant but not fire resistant. Shade-intolerant oaks were excluded from mesic sites because they were unable to compete with the shade-tolerant mesophytes. On droughty and/or low nutrient sites, e.g., sites with sandy soil, steep upper slopes, or sites with shallow soils over bedrock, the mesophytes were unable to tolerate the site conditions. In contrast to the mesic tree species, most oaks are tolerant of droughty, low nutrient environments, and they probably dominated these locations (Figure 4).

During the Hypsithermal the combination of drought and fires eliminated mesic species from all but the most sheltered sites, and they were replaced by tallgrass prairie. Most oaks have fire-resistant bark, and all oaks have the ability to resprout after being top-killed by fire (Stearns 1991, Abrams 1992). The hot, dry conditions and frequent fires associated with the Hypsithermal were unable to eliminate oaks, but repeated fires kept their densities low, forming oak savannas and woodlands (Figure 4).

Following the Hypsithermal, and after about 3,500 BP, the climate became cool and moist, and there was a shrinking of the area of prairie in the Midwest (Delcourt and Delcourt 1981, King 1981). Stabilization of vegetation is accredited to fires set by native Americans and occasional lightning strikes under a climatic regime that could support prairie, savanna, or forest (Curtis 1959; Anderson 1990, 1991*b*). The mosaic of vegetation types including prairie, forest, and savanna that characterized the vegetation of the Midwest resulted from the interaction of climate, topography, and fire. The relative importance of these interacting factors determined the prominence of these vegetation types on the landscape.

Distribution of Savannas on the Landscape

Fire frequency determined the occurrence of the three vegetation types on the landscape, and fire frequency was largely controlled by topography. Fires spread rapidly on level to gently rolling topography. On these landscapes there were nearly annual fires, which supported tallgrass prairies that required frequent fires for their maintenance in the climate of the Midwest (Curtis 1959; Risser et al. 1981; Anderson 1982, 1990). In dissected landscapes, the spread of fire was reduced, permitting the establishment of trees. Fires rapidly move up slopes, driven by rising convection currents, but as fires move down slope the rising convection current moves against the direction of the fire (Figure 5). Closed forest occurred in areas sheltered from fires, such as ravines or along waterways that served as fire breaks. These sheltered locations supported shade-tolerant but fire-sensitive mesophytic tree species such as sugar maple, basswood, and beech in the eastern portion of the prairie-forest transition. Fire-tolerant oaks dominated woodlands and savannas in areas where fires occurred less frequently than in the prairies, but with shorter return time than in closed mesophytic forests (Gleason 1922, Curtis 1959, Anderson and Anderson 1975, Rodgers and Anderson 1979, Grimm 1984, Anderson 1990, Abrams 1992).

Waterways also functioned as firebreaks. The west side of streams and rivers tended to be vegetated by prairie, because fires tended to be carried by prevailing westerly winds, whereas the sheltered east side of waterways supported forests (Gleason 1913). Easterly winds could have carried fires to eastern sides of waterways. However, east winds originate from the back side of passing high pressure systems and are associated with low pressure systems that bring in high humidity and precipitation that reduce the likelihood of fire.

Using a map (Figure 6*a*) of the historic distribution of forest/savanna and prairie in Illinois (Anderson 1970) and a map of the

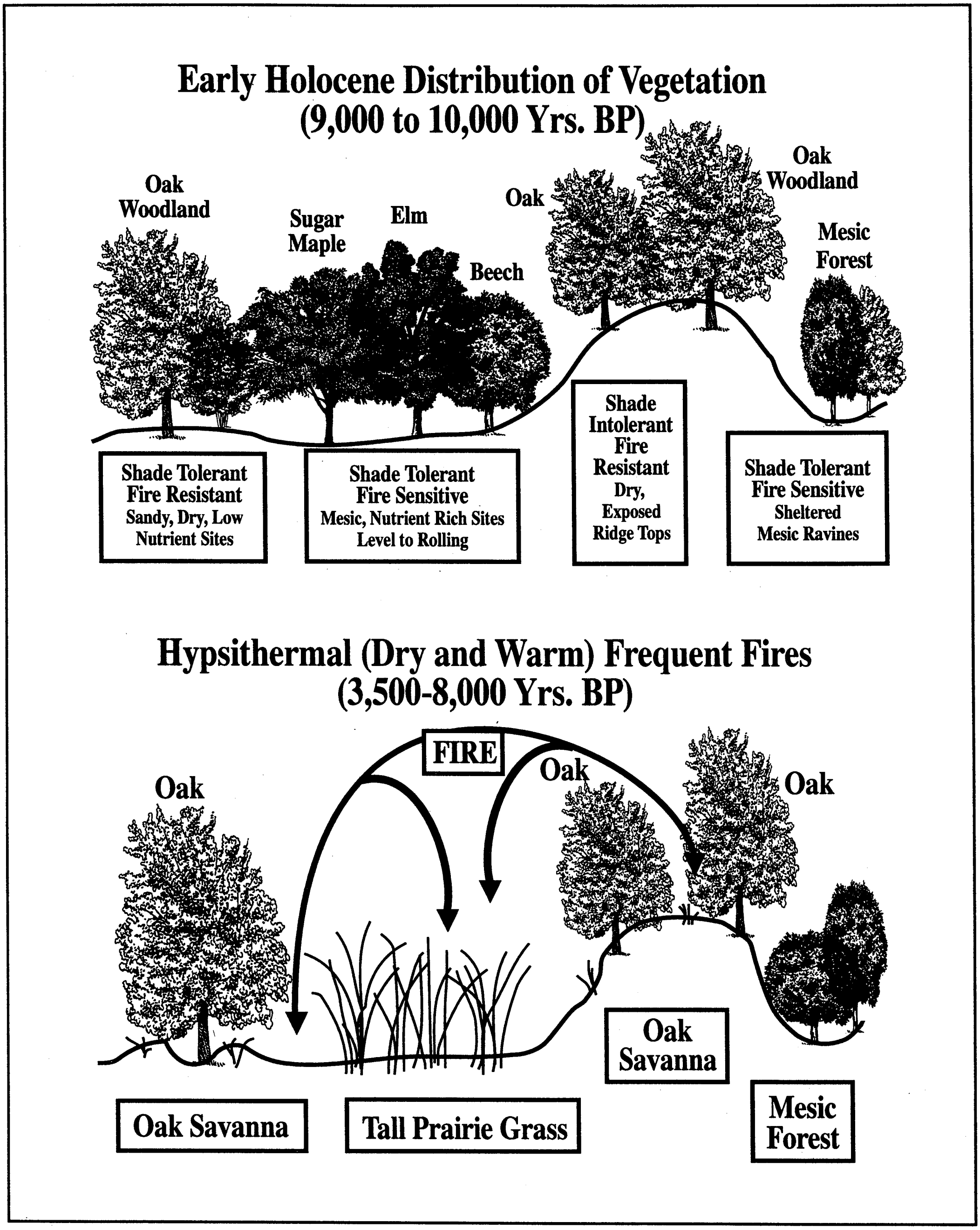

Figure 4. Possible change in vegetation distribution on the landscape from the early Holocene when the climate was cool and moist to the Hypsithermal that was associated with a warm, dry period with an increase in fire frequency.

average slope range for the state (Figure 6*b*), Anderson (1991*b*) examined the relationship between topographic relief and vegetation patterns. Forests-savanna were areas described in plat maps associated with the Government Land Office survey records as being "timber" and included varying mixtures of forest and savanna (Anderson and Anderson 1975, Moran 1976). Average slope range, given in three categories (2–4%, 4–7%, and >7%), was assumed to be a measure of topographic relief. Most prairie vegetation (82.3%) occurred on landscapes in the 2–4% category (Table 1). Only 23% of the forest-savanna vegetation was associated with 2–4% slope category, and most of these forests-savannas were on flood plains. In contrast, 77% of the timbered vegetation occurred on sites that had average slope ranges greater than 4% (4–7% slope = 35.2% and >7% slope = 41.8%). Most of these sites were associated with the highly dissected portions of the Illinoian glacial till plain, unglaciated areas, glacial moraines, and waterways.

Dry Savanna

On extensive areas in the Midwest, savannas and open woodlands also occurred on sites that had sandy, acidic soils with low nutrient availability and poor water-holding capacity. These sites were associated with glacial outwash plains (Curtis 1959, Pregitzer and Sanders in press, Will-Wolf and Stearns in press) and deep sand deposits in river flood plains (Anderson and Brown 1986). These sites supported herbaceous vegetation with low fuel loading. However, they were prone to fire, because the low water-holding capacity of the soil resulted in frequent and rapid drying of fuels that increased

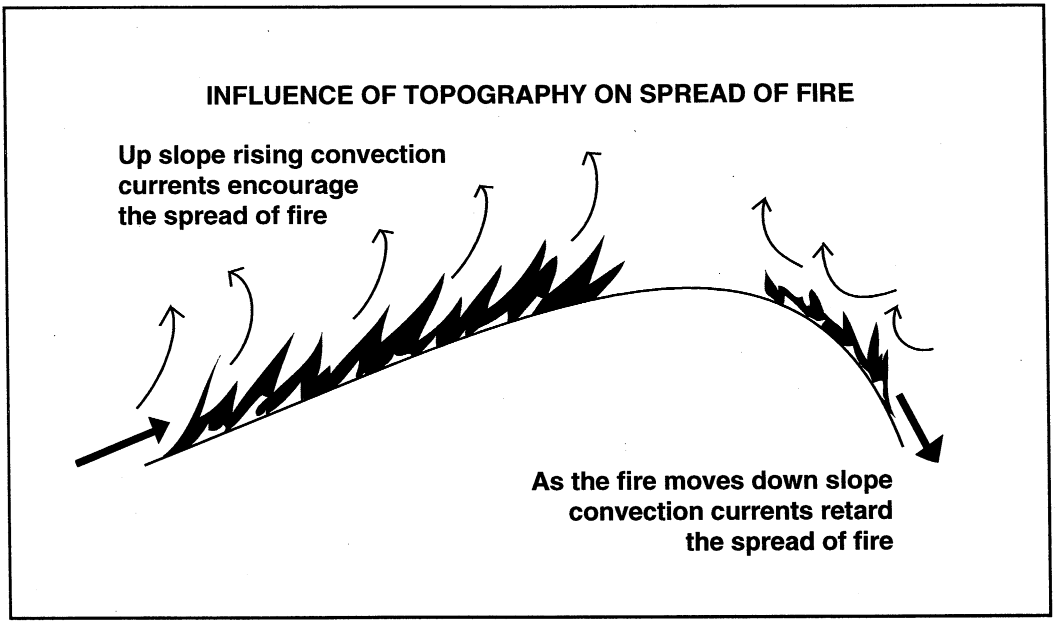

Figure 5. Influence of topography on the spread of fires. Rising convection air currents move fire rapidly up slope, but as fire move down slope the direction of the convection currents works against the spread of the fire.

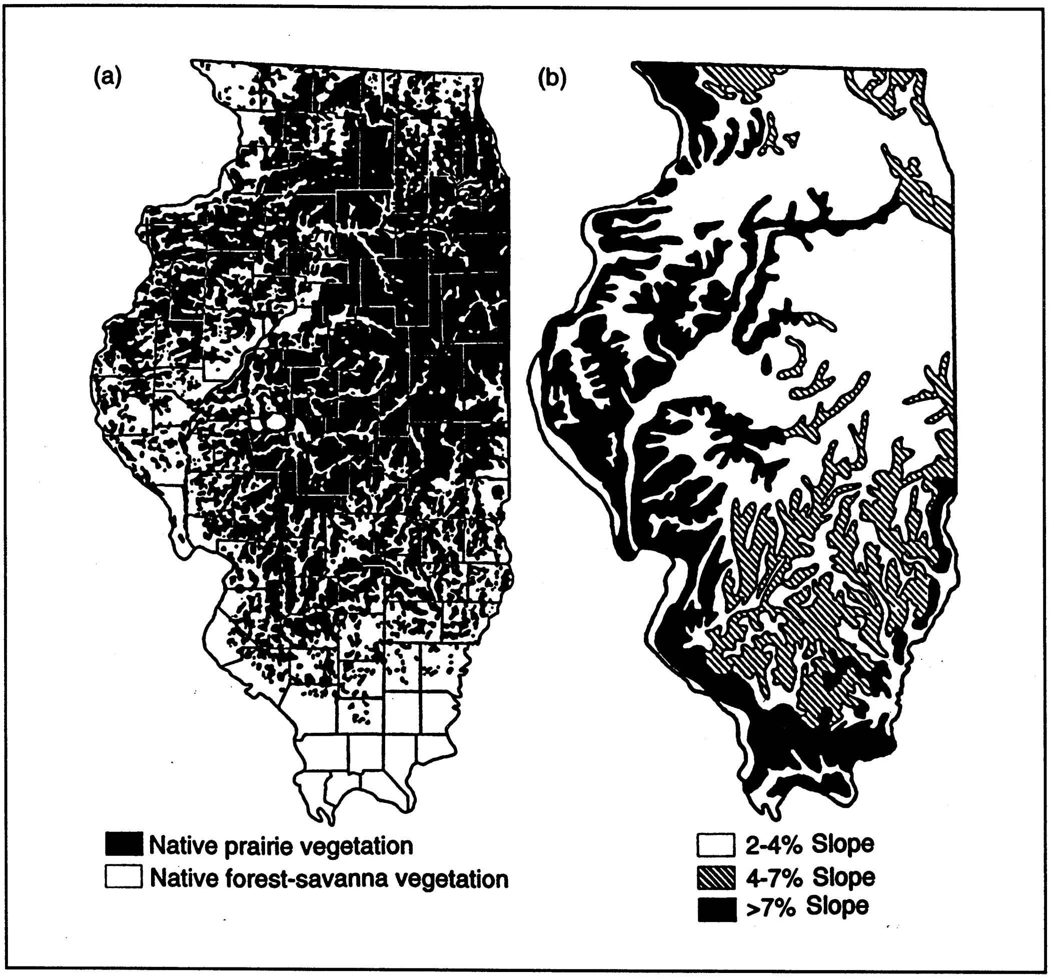

Figure 6. The relationship between landscape dissection and vegetation in Illinois near the time of European settlement from Anderson (1991*b*).

susceptibility to fire. With frequent fires that impeded the buildup of woody plant fuels, the fires were of lower intensity than those occurring on mesic sites with silt loam soils that supported tallgrass prairies with high fuel loading. These conditions permitted the co-existence of a mixture of sand prairie grasses and forbs and oak trees. Black oak was a common savanna tree in southern locations, and jack pine and Hill's oak were important trees in savannas in the northern Great Lakes Region (Curtis 1959, Grimm 1984, Anderson and Brown 1986, Pregitzer and Sanders in press, Will-Wolf and Stearns in press).

Calcareous dry savannas occurred on sites with thin soils over calcareous bedrock or gravels. White oak and bur oak were important tree species in these savannas that tended to occur in small scattered patches (Will-Wolf and Stearns in press). Cedar glades were another type of dry calcareous savanna that had an understory of dry prairie species and scattered red cedar trees *(Juni-*

Table 1. Percentage historic forest-savanna and prairie vegetation occurring with various slope-range categories in Illinois from Anderson (1991*b*).

Vegetation Type	*Average Slope Range Categories*		
	2–4%	*4–7%*	*>7%*
Prairie	82.3%	12.4%	5.3%
Forest-savanna	23.0%	35.2%	41.8%

perus virginiana). These savannas usually occurred on south- to west-facing slopes on sites with shallow soils over limestone bedrock. In the absence of periodic fires, limestone glades tend to undergo vegetation change forming nearly closed stands of the fire-sensitive red cedar with little ground cover vegetation. The open cedar glades grade floristically into hill prairies or high lime prairies (Curtis 1959).

Current Status of Savannas

Deep-soil (Mesic) Savannas

After European settlement, savannas on mesic sites with deep soils rapidly degraded as woody succession followed fire protection and gave rise to closed oak forests (Cottam 1949, McCune and Cottam 1985, White 1994, Anderson and Bowles in press). Consequently, most dry and dry-mesic oak forests and woodlands occurring in the eastern prairie-forest transition today were derived from savannas. In some cases, the derivation of oak forests/woodland from savanna is indicated by the presence of large open-grown trees surrounded by smaller forest-grown trees whose origin dates to the time of European settlement and fire protection. Similarly, oak trees with multiple stems that arise from a large root crown often originated from oak grubs and provide evidence of the former occurrence of savanna on a site (Cottam 1949, Curtis 1959). On some sites overgrazing by domestic cattle nearly or completely eliminated understory vegetation, while agriculture and urbanization fragmented and destroyed remnants. Thus, few, if any, intact savannas survive on deep silt-loam soils in the Midwest (Curtis 1959, Madany 1981, Apfelbaum and Haney 1991, Packard 1991, Anderson and Bowles in press). Nuzzo (1986) estimated that there were about 12 million ha of original tallgrass savanna in the Midwest, of which only 0.02% (2,607 ha) remained.

Dry Savannas

Successional processes that would convert savanna to woodland and forest proceed at a slower rate on xeric sites than mesic ones. Additionally, agricultural development generally results in lower returns on xeric savannas than on mesic ones so less development tends to occur on xeric savannas. Consequently, savannas occurring on xeric sites, such as deep sand deposits, or in areas where there are shallow soils over bedrock, have a somewhat larger percentage of the original savanna remaining, albeit in an altered state, than do the mesic savannas (Taft 1997). For example, in pre-European settlement times, jack pine barrens occupied about 20,000 km^2 in northern Michigan, Minnesota, and Wisconsin. Of the 920,000 ha of historic pine barrens that occurred in Wisconsin about 3,500 ha or 0.38% of the original barrens remain (Vora 1993, Pregitzer and Sanders in press). Pine barrens were lost through lumbering, agriculture, and conversion to red pine plantations. Successional processes that resulted from fire cessation converted the barrens to closed forests with increased abundance of hardwoods, (e.g., white birch [*Betula papyrifera*], black cherry [*Prunus* *serotina*], maples [*Acer* spp.], and oaks [*Quercus* spp.]) and red and white pines [*Pinus resinosa* and *P. strobus*]) (Curtis 1959, Vogl 1970, Pregitzer and Sanders in press). Nevertheless, the potential to restore substantial areas of these barrens to historic conditions remains.

Historic jack pine barrens had tree densities less than 49/ha (20 trees/acre) with the dominant trees in the historic barrens being jack pine and Hill's oak. The patchy environment in the understory, which varies from open areas to closed canopy conditions, creates habitat for an unusual ground layer vegetation. The flora includes sand prairie and northern forest forbs, graminoids such as big and little bluestems (*Andropogon gerardii* and *Schizachyrium scoparium*), wild mountain rice *(Oryzopsis asperifolia),* poverty grass *(Danthonia spicata),* and sedges with Pennsylvania sedge *(Carex pensylvanica)* often being prominent. Important shrubs on pine barrens are blueberries *(Vaccinium angustifolia)* and sweet fern *(Comptonia peregrina)* (Curtis 1959, Pregitzer and Sanders in press).

Ecosystem Management of Savannas.

In the Midwest, few remnant savannas are sufficiently large to be managed on a landscape scale. An exception may be areas historically occupied by jack pine barrens in the northern lower peninsula of Michigan. In this region, the United States Forest Service and the Michigan Department of Natural Resources manage jack pine plantations to produce wood products and habitat for the federally endangered Kirtland's warbler (Probst and Weinrich 1993). Jack pine plantations are managed on a fifty-year rotation with pines planted in a sine wave pattern to create openings that are utilized by the bird as nesting areas when the plantations are 5 to 20 years in age. The bird's listing as one of the first species protected under the Federal Endangered Species Act was prompted by a precipitous decline in the population of singing males from over 500 in 1961 to approximately 200 in 1971 (Weinrich 1995). Nevertheless, there was a marked increase in the number of male birds singing on territories following a 10,000 ha (24,000 acres) wildfire (Mack Lake) in 1980, with the highest number of males (765) being counted in 1995. The number of singing males declined slightly since 1995, 692 and 728 in 1996 and 1997, respectively, as the area of the Mack Lake burn developed beyond the stage of optimum nesting habitat.

The marked increase in birds following a single large wildfire suggests that designating substantial areas of potential jack pine barrens solely to create habitat for Kirtland's warbler would benefit the bird more than devoting all management areas to multiple-use functions. Fire-return intervals in the historic barrens were in the range of 25–50 years, and burns undoubtedly covered areas that were more extensive than the area of the Mack Lake burn (Curtis 1959, Vogl 1970, Whitney 1986, Pregitzer and Sanders in press). Management that stimulates historic fire regimes would probably benefit the warbler through the restoration of the historic barrens and maintain ecosystem processes to which the bird is adapted. Single species management for endangered species is likely to be less successful than management to restore ecosystem function and structure to the historic landscape to which the species is adapted. Moreover, ecosystem management in units that are sufficiently large to re-establish natural process, such as fire, has the salutary effect of benefiting organisms other than the target species that are also dependent on this ecosystem (Robertson et al. 1997, Taft 1997).

Conclusions

The savannas of the Midwestern United States are of recent development, having originated in the warm, dry, postglacial Hypsithermal period about 8,000 to 3,500 years before present. Savannas are transitional between eastern deciduous forest and tallgrass prairie and contain species from both vegetation types. There is no single definition of savannas, and varied vegetation types are called savannas. However, Midwestern savannas share several features in common. Savannas have a discontinuous tree canopy that is dominated by members of the oak genus *Quercus*. The ground cover often has a high component of species associated with tallgrass prairie, and a majority of the plant diversity occurs in the ground cover. Historic savannas required landscape-scale disturbance (repeated fires) for maintenance of diversity and stability. Most of the historic savannas, especially those on mesic sites, were destroyed at the time of extensive European settlement through agricultural development and cessation of fires that allowed conversion of savannas to closed oak forests. The remaining remnant savannas are small, fragmented, and have experienced loss of species due to fire suppression, grazing by cattle, and invasion of exotic species. Nevertheless, interest in restoring remnant savannas to historic conditions has grown in the past decade, and progress is being made on developing techniques for restoration and understanding the nature of savanna ecosystems (Fralish et al. 1994, Packard and Mutel 1997, Taft 1997, Anderson et al. in press).

Acknowledgments

I thank M. Rebecca Anderson and two anonymous reviewers for reviewing the manuscript.

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Stephen Budiansky

Some Historical Influences on Modern Views of Nature in America

Abstract *Many widely accepted contemporary views of nature, which emphasize the idea that human interference in ecological processes is invariably harmful, stem from the historical circumstances under which the nature appreciation movement first arose in the late eighteenth and early nineteenth centuries. Nature was romanticized as the embodiment of perfection and a mirror of God, if not the literal dwelling place of God. What moved early nature admirers to seek out "wild places" was precisely the absence of man and the sense of solitude that conferred. This view, which persists today, has led many to ignore or denigrate the significant historical influence that the North American Indians had on their environment through extensive burning of forests and hunting of ungulates; and, further, to adhere to an ahistorical paradigm of strict nature "preservation" that opposes any active management by humans, even for nonexploitive, ecological goals.*

1

Francis Parkman, a great nineteenth-century popularizer of cowboys, Indians, mountain men, and sundry other icons of the romanticized American wild lands, portrayed the ancient forests of the New World as vast, dark, and untrodden. In "the depths of immemorial forests, dim and silent as a cavern," "wrapped in the shadow of the tomb," not a flicker of sunlight ever touched the ground; they were "ancient as the world," to whose "verdant antiquity the pyramids are young." Only where Europeans had intruded was it otherwise. Between the bits of rough civilization the settlers had carved out of the virgin land lay "a broad tract of wilderness, shaggy with primeval woods" (Day 1953). A squirrel, it was said, might in the days before the white man arrived have traveled from Maine to Louisiana never once setting foot on the ground, but leaping from tree to giant tree.

A very different metaphor came to the mind of more than one early explorer who actually set foot in America's "primeval woods." A stagecoach, said one, might be driven from the east coast to St. Louis without first clearing a road. "A man may gallop a horse amongst these woods any waie, but where creekes or Rivers shall hinder," agreed Captain John Smith of the Jamestown, Virginia, settlement. If there is one point on which the early European travelers and settlers who set down their observations of the New World agree, it is that the forests of eastern North America reminded them of nothing so much as the carefully tended parks of the great estates of their homelands. An explorer in 1607 observed the trees around present-day Portland, Maine, "growing a great space asunder one from the other as our parks in England and no thicket growing under them." In the early days of the Plymouth colony the Pilgrims found the woods "thin of Timber in many places, like our Parkes in England." In New Jersey in the mid-seventeenth century, the woods were described as "but thin in most places, and very little Under-wood"; another explorer noted an abundance of high grass and trees that "stand far apart, as if they were planted." In such open, parklike wood, deer and turkey could be seen a mile away, cattle three miles (Martin 1973; Pyne 1982:46–47).

Parkman romantically portrayed the sixteenth century Italian navigator Verrazano lying off the coast of New England espying one of his mighty literary forests, full of "shadows and gloom." Yet Verrazano himself told of marching inland fifteen miles from Narragansett Bay, in what would become Rhode Island, and finding "open plains twenty-five or thirty leagues in extent, entirely free from trees or other hindrances." Where the explorer did encounter forests, they grew so open and unencumbered by underbrush that they "might all be traversed by an army ever so numerous," he marveled (Maxwell 1910, Day 1953).

The Europeans marveled at these open woods and meadows, but they did not have to search far for an explanation. If the land reminded them of carefully tended parks at home it was for a good reason. One of the earliest explanations was set down in 1632 by Thomas Morton, an English fur trader and adventurer who traveled the backwoods of eastern central Massachusetts and settled in what is now Quincy, Massachusetts. (He did not remain long. A free-thinker, he was always in trouble with the local authorities. After being repeatedly arrested, he was finally expelled for licentiousness, selling firearms to the Indians, and penning a satiric tract against the Puritans). Morton was a keen observer, and his travels off the beaten path gave him a first-hand knowledge of the ways of the Indians. He explained that it was deliberate management by the native inhabitants that kept the woods as they were:

> The Salvages [sic] are accustomed to set fire of the country in all places where they come; and to burn it, twize a yeare, vixe, at the Spring, and at the fall of the leafe. . . . The burning of the grasse destroyes the underwoods, and so scorcheth the elder trees, that it shrinks them, and hinders their growth very much. . . . And this custome of firing the country is the means to make it passable, and by that meanes the trees growe here and there as in our parks: and makes the country very beautifull, and commodious. (Bromley 1935)

The practice appears to have been extremely widespread. In Virginia, through a combination of burning and fuel-wood cutting, the Indians had managed to clear some thirty or forty acres of land per capita at the time the first Europeans arrived; three centuries later, although the total area cleared was obviously much greater, it amounted to considerably less per capita—only six or seven acres of treeless land per person. The dominant nineteenth and early twentieth century view that the Indians were ragged bands of backward savages incapable of having any significant impact on the land—and the more recent view that they were intuitive ecologists whose religious respect for nature forbade them to tamper with it—is certainly called into question by the testimony of the early settlers.

Of course along with the open woodlands and meadows there were certainly stands of denser, older forest; the landscape was a shifting mosaic through time and space, the product of many competing forces. But the accounts of early travelers and other evidence suggests that Indian-set fires had a major effect in shifting the balance toward younger stands on a very broad scale. An analysis of early land surveys concluded that at the time the European settlers arrived in the Pacific Northwest in the nineteenth century, stands older than 200 years occupied only about 5 percent of southwest Oregon—hardly the "sea of old growth" that modern environmental activists claim once existed (Zybach 1994). Even supposedly uninhabited regions were frequented regularly by Indian war or hunting parties that left their mark. In southwestern Virginia William Byrd reported seeing the sky filled with smoke so dense that it blocked out the mountains. "This happened not from haziness of the sky," he said, "but from the firing of the woods by the Indians, for we were now near the route the northern savages take when they go to war with the Catawbas and other southern nations. On their way, the fires they make in their camps are left burning, which catching the dry leaves which lie near, soon put the adjacent woods in a flame" (Maxwell 1953). Other travelers reported finding vast, open savannas far inland from the heavily occupied eastern seaboard; the only trees that they found growing there were confined to low swamps or wet areas along streams, which escaped the flames. Fire scars left in the annual growth rings of old trees in New Jersey confirm the settlers' observations, testifying to fires every ten to fifteen years (Little 1974). Careful studies of the fire history of the Rocky Mountains offer convincing evidence for frequent Indian-set fires in that region, too. When tree rings of old-growth stands in western Montana were analyzed, it became clear that fires were much more frequent (once every nine years) in areas that had been heavily used by Indians, as compared to similar but more remote sites (every 18 years). And more frequent burning had major ecological implications: Stands that burn every seven years or so are dominated by tall ponderosa pines and a grassy undergrowth. Older stands, by contrast, become rapidly clogged with woody shrubs, an understory of shade-tolerant Douglas fir, and a build-up of insect and disease pests (Barrett and Arno 1982).

Perhaps the most telling evidence for the dominant role that Indian-set fires played in shaping the American landscape is what happened when the Indians were pushed off the land. One early Massachusetts settler observed that "in some places where the *Indians* dyed of the Plague some foureteene yeares agoe, is much underwood . . . because it hath not been burned" (Thompson and Smith 1970:259). One of the great ironies in the myth of the forest primeval is that the dense, thick woods that later settlers did indeed encounter and arduously cleared were not remnants of the "forest primeval" at all. They were the recent, tangled second growth that sprung up on once-cleared Indian lands only after the Indians had been killed or evicted and the Europeans began to suppress fire. What later settlers took for the forest primeval was in fact much closer to being an abandoned ranch. "The virgin forest was not encountered in the sixteenth and seventeenth centuries," writes one historian; "it was invented in the late eighteenth and early nineteenth centuries" (Pyne 1982:46–47).

2

What, then, explains this late-eighteenth and early-nineteenth century urge to revise this history, to romanticize nature, to reinvent the American landscape as a virgin wildland and the Indians as ecological saints who trod softly on moccasined feet without snapping a twig?

The admiration for nature that has emerged as a prominent and broadly accepted feature of Western culture over the last 200 years or so finds little counterpart in the previous 2,000 years of Western civilization. Cultural beliefs of course rarely spring into existence fully formed; it is almost always possible to find hints and foreshadowings of any era's characteristic sentiments, beliefs, and ideologies; indeed it is not uncommon to find certain beliefs and their antitheses coexisting for thousands of years, with one or the other predominating at different times. There is much enthusiasm among environmentalists today for tracing a human love of nature even to our genes—it is, we are told, a "biophilia" that reflects an evolutionary adaptation of stone age man. Maybe so, and likewise perhaps a love of freedom is in our genes, too. But that tells us nothing about why American democracy arose when it did after centuries in which kings and despots reigned. Similarly, however ancient the roots of modern affinity for nature may be, the fact remains that for most of recorded history, the *dominant* mode of feeling toward nature expressed in Western civilization was one of hostility. Before the end of the eighteenth century, mountains, when they were commented upon at all, were generally described with abhorrence. They were "warts," "wens," "the rubbish of creation." Dr. Johnson, in 1738, expressed the opinion that the Scottish hills "had been dismissed by nature from her care." Other seventeenth and early eighteenth century writers were hardly less sparing in their censure of mountains: The Alps were "high and hideous," "monstrous excrescences of nature," the place where nature had "swept up the rubbish of the earth to clear the plains of Lombardy." An early visitor to Pike's Peak wrote, "The dreariness of the desolate peak itself scarcely dissipates the dismal spell, for you stand in a confusion of dull stones piled upon each other in odious ugliness" (Rees 1975).

The very word *wilderness* was a term of clear disapprobation. It meant an unimproved wasteland, a place devoid of value, a place to be shunned and hurried through. Mountains were places of wolves, bears, bandits, bad roads, and violent and unpredictable weather. The North American forests harbored wild animals and hostile Indians. To a farmer who needed to clear fields to feed his family and graze his livestock, the woods were a back-breaking obstacle; felling trees and pulling stumps was the most arduous job a settler faced.

In Medieval Europe, affection for nature carried with it the further suspicion of sacrilege; axe-wielding monks leveled forests to extirpate sacred groves or other sites of pagan nature-worship (Oelschlaeger 1991:70–72). Landing at Plymouth, William Bradford beheld the New World—and called it "a hideous & desolate wilderness, full of wild beasts & wild men." The forests of New England were a "howling" and "dismal" place, gloomy and sinister, full of evils real and spiritual. In 1653 the English historian Edward Johnson described the forests of North America as a "remote, rocky, barren, bushy, wild-woody wilderness," and he was not being complimentary (Cronon 1983:5).

So, again, what explains the great change of heart between the eighteenth century and now? How did nature change from a place of chaos, ugliness, and evil to one of order, harmony, and beauty?

Rarely has there been such an abrupt and sweeping transformation in dominant social attitudes. Yet in its very abruptness lies the explanation of how an ecologically unsubstantiated and ahistorical belief in nature as perfect, orderly, harmonious, and separate from man came to be virtually synonymous with a love for nature, and why even today this special vision of the natural world holds such a grip upon us. Nature—or at least the Arcadian vision of nature as a place of towering, ancient woods, majestic beasts, and timeless hills, a place where man may enter only as an intruder, observer, or worshipper—was an invention of the imagination of man. To love nature, man first had to invent a nature worth loving. And in inventing nature he perhaps inevitably consulted the romantic yearnings of his soul, not the miserable experience of thousands of years of grim reality. It was "the literary gentleman wielding a pen, not the pioneer with an axe" who could afford to romanticize nature (Nash 1982:44).

For the early nature appreciation movement was both self-conscious and self-consciously elitist. Those eighteenth century aristocrats—for aristocrats they almost exclusively were—who suddenly and unexpectedly began to express an admiration of mountains and other natural scenery were explicit in their belief that the ability to appreciate such beauty was not innate, but acquired. Nature was something that only the cultivated, trained through an appreciation of fine painting and landscape gardening, could truly understand and value. It was a sort of connoisseurship; one could no more expect a ploughman to properly appreciate the Alps than one could expect him to appreciate a glass of fine old port. As late as 1844, the poet William Wordsworth was complaining in a letter to an English newspaper about a proposed railroad that was to be built to the Lake District. His concern was not, as a modern-day preservationist might expect, that the railroad itself would mar the countryside; the problem was rather that it would bring trainloads of untutored sightseers who were not equipped to value what they were seeing. "The perception of what has acquired the name of picturesque and romantic scenery," he sniffed, "is so far from being intuitive that it can be produced only by a slow and gradual process of culture" (Rees 1975).

The tastes of the aristocratic nature lovers of the eighteenth and nineteenth centuries were perfectly revealed in the English landscape movement, which rejected the tame, artificial symmetry and formality of traditional gardens in favor of the wild and "natural." But the flowing landscapes that replaced the rigid lines of trees in pots and clipped hedges were an invented nature, an aesthete's nature. Every curve and vista was calculated to offer "insights" and "subjects of meditation"; streams were dammed to form poetic lakes, trees were set in artful clumps, and garden buildings were pressed into service as moral or philosophical allegories. There was a great truck in Classical and Gothic ruins, real and synthetic. "English landscape was invented by gardeners imitating foreign painters who were invoking classical authors," mocks the character Hannah in Tom Stoppard's play "Arcadia," and she has it about right (Stoppard 1993:25).

The carefully crafted landscapes of ruined abbeys, jagged cliffs, unkempt trees ("everything but vampires," Hannah says) betrayed a motive that beclouds our thoughts about nature to this day. The natural world's ability to stir the soul, even fill it with terror, was the prime attraction. This was nature as escapism—the place that "can stir you up as you were made to be stirred up," as the Sierra Club's David Brower would still describe it two centuries later (Hamilton 1994). Much the same taste accounted for the popularity of the Gothic novel; indeed the English landscape garden was almost a Gothic novel come to life, in crags and unkempt trees and "druidical" huts. The eighteenth century English landscape architect William Kent went so far as to plant dead trees in Kensington Gardens "to give a greater air of truth to the scene." The idea was to create a garden that looked old, as if it had been neglected for centuries. In a few particularly wonderful instances the Gothic touches went completely over the top. The owner of Pain's Hill in Surrey had a hermitage, complete with resident hermit, installed on his redone grounds. The hermit signed a seven-year contract at £700; he was supplied food, hassock, and hourglass, and undertook not to cut his hair, beard, or nails and to eschew speech. It was perhaps only inevitable that he was caught sneaking down to the pub after just three weeks on the job (Elliott 1994; Johnson 1979:226–27).

By the end of the eighteenth century, the well-to-do English seekers of soul-stirring experience were beginning to venture forth from their libraries and gardens into the genuine "wilderness," too. They were doing what seems perfectly commonplace now, but what was an exceptional departure then. English tourists began visiting Scotland and its wild hills in significant numbers only around 1810; it was in 1818 that the first English-language guidebook to Switzerland and the Alps was published. The motive of these pioneering nature tourists was virtually indistinguishable from that of the landscape gardeners. In expressing a love of the natural world, both were expressing a hunger for heightened experience, and it was only a very particular and idealized conception of nature that could fit that bill—a nature vast, ancient, eternal, separate, and awe-inspiring, a nature that at least presented the illusion of being beyond the touch of man. Such a wilderness proved the "ideal stage for the Romantic individual to exercise the cult that he frequently made of his own soul," as the historian Roderick Nash put it. But it is telling that these connoisseurs of the "sublime"—an odd word that came to be used at the time to express the contradictory emotion of fear and thrill (the notion also crops up in a predilection for deliberately contradictory phrases such as "delightful horror," "terrible joy")—were as apt to visit coal mines and quarries as mountains to satisfy this penchant (Rees 1975; Worster 1977:81–83; Nash 1982:47).

Again, we are dealing with degrees, not absolutes. Not all of the early environmentalists were aristocrats; John Muir notably was of humble origins. But if one looks through the rolls of the nature preservation societies in Britain and America in the nineteenth century the pattern is undeniable (Lowe and Goyder 1983, Bramwell 1989).

3

Indians only fit into the romantic picture of a wild, untouched wilderness to the extent that they could be seen as creatures of nature themselves, living in perfect harmony with nature's harmonious perfection. Many modern-day nature lovers assiduously perpetuate the myth of the noble savage in parallel to the myth of pristine nature. Ancient hunter-gatherers, who lived in a state of "balanced and harmonious" existence, altering "neither the natural firmament nor the animals and plants that share the land with them," were the original lovers and worshipers of nature, writes the environmental historian and philosopher Max Oelschlaeger, for one (Oelschlaeger 1991:34).

Yet ecological and archaeological evidence strongly suggests not only that Indians practiced landscape management on a truly heroic scale with the use of fire, but also that they were perfectly capable of drastically altering the size and distribution of ungulate populations, and even hunting a number of species to extinction (Kay 1994). Estimates of the pre-Columbian population of America are notoriously uncertain, but credible calculations place the number of people living north of the Rio Grande as high as 12 million (Dobyns 1966, Denevan 1992). Far from being a small band of harmonious stewards of the land, they dramatically modified their environment. Camels, woodland musk oxen, mammoths, mastodons, stagmoose all vanished shortly after the first major occupation of North America by man, 12,000 years ago. All were species that had evolved for a million years in North America in the absence of human hunters; the species that survived, by contrast (moose, elk, caribou, deer), were all recent arrivals from Asia and whose evolutionary history included defensive adaptations to human predation (Pielou 1991:254–57).

The determination to ignore such uncomfortable facts and to idealize the Indians as precocious environmentalists remains strong and may explain the credulity with which many have accepted and propagated the now-famous speech of Chief Seattle, a nineteenth-century American Indian whose prophetic warnings of the coming ecological crisis first came to wide public attention when they were used to narrate a 1972 television movie about pollution, called *Home.* "This we know—the earth does not belong to man, man belongs to the earth," the chief declares in one of the many versions of the speech that were subsequently reprinted. "All things are connected like the blood which unites one family. Whatever befalls the earth befalls the sons of the earth. Man did not weave the web of life; he is merely a strand in it. Whatever he does to the web, he does to himself."

To a few experts on American Indians, this all smelled a bit fishy. The real Chief Seattle did make a speech in about 1855, which was recounted thirty years later in a newspaper article by an American who had been in the audience; but according to this account, Seattle merely praised the generosity of the "great white chief" for buying his lands and offered not a word of ecological insight. (Seattle was also known to historians for his dignified refusal to allow the grateful white settlers to name their town after him; he objected that his eternal sleep would be interrupted each time a mortal uttered his name. The objection vanished when the whites proposed levying a small tax on themselves to provide the chief with some advance compensation for his troubles in the hereafter.) Nowhere was there any record of Seattle as a prophet of environmentalism.

A little research eventually cleared up the mystery. The reason Chief Seattle's speech sounded remarkably like the words of a twentieth-century, white, middle-class environmentalist, it turned out, was because they were the words of a twentieth-century, white, middle-class environmentalist. Ted Perry, a professor of film at the University of Texas at Austin, had written the script for the movie and had never claimed that the words he put in Chief Seattle's mouth were anything but fiction. But the truth has never quite managed to catch up, and even though the spuriousness of Chief Seattle's speech has been widely publicized, Seattle's anachronistic warnings about the fragile balance of nature *continue* to be reprinted and quoted in environmental magazines, sermons from the pulpit, classroom study kits, posters, textbooks, and bumper stickers. As a seemingly far-seeing anticipation of the central credo of modern environmentalism by a representative of an ancient way of life, Chief Seattle's speech has attained the status of what one admiring environmentalist thinker—Theodore Roszak, a professor of history at California State University—has called "a piece of folklore in the making, a literary artifact mingling traditional culture with contemporary aspiration." Roszak is aware that the speech is a twentieth-century concoction, and admits that he "initially had some scholarly qualms about citing the chief" in his writings, but decided to go ahead anyway: Seattle's "semilegendary" words, Roszak explained, "have become precious to the environmental movement" (Murray 1993; Roszak 1993:50,338–39).

4

There was another force that played a role of great importance in converting new followers to a love of nature in the late eighteenth and early nineteenth centuries, and that was religion. Petrarch climbed a mountain in 1336 and found himself "abashed" at taking pleasure in nature, fearing that to do so was sacrilege. Five centuries later the American theologian Jonathan Edwards proposed a different solution to the conflict between God and nature. Admiring nature was permissible, even admirable, he argued, precisely because nature was "God speaking to us." The feeling of sublime terror inspired by wilderness was a reminder of God's power and wrath. Even the dirt that covers everything and "which tends to defile the feet of the traveler" is a salutary moral lesson from God, a reminder that "the world is full of that which tends to defile the soul" (Albanese 1990:43–45). Others were less explicit about the precise moral lessons of nature and began to suggest simply that sublime landscapes were suitable objects of contemplation as stirring reminders of God's magnificence and grandeur.

This was a significant departure from the recent Puritan past. The wild and terrible in nature was no longer the rubbish left over from the creation or the unenlightened province of the devil. It was a testimonial to the greatness of God. Climbing a mountain was no longer an act of sacrilege, but an act of moral instruction.

If it was not yet an act of worship, that was coming. To Henry David Thoreau, nature's value was above all what it would do for man's soul. "I derive more of my subsistence from the swamps which surround my native town than from the cultivated gardens in the village," he wrote. "My spirits infallibly rise in proportion to the outward dreariness. . . . When I would recreate myself, I seek the darkest wood, the thickest and most interminable and, to the citizen, most dismal swamp. I enter a swamp as a sacred place, — a sanctum sanctorum." His motive was a "desire to bathe my head in atmospheres unknown to my feet" (Emerson and Thoreau 1991:94–100).

For Thoreau, nature's chief value was that it was not the town. The woods were an escape from social corruption, or, more to the point, people. "Society is always diseased, and the best is the most so," he wrote in *The Natural History of Massachusetts.* The conventions of social intercourse were stultifying. "Politics . . . are but as the cigar-smoke of a man." Commerce was frivolous. Labor was degrading, farming no better than serfdom. Even man's amusements were nothing but a sign of the depths of his despair. "The greater part of what my neighbors call good I believe in my soul to be bad." The word *village,* he said, comes from the same Latin root as *vile* and *villain,* which "suggests what kind of degeneracy villagers are liable to." Thoreau wanted to "shake off the village," where men spent empty, monotonous, vacuous, and spiritually impoverished lives. "I confess that I am astonished at the power of endurance, to say nothing of the moral insensibility, of my neighbors who confine themselves to shops and offices the whole day for weeks and months, aye, and years almost together," he wrote. It was the freedom that nature had to offer that was its chief attraction. Thoreau went to live at Walden Pond, he said, "to transact some private business with the fewest obstacles."

If nature's value rested upon its being a spiritual refuge from the evils of society, then nature, by definition, meant its separation from man and the absence of man. It was the very fact that man and all his follies were *not* to be found there that made nature estimable. What Thoreau disliked about man's presence was not that it would interfere with or degrade critical biological processes; what he disliked about man's presence was its presence. Thoreau likewise disapproved of wealth, church, rules, voting, dinner parties, and young men not as smart as he who sought to join him on his walks. He would tell the latter that he "had no walks to throw away on company" (Emerson 1862, Stevenson 1880). The link between environmentalism and escapism is an enduring one, and Thoreau's admiration of the wild as a place to turn one's back on the town can be heard in the words of David Brower, Bill McKibben, and other nature writers of our day.

Thoreau's declaration that "in wilderness is the preservation of the world" is one of the most quoted in modern environmental writing. Time and again it is cited in an utterly anachronistic fashion, however, wrenched from the clearly spiritual context of the passage in which it appears. When Thoreau was talking about "the preservation of the world," he did not mean the physical or ecological world at all, but rather the spiritual world of man. Those who cite this passage to lend authority to modern calls for preserving tropical biodiversity are misunderstanding what Thoreau was saying.

Thoreau's spiritual aversion to society readily explains some of the appeal that the woods held for him. But nature's stock was rising at this time for other fundamentally spiritual reasons, too. Many of the early American nature worshippers, including Thoreau's fellow townsmen in Concord, Ralph Waldo Emerson and Asa Bronson Alcott, were deeply involved in many reform-minded causes—temperance, abolition of slavery, dietary reform, alternative medicine—that were seen by their adherents quite explicitly as a moral and spiritual rejection of artificial evils and a return to the uncorrupted purity of nature. Just as "natural law" had shown Americans the falseness of monarchy, slavery, and other political systems that denied men their God-given rights, so natural foods and natural healing would show the falseness of alcohol and artificial medicines that denied men their God-given health. Rather than try to rise above nature and the "brute" or "animal" instincts, as Christianity had so long seemed to urge, the message of these "Christian physiologists" was that man must give up the sinful luxuries and excesses of civilization and return to nature (Albanese 1990:130–42; Furnas 1969:441–42).

The point is not to suggest that nature

lovers were cranks (though some certainly were). But it is crucial to recognize that the impulse that gave rise to such feelings for nature was fundamentally spiritual, not ecological. To these pioneering nature enthusiasts nature was but a means to an end. The spiritual ends they saw in nature were the *justification* for paying attention to nature at all. They were spiritual pilgrims first, birdwatchers second. And this attitude further drove home the conviction that nature—defined explicitly for this purpose as the world uncorrupted by man's artificial evils—embodied God's perfection. Thoreau was surely tongue-in-cheek when he and a few fellow drop-outs from Concord society formed the "Walden Pond Society" as an alternative church for Sunday morning meetings and proposed plucking and eating wild huckleberries as a substitute for the more conventional sacrament of communion. But there was no hint of irony in Emerson's transcendental conviction that nature was the literal dwelling place of God: "The aspect of nature is devout. Like the figure of Jesus, she stands with bended head, and hands folded upon the breast. The happiest man is he who learns from nature the lesson of worship." Emerson believed that nature was both a source of moral instruction and discipline, and the holy of holies where man would become "part or particle of God" himself (Emerson and Thoreau 1991:53,63–64; Alcott 1872:42).

5

Such feelings toward nature are real and earnest and genuine. Thoreau and Emerson and later, John Muir, struck a deep chord that resonates yet. Those who fight for more wilderness areas these days will speak of experiencing a sense of connection with something greater than themselves, something "primeval, threatening, and free of jarring reminders of civilization" (Mardon 1993).

Satisfying human needs, including a need for spiritual solitude, is a valid end. But what is good for the soul is not always what is good for nature. Some ecological goals are consistent with a goal of wilderness-as-solitude, but many are not. Setting a goal of providing the experience of solitude tells us nothing about what measures might be required to manage an ecosystem effectively to preserve endangered species, to reestablish disturbance processes that have been lost or suppressed by the advance of civilization, to restore vanished ecosystems such as the midwest oak savannas, to counter the effect of exotics, or to keep ungulate populations within the range of historical variation that had obtained since the end of the Ice Age—under the influence of heavy human predation—until the genocide of the Indians and preservationist policies allowed their numbers to explode.

Of course there has long been a wide spectrum of thought within the conservation and environmental movements, and paralleling the nature religion of Thoreau and Muir there early on arose a scientific and practical strand of thought represented by Theodore Roosevelt, Gifford Pinchot, and Aldo Leopold to name but a few. Many environmentalists and conservation biologists insist that environmentalism today has moved beyond romantic sentiment and simplistic formulations about the "balance of nature"; they insist that romanticism plays little part in modern, scientifically based advocacy for wilderness (Waller 1996). Unfortunately, one does not have to search very hard to find simplistic, romantic notions aplenty in contemporary debates over wilderness. Fundraising literature from mainstream environmental groups regularly invokes the theme that human intrusion is wrong and unnecessary, that wilderness is a sacred concept, that excluding "jarring reminders of civilization" is indeed what it is all about. The "balance of nature" idea and simplistic, deterministic notions of succession and climax may be a dead letter among scientists, but it is very much alive among influential nature writers of our day. The environmental historian Donald Worster, for example, claims not only that nature literally *has* a set order and purpose that mankind has a moral duty not to interfere with; he goes on to make the purely political argument that scientists who point out the simplistic myths embodied in the notion of wilderness or the inherent balance of nature should not do so because they are thereby abetting "members of the Farm Bureau" and other such "fierce private property and marketplace advocates" who lack a proper "ethic of environmental restraint and responsibility" (Worster 1997). Worster elsewhere insists that ecologists must, on moral grounds, adhere to concepts such as climax and succession (which he sees as under siege by modern "permissive"—his word—concepts such as disturbance and patch dynamics) because to abandon "climax ecology" "would be to remove ecology as a scientific check on man's aggrandizing growth" (Worster 1993; Worster 1977: ix–x, 240–42). The environmental writer Bill McKibben writes that man's intrusion in nature destroys its very meaning, which is its "independence" (McKibben 1989:70,73,104). Others have criticized even ecological restoration on similar grounds, arguing that the value of nature rests solely and completely in its freedom from "the domination of human technological practice" (Katz 1992).

Such thinking has had very real effects on contemporary public debate and public policy. Land managers who have attempted to institute prescribed burns, carry out salvage logging to reduce fuel buildup, or, most controversially, cull ungulates can testify that nature romanticism is a force that is alive and well, with a vengeance. Even in large parks, forests, and wilderness areas, explosions of ungulate populations have wreaked havoc on rare songbird species, on endangered plant populations, and on forest regeneration, yet attempts to limit their numbers have been repeatedly met by opposition from environmental groups decrying any "intrusion" into nature—and such views increasingly prevail (McLaughlin 1993, Maryland Cooperative Extension Service 1994).

But even a number of prominent scientists who advocate expanded wilderness areas on purportedly scientific grounds frequently invoke romantic arguments to justify their position. The so-called "Wildlands Project," an audacious proposal to convert as much as half the land area of large regions of the United States into protected wilderness, is based on a scientific analysis of land areas required to sustain minimum viable populations; yet these analyses contain huge uncertainties, and Michael Soulé, a biologist and project founder, has been quoted as defending the project's basis and aims in explicitly spiritual terms—as providing people with the experience of "wildness," "bigness," and "fierceness" (Mann and Plummer 1993).

Likewise, Edward O. Wilson argues that biodiversity needs to be protected because it is critical for the human soul—that mankind supposedly has an instinctive need to bond with the rest of creation (Wilson 1991:350; Kellert and Wilson 1993). Indeed, a number of writers have recently argued quite explicitly that spiritual feelings of peace and solitude in undeveloped wilderness are *the* prime case for protecting biodiversity; indeed, that such spiritual feelings are one and the same with the scientific case for preserving biodiversity. Stephen Kellert, for example, equates his feelings of solitude and escape from civilization during a walk in the woods with a feeling of "intimate affiliation with living diversity." (Kellert, 1996). Part of why this is so unconvincing is that the feelings these writers describe in such rich Thoreauvian prose have everything to do with the romantic yearning for solitude and essentially nothing to do with any actual feelings that people might be able to summon up for the insects, bacteria, fungi, parasites, and other interesting life forms that make up the overwhelming bulk of "living diversity."

There are many valid and important ecological goals which require management practices that simply will not sit well with those who nurture the romantic yearning for "unspoiled" wilderness. Some of these management practices are ugly and intrusive and violent. Some of the important scientific goals of ecological management are simply not going to evoke feelings of reverence and "intimate affiliation" with nature. I personally believe that protecting even very ugly endangered species is an important goal, and would hate to have to rely on romantic or religious impulses to support it. As some astute critics have pointed out, there is a very grave danger of confusing goals here. Cloaking what is fundamentally a political, sentimental, or religious position in modern scientific trappings is ultimately corrupting to science (Cronon 1995).

A more pressing problem is that a goal of "protecting biodiversity" or creating "wildlands" tells us no more about how to set realistic ecological priorities than does a goal of providing people with opportunities to experience solitude. Wilson's "theory of island biogeography," a simple formula relating species diversity to land area, has been strongly criticized both for its biological infidelity and mathematical naiveté (Connor and McCoy 1979, Heywood and Stuart 1992, Budiansky 1994) and for diverting attention from the studies that are actually needed to help identify biodiversity hotspots and to set priorities. A significant point is that areas that people value for their "wildness" often do not correspond well with biodiversity hotspots. Nor has a clear scientific case been made that vast contiguous "wilderness" areas are always required for preserving biodiversity effectively (Mann and Plummer 1995). Daniel Simberloff, a former student of Wilson's who has conducted extensive research on this subject, has written: "It is sad that the unwarranted focus on island biogeography has detracted from the main task of refuge planners, determining what habitats are important and how to maintain them." (Simberloff 1992). Indeed, the only specific recommendation that Wilson derives from his species-area analyses is a proposal to halt "all" further development of land in the world (Ehrlich and Wilson 1991).

This seems unlikely to happen. In the United States, which can afford to set aside far more land than arguably any country in the world, about 5 percent of land is in parks and wilderness areas; about 70 percent is in pasture, cropland, and producing forests (Waggoner, Ausubel, and Wernick 1996). Even under the most optimistic population control scenarios, world population is likely to reach about 10 billion sometime in the next century before leveling off (Bongaarts 1994). It seems clear that achieving the ecological ends that are widely shared today—such as preserving endangered species—will require active management of many land area that do not fit the definition of "wilderness."

Far from being compatible with the scientific demands of ecological management, the tenaciously lingering romanticism toward nature is often at odds with what is needed. True, if we could set aside half the United States as "wildlands," size alone could accomplish a lot—it could allow for the establishment of large metapopulations, capture natural disturbance processes on a broader scale, and provide needed habitat for certain endangered species such as grizzly bears and wolves that need large individual ranges. But even then there would be problems that would demand active human intervention if our ecological goals are to be met. Disturbance processes upon which many species depend have been curtailed, if not within parks or wilderness areas, then in surrounding areas. Exotic species have intruded. Animals' migration routes have been cut. And the part played by humans for ecologically significant timespans would still be eliminated from such "wild lands." To have a "functioning ecosystem," we would have to make it happen. Intrusion is ecologically sound policy; "wilderness" is not.

Yet the resilience of an artificial view of wilderness, with its deep historical roots, may well explain why "hands-on" management of ecosystems, even for the purest and noblest of environmental ends, so often meets harsh resistance from those who equate any intrusion of man with sacrilege against the credo of nature's perfection, its unity, and its symbolic value as a critique of the shortcomings of human society.

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Angela E. Collada and Alan Haney

Vegetation Changes Associated with Oak Wilt in a Wisconsin Sand Savanna

Abstract *This study evaluates the effects of oak wilt, a disease caused by the fungus* Ceratocystis fagacearum *on plant species abundance, composition, and structure in degraded oak barrens at Necedah National Wildlife Refuge. Open patches created by oak wilt are compared to degraded barrens immediately surrounding each patch. Patches are also compared to Old Barrens, a savanna community in the Refuge that has remained open since a wildfire in 1936. Two soil associations predominate in the study area: the better drained Plainfield-Friendship association supported significantly more patches and more prairie/savanna species than the poorly drained Meehan-Newson soils. As predicted, more prairie/savanna species occurred in patches than surrounding woods, but far more occurred in Old Barrens than in patches when comparing within the same soil type. Total herbaceous cover was higher in patches than Old Barrens, and deciduous shrub cover was higher in Old Barrens than in patches; total herbaceous cover was also higher in patches than in woods. Total deciduous and coniferous tree cover was lower in patches than woods, although significant only when comparing patches to woods on Plainfield-Friendship soil. Total herbaceous cover was negatively correlated to total tree cover.*

The dependence of savanna ecosystems on disturbance is well known (Curtis 1959, Anderson 1982, Nuzzo 1986, Haney and Apfelbaum 1991, Skarpe 1992, Heikens and Robertson 1994, Huston 1994). Fire effects, the primary disturbance associated with savannas, have been studied extensively. Fire reduces the litter layer and canopy cover by killing shrubs and small trees, thereby allowing more light to reach the ground (Dyksterhuis 1957, Daubenmire 1968, White

1983, Hulbert 1986, Skarpe 1992, Huston 1994). Warmer soil temperatures and increased light, in turn, encourage the germination and growth of fire-adapted and shade-intolerant species (Daubenmire 1968, Tester 1989, Huston 1994).

Depending upon intensity and the initial successional stage of the savanna, grazing, in conjunction with fire, also discourages the invasion of woody species and alters species composition in favor of those characteristic of open sites (Dyksterhuis 1957, Daubenmire 1968, Anderson 1982, Dyer et al. 1982). Effects of other forms of herbivory, particularly by insects and soil fauna, have yet to be studied (McPherson 1993). While the ecological role of disease, in general, is poorly understood (Burdon 1994, Castello et al. 1995), the localized, host-specific impact of oak wilt is well documented (Gibbs and French 1980, Menges and Loucks 1984, Webber and Gibbs 1989).

Ceratocystis fagacearum, the fungus that causes oak wilt, was first identified in Wisconsin over a century ago (Warder 1881). The principle long-distance vector of the fungus is the picnic beetle (Coleoptera: Nitidulidae) (Buchanan 1960, Gibbs and French 1980, Webber and Gibbs 1989, Bruhn and Heyd 1992), which is attracted to wounded but otherwise healthy trees. Picnic beetles can transfer spores up to 1 mile from an infected oak (Juzwik 1983 cited in Bruhn and Heyd 1992). Local spread occurs through root grafts (Kuntz and Riker 1961, Bruhn and Heyd 1992), the fusing of the roots resulting in functional vascular connections (Graham and Bormann 1966), and is the primary means of transmission (Gibbs and French 1980). Root grafts account for the patches of dead oaks that characterize an infected area (Worf and Kuntz 1978, Gibbs and French 1980).

The extent of root grafting varies by species and is influenced by soil (Gillespie and True 1959, Graham and Bormann 1966, Bruhn et al. 1991, Bruhn and Heyd 1992). Red oaks (genus *Quercus,* subgenus *Erythrobalanus*), the dominant deciduous trees of oak barrens (Curtis 1959, Whitford and Whitford 1971), are especially prone to root grafting (Worf and Kuntz 1978), and the incidence of root grafts increases on sandy, well-drained soils (Gillespie and True 1959, MacDonald and Hindal 1981, Bruhn and Heyd 1992).

Studies of *C. fagacearum* to date have fallen into two broad categories: epidemiological studies, including the impact of oak wilt on oaks (Henry et al. 1944, Struckmeyer et al. 1954, Buchanan 1960, Kuntz and Riker 1961, Worf and Kuntz 1978, Gibbs and French 1980, Jacobi and MacDonald 1980, MacDonald and Hindal 1981), and models of the spread of the fungus (Menges and Loucks 1984, Menges and Kuntz 1985, Appel et al. 1989, Bruhn et al. 1991).

This paper examines the effect of oak wilt on the vegetation in a successionally advanced oak barrens at Necedah National Wildlife Refuge (NNWR) in west central Wisconsin. Barrens are a type of savanna characterized by stunted trees and coarse or shallow soils (Curtis 1959, Haney and Apfelbaum 1991, Heikens and Robertson 1994). Curtis (1959) described the vegetation of the Central Sands region as pine barrens, a true savanna dominated by scattered, slow-growing oaks, primarily *Quercus ellipsoidalis* and *Q. velutina* and *Pinus banksiana* and *P. resinosa.* Historically, fire, in conjunction with disease and grazing by both ungulates and insects, maintained the unique physiognomy and structure of barrens; fire suppression at NNWR allowed the barrens to develop into mixed oak and pine woodlands.

Speculation about the historical effect of oak wilt as a natural disturbance (Anderson 1982, Warder 1991, Heikens and Robertson 1994) as well as our own observations of structure and the presence of open-site species in oak wilt patches led us to hypothesize that the impact of oak wilt on barrens communities was similar to the effects of fire. We expected to see more savanna forbs in the ground layer of patches than in the woods. We also expected total herbaceous cover in patches to approximate cover in well-maintained barrens and to be higher than in the surrounding woods. *Carex pensylvanica,* a species of open, upland woods, was expected to be the dominant herbaceous species in the woods, and woodland species in general were expected to be less abundant in patches. We also predicted that *Pinus banksiana,* an early successional species, would be more common in the ground, shrub, and tree layers in patches than in the surrounding forest, comparable to open barrens, reasoning that opening the canopy through the loss of oak trees would favor *P. banksiana* regeneration.

Methods

Study Site

The Necedah National Wildlife Refuge is located in the Central Sands region of Wisconsin, in Townships 18-20 North, Ranges 2-3 East. The NNWR was established in 1936 and currently includes 18,211 ha that are managed primarily for biodiversity and recreation. Barrens restoration became a priority in 1993 in response to concern over the federally endangered Karner blue butterfly *(Lycaeides melissa samuelis)* and other rare species. Currently, 227 ha of mixed oak woodland have been restored to savanna by reducing canopy cover in woodlands from about 90% to approximately 50% through tree removal and fire. A total of 1,441 ha is planned for restoration and management as oak and pine savanna.

Oak wilt was first identified at NNWR in 1975, and aerial photographs were taken in 1978 to assess the extent of spread of the fungus. Initial oak wilt research in 1979–1981 focused on methods for controlling the spread of the fungus (J. Walters, unpublished report). No other research was conducted to determine the impact of oak wilt on the NNWR, and we found no published studies of the ecological effects of *C. fagacearum.*

Two associations comprised the majority of soils at our study site. Plainfield-Friendship soils are well drained and located on higher ground, typically a minimum of 1.5 m above the water table (Gundlach et al. 1991, D. Omernik, personal communication). Meehan-Newson soils are poorly drained and occur in lower lying areas. The five soil series form a gradient from well-drained ridges to poorly drained sedge meadows.

Patch Selection and Sampling

Five of the 69 sections comprising NNWR were randomly selected for sampling. Management history of selected sections was researched, and sections were discarded if disturbed since 1968 by events such as fire, logging, or hydrological change. All sections included in the study contained a minimum of seven oak wilt patches, of which at least five were randomly selected for sampling.

Oak wilt patches were identified primarily by the proximity of several dead oak trees, typically in a circular or elliptical pattern. A minimum of three to four adjacent dead oaks were required to qualify an area as a patch. Areas with fewer than three to four dead oaks qualified if wilting leaves were present on at least one of the trees, indicating an active oak wilt site. Ten patches were sampled in the first section to ensure that sufficient data were collected, and six patches were sampled in another section because one patch was extremely small. A total of 31 patches were sampled in May and August 1995 and July 1996.

The center of each selected patch was identified and line transects established along 0, 90, 180 and 270 degree azimuths from the center. Transects began 1 m from the patch center and extended a minimum of 50 m beyond the edge of the patch into the surrounding woods unless vegetation graded into wetlands, pine plantations, or other habitat unsuited for growth of oaks, at which point transects were terminated. Soils were identified for each 10 m segment along each transect.

Percent cover for each species in the ground layer (vegetation < 1 m tall) was estimated using 1 m^2 circular plots centered at 10 m intervals beginning 1 m from the center of the patch. The number of plots varied with the length of each transect. Coarse litter, fine litter, and bare soil were also estimated. Bryophyte and lichen cover was estimated but not evaluated.

Tree (> 1 m tall, > 5 cm dbh) and shrub and small tree (> 1 m tall, < 5 cm dbh) cover were recorded by species for each 10 m segment using a line intercept method (Kent and Coker 1992). Because hybridization of *Quercus ellipsoidalis* and *Q.velutina,* both of which are in the red oak subgenus, was so extensive and rendered the two species virtually indistinguishable (Curtis 1959), these trees were identified as their hybrid, *Q. paleolithicola* (Gleason and Cronquist 1991).

Old Barrens, also located on Plainfield-Friendship soil, is a floristically diverse unit on the Refuge that appears to have been maintained by oak wilt (R. King, personal communication) since a wild fire restored it in 1936. Vegetation at Old Barrens was sampled by Refuge staff in 1995 using a sampling protocol similar to ours. We compared their data to that we collected from oak wilt patches on Plainfield-Friendship soils.

Analysis was conducted at two levels: vegetation in oak wilt patches was compared to the undisturbed woodlands immediately surrounding the patches, and comparisons were made of vegetation on patches occurring on Plainfield-Friendship soils to vegetation on Old Barrens. The distribution of patches and woods across the two soil associations was examined using a chi-square test. Preliminary analysis of vegetation data indicated that even the most common species had skewed distributions; that and uneven sample size led us to compare the abundance of species using the Mann-Whitney U test ($P \leq 0.05$) (Sokal and Rohlf 1981). We used the Spearman correlation coefficient to determine the effect of canopy cover on total herbaceous cover (Sokal and Rohlf 1981). Designation of prairie/savanna species is based on Gleason and Cronquist (1991) and a list compiled by Will-Wolf and Stearns (in press).

Results

Soils

Chi-square tests of the distribution of patches and woods by soil type confirmed ($P \leq 0.0001$) that most oak wilt patches are on Plainfield-Friendship soils. Not only did patches occur with much greater frequency on the better drained soils, they also tended to be larger (not significantly) on average. Patches ranged in size from 22–78 m in diameter (mean = 52 m) on Plainfield-Friendship soils while patches on Meehan-Newson soils averaged 23–63 m in diameter (mean = 40 m).

Structure

Comparisons between Old Barrens and oak wilt patches on Plainfield-Friendship soil of the three strata (total ground, woody sapling and shrub, and tree layers) revealed significant differences in the ground and shrub layers (Table 1). Sedges, primarily *Carex pensylvanica,* were almost twice as abundant in patches as in Old Barrens ($P \leq 0.0012$) whereas grasses were ten-fold more abundant in Old Barrens ($P \leq 0.0004$). Deciduous shrubs were more prevalent in Old Barrens than in patches ($P \leq 0.0214$).

Comparisons of patches with surrounding woods by soil type showed greater structural variation at several levels (Table 2). Significant differences ($P \leq 0.05$) in total cover occurred only in the ground layer, which was greater in patches than in woods. Total forb cover was significantly higher on Meehan-Newson soils, but total graminoid cover was higher on Plainfield-Friendship soils. Sedge cover was consistently higher on Plainfield-Friendship soil, but grass cover, which was low compared to sedges, displayed no clear pattern in distribution across soils or location. Total tree cover ($P \leq 0.0082$) and deciduous tree cover ($P \leq 0.0240$) were both lower in patches than in woods, as expected.

An examination of total ground layer cover as a function of total tree cover verified that herb cover decreased as canopy cover increased ($P \leq 0.001$) (Figure 1). Ground layer cover as a function of canopy cover in Old Barrens and patches on Plainfield-Friendship soil was not significantly different ($P \leq 0.303$).

Individual Species Distribution

Standardized species richness, the average number of species per 10 m transect, was calculated to take into account the varying unit sizes in the oak wilt study area and Old Barrens (Table 3). Standardized richness was significantly higher ($P \leq 0.0003$) in Old Barrens than in patches on Plainfield-Friendship soil; there was no statistical difference between patches and woods on either soil type.

Table 1. Total mean percent cover and standard deviation for growth forms and subsets of growth forms for Old Barrens and patches on Plainfield-Friendship soil.[1]

	Old Barrens		*Patches*	
Growth Form or Subset	*Mean*	*S.D.*	*Mean*	*S.D.*
Total ground layer	83.360	20.408	104.378	45.580
Forbs	20.120	9.166	27.665	25.995
Graminoids	58.480	7.685	67.994	16.138
Sedges	36.080	10.324	65.973	15.731
Grasses	22.400	6.554	2.021	3.143
Woody cover	4.760	4.736	8.720	8.315
Woody sapling and shrub layer	10.760	8.568	4.001	4.976
Coniferous cover	1.000	2.236	1.629	2.324
Deciduous cover	9.760	7.093	2.371	4.798
Tree layer	35.656	38.518	27.862	20.734
Coniferous cover	16.920	20.496	16.126	15.568
Deciduous cover	18.736	28.527	11.736	13.616

[1] Significant differences are underlined.

Table 2. Total percent cover and standard deviation[1], for growth forms and subsets of growth forms by soil and location for oak wilt patches and woods.

	Plainfield-Friendship Soil				*Meehan-Newson Soil*[1]			
	Patches		*Woods*		*Patches*		*Woods*	
Growth Form or Subset	*Mean*[2]	*S.D.*	*Mean*[2]	*S.D.*	*Mean*[2]	*S.D.*	*Mean*[2]	*S.D.*
Total ground layer	104.378^{a}	45.580	75.573^{b}	40.393	103.394^{ab}	61.518	72.821^{b}	48.297
Forbs	27.665^{ac}	25.995	25.693^{a}	20.216	68.281^{b}	40.542	44.569^{c}	30.654
Graminoids	67.994^{a}	16.138	42.401^{b}	17.695	26.366^{b}	19.447	19.632^{c}	19.488
Sedges	65.973^{a}	15.731	41.673^{b}	17.406	26.306^{b}	19.382	17.397^{c}	20289
Grasses	2.021^{a}	3.143	0.728^{ab}	1.286	0.060^{b}	0.134	2.035^{c}	6.558
Ground layer cover	8.720	8.315	7.479	6.676	8.748	7.194	8.620	8.341
Total sapling and shrub layer	4.001	4.976	6.961	11.171	4.324	5.930	16.884	23.268
Coniferous cover	1.629	2.324	1.306	2.209	0.867	1.938	0.358	0.745
Deciduous cover	2.371	4.798	5.655	10.676	3.458	4.152	16.527	23.076
All trees	27.862^{a}	20.734	62.565^{bc}	29.418	45.764^{abc}	27.424	67.410^{b}	40.109
Coniferous trees	16.126	15.568	18.005	15.240	20.364	23.028	24.798	30.870
Deciduous trees	11.736^{a}	13.616	44.560^{b}	25.476	25.400^{ab}	28.219	42.612^{b}	33.744

[1] No significant difference was reported for any species; superscripts were applied without regard to possible significance or insignificance between species on these sites.

[2] Means with the same superscripted letter were not significantly different.

Thirty-seven species had significantly different distributions (Table 4) when patches on Plainfield-Friendship soil were compared to Old Barrens. Of those 37 species, 18 occurred exclusively in Old Barrens and one, *Gaylussacia baccata,* occurred only in the oak wilt patches. With few exceptions, the species listed (Table 4) are common to savannas. Several species, including *Rosa carolina* and *Pteridium aquilinum,* were not reported in Old Barrens, although we have observed them there.

Comparisons of vegetation in patches and woods by soil type revealed significant differences in the abundance of 10 species (Table 5), including *Acer rubrum* in all three strata. Species such as *Andropogon gerardii* and *Pinus banksiana* occurred exclusively on Plainfield-Friendship soil. *Carex pensylvanica* was more abundant on Plainfield-Friendship soil and in patches; *Andropogon scoparius, Achillea millefolium, Koeleria cristata, Helianthemum canadense, Poa pratensis, Sorghastrum nutans,* and *Solidago* spp., whose distributions were not significantly different, nonetheless, were more abundant in the well-drained Plainfield-Friendship soil. *Gaylussacia baccata* was more abundant on Meehan-Newson soil and significantly more abundant ($P \leq 0.0043$) in the patches than the woods on that soil type. *Pteridium aquilinum* also was more abundant on Meehan-Newson soil and in woods than in patches, but differences were not significant.

Discussion

Oak wilt is a localized disturbance which, as it spreads, creates small scattered patches throughout the woodlands that structurally begin to resemble a barrens. We found that oak wilt patches were intermediate to a well-established barrens and surrounding wood-

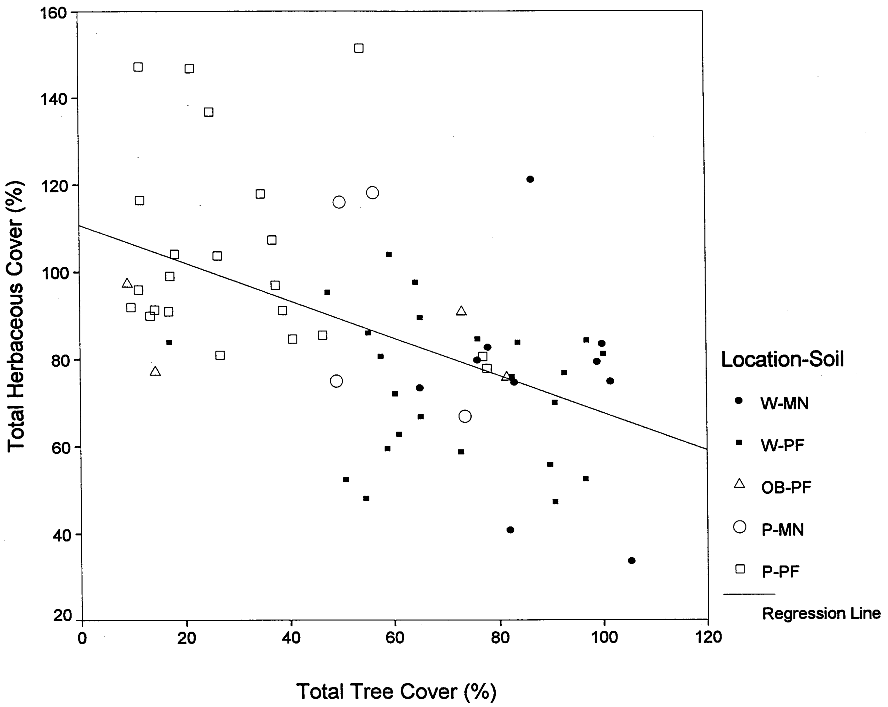

Figure 1. Total ground layer cover as a function of total tree cover for all oak wilt openings and Old Barrens sites. Locations are identified as patches (P), Old Barrens (OB), or woods (W), and soils are identified as Plainfield-Friendship (PF) or Meehan-Newson (MN).

lands in both structure and composition. Herbaceous cover in patches is much higher than in the surrounding woods and, depending on the soil type, was dominated by either forbs or graminoids. However, the ground layer in patches contained more weedy species such as *Galeopsis tetrahit* and T*araxacum officinale* and far fewer prairie/ savanna species than Old Barrens. Total shrub cover was consistently low across all sites. Total tree cover in patches approximated tree cover in Old Barrens and was considerably lower in both than in the woods. The cover of *Pinus banksiana,* which we hypothesized would increase across all strata in oak wilt openings, was significantly higher only in the ground layer on Plainfield-Friendship soil. Total herb cover was negatively correlated to tree cover and was similar in patches and Old Barrens.

Several factors may contribute to the results we observed in this study. Soil type was reported to be a significant factor in the occurrence of oak wilt (Gillespie and True 1959, Bruhn and Heyd 1992), and this was borne out in our study. Oaks in the shallow, droughty, nutrient-poor Plainfield-Friendship soil apparently experience a

Table 3. Average number of species by strata per 10 m segment by soil and location.

Soil	*Site or Location*	*Ground Layer*	*Shrub Layer*	*Tree Layer*
Plainfield-Friendship	Patch	2.57	0.19	0.34
	Old Barrens	4.52	0.24	0.32
	Woods	2.30	0.22	0.50
Meehan-Newson	Patch	4.23	0.46	0.50
	Woods	3.65	0.35	0.76

Table 4. Mean and standard deviation of percent cover for species occurring in Old Barrens and oak wilt patches on Plainfield-Friendship soil.

	Old Barrens		*Patches*	
Species[1]	*Mean*	*S.D.*	*Mean*	*S.D.*
Achillea millefolium	1.1600	1.9667	0.0113	0.0412
Agrostis hyemalis	0.2400	0.1673	0.0000	0.0000
Andropogon gerardii	2.1600	1.2973	0.7037	2.2400
Andropogon scoparius	14.3200	6.0039	0.0515	0.1269
Asclepias tuberosa	0.0600	0.1342	0.0000	0.0000
Aster azureus	0.7600	0.4278	0.0161	0.0609
Baptisia lactea	0.4800	1.0733	0.0000	0.0000
Carex spp.	36.0800	10.3239	65.9729	15.7314
Comptonia peregrina	0.9600	1.8298	0.0000	0.0000
Convolvulus spithamaeus	0.7800	1.3864	0.0000	0.0000
Coreopsis palmata	1.0400	2.2154	0.0000	0.0000
Danthonia spicata	0.5600	0.8173	0.0458	0.2043
Fragaria virginiana	0.1200	0.2683	0.0000	0.0000
Gaylussacia baccata	0.0000	0.0000	4.8140	12.7124
Helianthus occidentalis	3.9200	3.3804	0.0000	0.0000
Houstonia longifolia	0.1600	0.2191	0.0076	0.0260
Koeleria cristata	2.4200	2.5509	0.0327	0.1153
Lechea intermedia	0.1600	0.3050	0.0000	0.0000
Lespedeza capitata	0.0600	0.1342	0.0000	0.0000
Liatris aspera	0.2000	0.2449	0.0000	0.0000
Liatris cylindracea	0.1200	0.2683	0.0000	0.0000
Panicum ssp.	0.3800	0.5848	0.0083	0.0408
Pedicularis lanceolata	0.1400	0.3130	0.0000	0.0000
Physalis virginiana	0.1800	0.2490	0.0000	0.0000
Pinus banksiana	0.4800	0.5450	0.2005	0.5205
Poa pratensis	1.3800	1.5928	0.6374	1.9035
Populus grandidentata (shrub)	2.7600	3.7799	0.0093	0.0454
Populus grandidentata (tree)	1.0230	3.8278	13.8000	23.0634
Rubus spp.	3.4270	7.6789	0.1400	0.3130
Solidago juncea	1.7800	1.5563	0.0035	0.0170
Solidago nemoralis	0.3600	0.4980	0.0000	0.0000
Sorghastrum nutans	0.7800	1.1145	0.0208	0.1021
Spiranthes gracilis	0.0200	0.0447	0.0000	0.0000
Vaccinium angustifolium	2.5000	2.8723	10.8920	8.5607
Viola pedata	0.6000	0.5788	0.0240	0.0690

[1] Only species whose distributions were significantly different are listed.

Table 5. Mean, standard deviation, and significant differences ($P \leq 0.05$) of percent cover for species in oak wilt patches and woods.

	Plainfield-Friendship Soil				*Meehan-Newson Soil*[1]			
	Patches		*Woods*		*Patches*		*Woods*	
Species	*Mean*[2]	*S.D.*	*Mean*[2]	*S.D.*	*Mean*[2]	*S.D.*	*Mean*[2]	*S.D.*
Acer rubrum (ground layer)	0.000^{a}	0.000	0.221^{b}	0.392	0.317^{b}	0.435	0.182^{b}	0.343
Acer rubrum (shrub layer)	0.006^{abc}	0.029	0.000^{a}	0.000	0.800^{b}	1.789	1.729^{b}	5.513
Acer rubrum (tree layer)	0.000a	0.000	1.589^{ab}	4.635	2.000^{b}	4.472	4.987^{b}	9.374
Andropogon gerardii	0.704^{a}	2.240	0.207^{ab}	0.712	0.000^{ab}	0.000	0.000^{b}	0.000
Aronia melanocarpa	0.010^{a}	0.051	0.012^{a}	0.049	0.000^{a}	0.000	1.525^{b}	3.601
Corylus americana (shrub)	0.000^{a}	0.000	0.000^{a}	0.000	0.080^{b}	0.179	0.000^{a}	0.000
Gaylussacia baccata	4.814^{a}	12.712	5.733^{a}	9.909	24.499^{b}	11.199	13.520^{a}	17.947
Pinus banksiana	0.20^{a}	0.520	0.111^{a}	0.152	0.000^{a}	0.000	0.000^{b}	0.000
Pteridium aquilinum	4.012^{a}	7.976	5.089^{ab}	7.006	14.156^{ab}	16.960	13.209^{b}	15.528
Trientalis borealis	0.000^{a}	0.000	0.021^{a}	0.108	0.233^{b}	0.325	0.124^{b}	0.238

[1] No significant difference was reported for any species; superscript applied without regard to possible signifcance or insignificance between species on these sites.

[2] Means with the same superscripted letter were not significantly different.

higher incidence of root grafting, which in turn affects the extent of oak wilt spread and, consequently, patch size.

Most species occurring in Old Barrens are fire adapted and shade intolerant. We hypothesize that the effects of fire, including litter removal, nutrient release, increased pH, warmer soil surface temperatures, increased nutrient availability, and reduction of woody vegetation, will have a different effect than oak wilt alone. We predict, moreover, that fire will have a synergistic effect when combined with oak wilt.

Old Barrens, in addition to originating by fire, is a relatively unfragmented 227 ha area, whereas patches did not exceed 78 m in diameter (0.48 ha). The low richness of savanna species in patches may be influenced by both patch dynamics and fire; recruitment and proliferation of savanna species is more likely to occur in large areas that have existed for decades than in more recently established, small isolated openings scattered throughout a woodland.

This study provides a preliminary framework for understanding the ecological impact of oak wilt on the vegetation of degraded barrens. Oak wilt may restore some savanna species by creating barrens structure in small isolated patches, but other disturbances, notably fire, are probably required to restore a full complement of savanna species. We believe that studies of the interaction of oak wilt and fire will add greatly to our understanding of the successional importance of oak wilt in savannas.

Acknowledgments

The Department of Defense Legacy Resource Management Program and the Sand County Foundation funded this project. We wish to thank Rich King at Necedah National Wildlife Refuge for allowing us to use the Old Barrens data. Tiata Barbieri assisted with data collection. The authors appreciate the helpful suggestions of two anonymous reviewers.

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Linda DePaul and David Kopitzke

Incentives for Savanna Protection on Private lands: Past, Present, and Future

Abstract *In Wisconsin, as in most parts of the eastern one-half of the United States, about 80% of the land is owned by private individuals. These owners may be individuals, families, businesses, and organizations. Their diverse backgrounds, goals, and land ownership sizes create a mosaic of diverse land conditions across the state and present a challenge to landscape-level management. Yet, many of the state's rare species and their associated habitats occur on this land, including prairie brush clover* (Lespedeza leptostachya), *wooly milkweed* (Asclepias lanuginosa), *purple milkweed* (Ascelepias purpurascens), *orchard oriole (Icterus spurius), and loggerhead shrike* (Lanius ludovicianus). *Considering the large percentage of Wisconsin's land base that is privately owned, it is not surprising that many of the known remnants of oak savanna ecosystems occur on privately held acreages.*

Land ownership trends in the Great Lakes region indicate that in the future, private holdings will be more fragmented and will turn over more frequently (Sample et al. 1995). If these important remnants of our once vast oak savanna ecosystems are to remain part of Wisconsin's natural heritage, private land owners must be motivated to play a significant role in their protection. Apart from forestry and agriculture programs, conservation activities traditionally have been largely the province of government agencies or private environmental organizations. Recently, however, the private landowner's contribution has grown in importance and is being recognized. Usually this contribution has depended solely on the goodwill and generosity of a small percentage of concerned landowners.

Encouraging a larger percentage of landowners to commit themselves to savanna restoration, management, and protection requires more compelling incentives than have previously been available. We have listed a variety of currently available incentives offered by private conservation organizations and government agencies, including legislation, technical assistance, payments, and

education. There is much that we can learn from the past and current successes and failures. We will discuss the relative success of each of these methods and will also describe the practical potential types of incentives that could be instituted to encourage private landowners to protect savannas. Continued research, local involvement, and integrated approaches toward savanna management on private lands are all needed to protect this valuable ecosystem.

Birch (1994) states that close to 84% of the land in Wisconsin is privately owned, which is close to the 80% figure that is frequently quoted for all states in the eastern one-half of the United States. Even in western states, rich in public land, usually the majority of the land is privately owned. Nor is this the case only in the United States. In Australia, for example, 70% of the land is in private ownership (Clairs et al. 1997).

It is not surprising, then, that many, if not most, of Wisconsin's rare species and their habitats occur on private lands—owned by individuals, families, businesses, and organizations. This is certainly true of oak savanna plant communities. If this very rare group of plant communities is to remain a healthy part of Wisconsin's biota, then private landowners must play a significant role in its protection.

We adopted a broad definition of a savanna: a grassland with scattered trees. This definition encompasses those communities that John Curtis (1959) called oak openings, scrub oak barrens, pine barrens, and cedar glades. Curtis estimated that at the time of settlement Wisconsin boasted 9,602,500 acres of savanna—more than 25% of the state's total area. Currently, estimates indicate that there are 1,920 acres of savanna, only 0.02% of its former area and, of the total state's acreage, a mere 0.005% The figures show clearly that savannas were once among the most common of plant communities in the state; now they are the rarest.

While some essentially intact oak savanna communities occur on public land, this does not automatically assure their protection or long-term survival. Not all public land managers are trained to recognize savanna structure and species, and oak savanna management techniques are by no means clear. Even the most ardent of oak savanna enthusiasts cannot always be sure if burning is indicated, when to burn, which pesticides are best in all cases, and which species to encourage or discourage. Furthermore, there are not enough public employees who are savanna ecologists to manage all the potential savanna habitat on public land.

This underscores the pressing need for educating the public, especially landowners, on how to identify, protect, and manage (as well as we know how) savannas. In addition, restoration projects are often expensive and labor intensive for the landowner. If we really want to see savanna communities maintained or restored, we should assist the landowner at two levels, education and implementation. What incentives have there been to encourage landowners to take an interest in savannas? To answer this question adequately, we must first look at the history of conservation incentives for private landowners.

History of Government Incentives

Incentives to private forest landowners have appeared in many forms and have a long and rich history. In 1864, George Perkins Marsh published an influential book entitled Man & Nature. Nearly one-half of this book was devoted to the ravages of the forest lands. During 1872 the first set-aside of more than two million acres of spectacular forest lands for preservation from development occurred. This was contrary to the government programs of the day that were targeted at encouraging homesteading. These types of programs essentially gave land away for mining, farming, and rural development.

In 1911 the first public forest policy was passed to encourage specific practices on lands owned by private individuals and businesses. However, since large portions of the American public would not support extensive federal domination on private lands, forest managers and politicians were forced to propose programs limited to "encouraging" better management practices.

Over the last 220 years of our country's history, the acceptance of a larger role for government on private lands has grown. Some of the more important reasons for this acceptance include increasing population numbers, rising incomes and living standards, increased competition for limited resources, broader education, wider suffrage, and growing conservation and environmental concerns. The broad goal of these environmental incentive programs has been to protect the land values that society has determined to be important. Our nation has only 7% of the world's forests but 40% of the world's privately owned forests (Moulton 1994).

The types of incentives that have evolved over time all have both positive and negative aspects associated with them and have limited applicability. There has been no single type of incentive that has proven effective for the majority of landowners and land situations, although attempts have been made consistently to craft just such a program. The most notable type of incentive program that has all too frequently been misapplied is strict regulation by law. These incentives gained much of their momentum out the environmental era of the 1960s, but did not remedy the situations they were created to protect. The basic problem, as George Reiger (1992) states, is that "such legislation . . . was based on the naive premise that only the federal government is big enough and fair-minded enough to deal with problems created with the Corporate State. Unfortunately, just the opposite is true."

Other types of incentives involve purchase of fee simple title, conservation easements, lease and management agreements, registry/awareness programs, and cost-sharing programs. With the large number and types of incentive programs, most with different enabling legislation, intended audiences, rules, and goals, it is not surprising that the programs that were intended to benefit the environment sometimes overlap, confuse, compete, and actually counter each other.

Counterproduction Incentives

With the plethora of incentive programs administered by a variety of agencies, each with a slightly different mission, at times these incentives are diametrically opposed to each other, as in tree planting versus prairie maintenance or animal damage control. The narrow focus or "quick fix" approach of the following incentive programs has led to numerous problems.

1. Tree Planting/Agricultural Planting on Open Sites. Foresters, wildlife biologists, and conservation specialists have historically focused on establishing quick "cover." Tree planting recommendations frequently rely on formulas for spacing and density that establish "full stocking" and straight, clean tree trunks. Such an approach has "fully stocked" as its goal. If tree density falls below 400–500 trees/acre, the planting is not considered successful.

Wildlife and soil conservationists historically have recommended cool season grasses, exotics, and even aggressive exotics because they can be quickly established. There are known techniques to establish them including formulas for planting rates and utilization of fertilizers and lime. Thus, we have treated natural resource management as an agricultural problem to be fixed rather than a complex community to be established, maintained, or restored.

Landowners are the other half of the equation. Because many landowners want instant results and low maintenance, we have more red pine plantations and alfalfa/clover fields than ever before.

Another problem is the paucity of sources of seeds and plants of native species. This results in the high cost of seed/stock when native materials are available. Ecologists encourage landowners to use native species. However, because of the cost, lack of ready availability of plant material, and low demand, it is hard to get nurseries interested in growing natives.

2. Fire Suppression. Public forest management agencies have done such a thorough job of fire prevention and promotion of Smokey the Bear, that every school child knows fire is bad. Unfortunately, we have concentrated on both human and natural-caused fires with little regard to where they occur or what threat they may present. Attempts at instituting "let burn" policies and prescribed burns have generally met with a lack of acceptance by the general public. The infrequent occasions when these fires have escaped have received much negative public attention. The result is that many fire-dependent communities—communities that have historically relied on maintenance of their successional stage through fire—are becoming increasingly rare.

Lightening-caused fires are infrequent in Wisconsin, and most likely, the same was true in the recent past. Because we know of the presence of nomadic hunting tribes throughout the state during most of the postglacial period, we may assume that man-made fires were an important, if not the sole, cause of forest, prairie, and savanna fires (Curtis1959). By eliminating man-caused fires, much of the former prairie and savanna lands are succeeding to brush or forested landscapes.

Some individuals maintain that fire-like conditions can be accomplished without fire. They cite herbicide use, grazing, and mechanical disturbances as safer alternatives. However, no herbicide, animal, or machine can fully mimic the structural and chemical changes a fire produces in the upper soil layer and seed bank.

3. "Perverse" Incentives. One problem that occurs when assistance programs are developed by different government agencies with narrow focuses and constituencies is that the government ends up actually paying landowners to destroy or damage valuable resources. For years environmentalists have pointed out that many government policies encourage or subsidize activities that lead to the loss of species and habitat.

For example, a study by the Environmental Working Group found that U.S. Department of Agriculture (USDA) payments to farmers totaled 108.9 billion dollars in ten years between 1985 and 1994. Despite this, agriculture remains the single largest contributor to water pollution and wetland conversions (Opperman 1997).

For ten thousand or more years, many North American terrestrial ecosystems were periodically burned by indigenous peoples. European settlers often continued this practice, but such fires were halted shortly after the turn of the century, mainly through the efforts of the U.S. Forest Service (USFS). In

1908, Congress passed a law that effectively gave the USFS a blank check for putting out fires. When a fire did take place, the agency could spend whatever it took to suppress the fire with confidence that Congress would reimburse the USFS at the end of the year. It could be argued this law created a perverse incentive that ended up doing far more damage to American forests than clearcutting. No matter how remote the forest, no matter how worthless the timber, fires were quickly suppressed. This radically altered the vegetative composition of the forests (Opperman 1997).

The USDA's Animal and Plant Health Inspection Service (APHIS) animal damage control program conducts active and often lethal campaigns against livestock predators such as coyotes and other animals that may damage agricultural interests. The APHIS program for controlling prairie dogs has resulted in damage to other species as well. There are an estimated 163 vertebrate species dependent on or closely associated with prairie dogs, either as a food source or for the habitat modifications that prairie dog towns provide. These include several endangered species (Opperman 1997).

4. Taxpayer Double Burden. This category includes subsidies that promote habitat conversion or degradation as a "double burden" because taxpayers must pay to subsidize a particular industry or activity and then pay again to recover species and protect them from the subsidized activities. Subsidized programs are those in which income is directly or indirectly transferred from taxpayers, in general, to specific beneficiaries or those in which the beneficiaries of a specific policy do not pay full costs for a project, access to resources, or for a service. We feel that many listed species on federal lands are threatened by subsidized activities.

For example, a series of dams built by the Bureau of Reclamation along the Missouri River inundated 390,000 acres of wetlands and oxbow lakes. These wetlands were homes for several listed species. At the same time 1.2 million acres of wetlands in the Everglades were opened for agriculture or development through the drainage and flood control provided by the Central and South Florida Project. Eighty percent of this project was financed by the Federal government. Both of these subsidized projects destroyed wetlands, homes for many listed species (Clairs et al. 1977). While these wetlands are being destroyed, the U.S. Fish and Wildlife Service spends taxpayer dollars to recover populations of rare species dependant on wetland habitats.

An indirectly subsidized activity that poses degradation threats is recreation. Users of recreation facilities on public lands rarely pay the market value for their activities. These types of activities, including off-road vehicle use, skiing, boating, hiking, or climbing, all have been shown to affect native species. Opperman (1997) states he discovered that 112 listed species found on federal land were affected by recreation, and for 22 species, this was the only or most significant threat.

Current Incentives

Current incentives to initiate conservation practices on private lands fall into two categories. The first depends on the good will of the landowner as it includes voluntary and non-monetary incentives. These include information, encouragement, recognition, and sometimes management assistance. The second category, many examples of which are described later, includes government programs in which management costs are shared between the government and the private landowner.

Voluntary Programs

In 1991 the Wisconsin Department of Natural Resources' Bureau of Endangered Resources initiated its Landowner Contact Project. Begun with a focus on the voluntary protection of two federally listed species, the dwarf lake iris (Iris lacustris) and the dune thistle (Cirsium pitcheri), it has since expended considerably. It now reaches out to assist private landowners on whose properties occur a variety of state and federally listed rare species. It also includes habitat protection for goat prairies and sand prairies.

The Landowner Contact project is simple in conception, but often involves considerable expenditure of time and effort to achieve its goals. Basically, eight steps are followed to achieve protection of rare natural resources on private lands:

1. Determining species and habitats of concern;
2. Doing research using personal contacts and the Natural Heritage Inventory on sites where the resource has been observed;
3. Determining current land ownership at the site;
4. Contacting the landowner via letter, phone call and/or face to face visits offering information and management assistance concerning the rare resource;
5. Visiting the site with the landowner's permission (and often in the company of the landowner) to verify the presence and status of the resource;
6. Negotiating a voluntary protection agreement between the landowner and the Bureau of Endangered Resources;
7. Recognizing the landowner with a certificate and matted illustration;
8. Continuing regular contact with the landowner with offers of further information and help.

So far, the Bureau of Endangered Resource's Landowner Contact project has not focused on savanna protection, though this is being considered.

The Blue Mounds Project uses much the same approach; its goal is to protect native species and their habitats, focusing on private lands in western Dane and eastern Iowa Counties. This eastern edge of the Driftless Area includes prairie, savanna, wetland, and woodland sites occurring amid farms, residences, and commercial woodlots. A key element of the program is the offer of a free four-hour hike over the land during which the landowner learns what plant communities and species currently may be found on the property. Following this may be further contacts during which management and native habitat restoration may be discussed and planned. Savanna remnants do occur in this area, and the possibility of savanna protection and restoration is always a consideration.

During the past few years, The Nature Conservancy (TNC) has focused its attention on a small number of biologically significant large-scale natural areas in the United States. These "Last Great Places" are defined as "the most important areas for biodiversity remaining in the western hemisphere." One of these projects, the Baraboo Hills, occurs in Wisconsin. Though largely forested, the bluffs also contain some prairie and savanna remnants. The Baraboo Bluffs themselves are far too extensive and expensive to be purchased by TNC. Certain "biological gems" are being acquired, but the majority of the bluffs will remain in private ownership; conservation activities on these private lands are being encouraged in several ways. Private landowners are being included in conservation efforts through educational and informational meetings. To augment these meetings, a publication entitled *Baraboo Bluffs Forest Owners' Handbook* (The Nature Conservancy 1995) has been widely distributed. TNC employees working in the Baraboo Bluffs make special note of savanna sites as well as other biologically significant plant and animal communities.

Yet another voluntary conservation option is discussed in *Technology Review* (Anonymous 1996), in which the author discusses outright payments made to private landowners who engage in specific activities. These payments are funded by the conservation organization, Defenders of Wildlife. Resources for such payments are clearly limited, especially in the case of private organizations. Nevertheless, with especially rare resources or resources threatened by unexpected, sudden developments, this is sometimes a suitable solution. An example of this program is the use of Defenders of Wildlife funding to pay for timber wolf damage to livestock as part of the timber wolf reintroduction in Yellowstone National Park.

In all these cases, benefits are multiplied if cooperating landowners have adjacent properties or the properties are clustered in ways that allow for more natural movement of plants and animals across political and ownership boundaries. Exchange of genetic material, adjustment to changing conditions, insect pollination of plants, and recovery from localized disturbances are all enhanced if large numbers of properties located near to each other are the sites of coordinated conservation activities.

Cost-Share Programs and Their Effects on Savannas

The variety of financial assistance programs that have been developed over the years usually focus on agriculture or forestry/forest production. None of the various programs have focused specifically on savannas, and in some instances, such programs have negatively impacted savannas (Haines 1995). A brief run-down of the traditional programs follows:

- Agricultural Conservation Program (ACP): This is sometimes called the "granddaddy" of USDA programs. Since the program started in 1936, it has been instrumental in the planting of more than seven million acres of trees (Moulton 1994). Although this program is no longer available, active contracts still exist. The ACP was developed to provide financial and technical assistance to help institute agricultural conservation and solve environmental problems.

- Forestry Incentive Program (FIP): Established in 1974, the primary objective of the FIP is to increase the nation's timber supply. It focuses specifically on tree planting, tree improvement, and preparation for natural regeneration. By 1994, the FIP had provided cost-share assistance to more than 126,000 private landowners. The emphasis is on "productive" forest land.

- Managed Forest Law (MFL): This is a tax incentive to encourage the management of private forest lands for the production of future forest crops for commercial use. Up to 20% of the land enrolled in the MFL program may be "non-productive," while 80% must be capable of producing a minimum of 20 cubic feet of merchantable timber per acre per year (Tlusty and Roberts 1991).

- Conservation Reserve Program (CRP): This program takes highly erodible and marginal cropland out of production. It provides up to 50% cost-sharing for approved practices during a 10-year (15 years for hardwood trees) contract payment period. Approximately 36 million acres were "retired" from crop production between 1985 and 1995 at an average rental cost of $50 per acre. While it can be expensive, the CRP has demonstrated benefits to endangered species by taking marginal and patchily distributed agricultural land out of production (Jelinski and Kulakow 1996). Farmers are paid to retire highly erodible lands for ten years and obliged to dedicate this acreage to wildlife and watershed protection. The CRP reaped numerous benefits for the flora and fauna of the Great Plains states, including the recovery of many bird populations (Opperman 1997).

- Stewardship Incentive Program (SIP): Established in 1990, SIP was intended to pay part of the cost of a variety of multiple-resource activities. SIP has cost-shared food plots for deer in areas where tree regeneration is already hard to achieve due to deer browsing. SIP can also cost-share tree shelters to protect seedlings. Thus, SIP is another example of a program that sometimes pays for diametrically opposed incentives.
- Environmental Quality Incentives Program (EQIP): This new program targets livestock producers but encourages total resource management.
- Wildlife Habitat Improvement Program (WHIP): This is another new program that has not yet been tested, but does offer some hope for the future. In Wisconsin, threatened and endangered species have been highlighted as a priority concern. Since the WHIP program is so new, there is a chance of adding communities into this category.

Future Management and Incentives

Simply getting landowners to commit themselves to savanna restoration and management is only the first step in a longer process. Indeed, landowners will be hesitant to commit themselves to savanna protection, regardless of the incentives, until they are fully informed about what specific management actions will take place on their acreage. Furthermore, it is necessary to know what management techniques are successful and whether restoration of a degraded site is possible. Currently, the state of our knowledge in this realm is still quite limited.

Some minimal amount of research on management options would provide much needed information for those committed to protecting savannas, whether private landowners or public land managers. Some ecological questions that need good answers include:

1. What are the best methods for clearing overgrown savannas? Do these vary according to invading species, slope, aspect, time of year, and surrounding land use?
2. Can mowing be an acceptable method for maintaining savanna habitats? When should this be done, how frequently, and at what height?
3. How frequently should a savanna in Wisconsin be burned? How does this vary with differences in overstory species, understory species composition, and site history? Can we assume that, like prairie burning, the burning of savannas should sometimes be in spring, sometimes in fall, and that it should be done in a patchy, random fashion to allow for the survival of pollinating insects?
4. Can grazing be a successful method for maintaining savannas? Which species of grazing animals are best for the plant community, in what numbers, and how often may they be released at a savanna site?

Once these questions are answered, planning management activities and creating new effective incentives will become easier.

Conclusions

Professional land managers do not have all the answers, but we are moving in the right direction. We must commit ourselves to doing careful and meaningful research. We must be ready to learn from amateurs and from landowners themselves. Following the model of Integrated Pest Management, perhaps we can devise an Integrated Land Management model that would take into account the needs of savanna plant and animal species along with the needs of landowners for financial and other returns from their property.

We need to continue to debate among ourselves concerning the appropriate balance of forests, savannas, prairies, agricultural land, and land devoted to residences, businesses and industry. Currently we are only hurting ourselves by fighting for limited resources that benefit special interests rather than concerning ourselves with the overall resource base and its needs.

Resource professionals must commit themselves to serving private landowners who own savanna habitat. This includes educating landowners about what a savanna is, why it is important, and how to maintain this rare habitat.

Creative use of existing incentive programs can go far toward savanna protection on private lands. But resource professionals and conservation organizations must also lobby for the enactment by governmental units of newer and more ecologically sound incentive programs. Ideally, a legislative proposal would provide incentives to protect whole native plant and animal communities: savannas, barrens, prairies, wetlands, and forests. The more flexible these programs are, the more likely they are to accommodate protection of diverse habitats and the flora and fauna existing there.

Government programs are only part of the solution to the challenge of protecting savannas. Incentives can be regarded as a stimulus to initiate proper management on private lands. Education and adaptive resource conservation can keep management going. But ultimately, the long-term survival of savanna plant and animal communities will depend on the goodwill, commitment, and intelligence of private landowners working cooperatively with resource professionals.

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Thomas A. Eddy and Cindy M. Moore

Effects of Sericea Lespedeza (Lespedeza cuneata *(Dumont) G. Don) Invasion on Oak Savannas in Kansas*

Abstract *Invasion of sericea lespedeza* (Lespedeza cuneata *(Dumont) G. Don) into oak savannas in southeast Kansas altered the composition, structure, and density of the native prairie component of the ecosystem and reduced the number of invertebrate species. Vegetation characteristics in clearings infested with sericea lespedeza were compared with uninfested clearings during the summer of 1996. Eighty 1 m^2 quadrats were randomly placed in each of the 2 site conditions. The number of grass species decreased from 12 in uninfested sites to 4 in infested sites. Native forb species declined from 27 in the uninfested sites to 8 in the infested sites. Canopy coverage of sericea lespedeza in the infested sites was 84%. Mean stem counts of sericea lespedeza were 352/m^2. Weight of clipped native grasses and forbs from uninfested sites was 92% greater than in infested sites. Numbers of invertebrate species declined from 65 at the uninfested sites to 24 at the infested sites. Implications of vegetation changes on wildlife populations and forage for livestock are considered.*

Invasions of plants and animals have been occurring in North America since the continents separated. Many of the introductions of exotic species have resulted in the displacement of native species and the disruptions of important ecological processes. Exotic species are one of the greatest threats to native species and to human-disturbed ecosystems in the world (Elton 1958, Fox and Fox 1986, Reid and Miller 1989, Whelan and Dilger 1992, Noss and Cooperrider 1994, Hunter 1996). Rangelands have proven to be especially vulnerable to exotic plant invasions. Exotic grasses and forbs from Europe, Asia, the Mediterranean, and the rest of the world have been a major problem in the native ecological systems of North America

(Baker 1986). Sericea lespedeza (*Lespedeza cuneata* (Dumont) G. Don) is in the initial stages of invasion of Kansas oak savannas and adjacent grasslands and threatens to destroy the quality and productivity of the tallgrass prairie.

Sericea lespedeza, a drought-hardy perennial legume, was first introduced from Japan in 1896 (Magness et al. 1971) and later in the 1930s through the 1950s as a forage crop for healing erosional scars on farmlands, establishing cover on mine spoil banks, and as cover for wildlife (Scott 1995). The long-lived plants are leafy and erect, standing from 0.5 to 1.5 m high. The leaflets are long, narrow and blunt at the terminals. The plant dies back in winter, and new growth arises from crown buds in the spring. It shows low tolerance for shade but thrives in full sun. The current range of this invasive plant has been estimated to be from the Atlantic coast west to Texas and Kansas and north to the Ohio River (Magness et al. 1971).

The invasive impact of this species on Kansas agriculture was recognized in 1988 when the state legislature declared sericea lespedeza a county option noxious weed (Scott 1995). The county-declared option allows the county to penalize land owners who do not control infestations. By 1995, 52 out of 105 counties in Kansas had declared sericea lespedeza a noxious weed. The Pest Risk Analysis (Scott 1995) states that the reported infestation has nearly doubled every 2 years since 1990 in Kansas. This increased reporting is generally agreed to have been generated by the public's increased awareness. Woodson County, where our study area is located, had a reported 21,130 ha infested with sericea lespedeza in 1995. The 1995 Pest Risk Analysis indicates that annual economic impact in the region would approach $29 million assuming a 75% reduction in quality forage available to livestock (Scott 1995).

Many plant species invade apparently because livestock grazing has changed the environment rather than because they are inherently better competitors (Elton 1958, Noss and Cooperrider 1994). Sericea lespedeza is unique in its ability to establish itself in grazed and ungrazed tallgrass prairie and oak savannas.

Our study assessed the changes in the tallgrass vegetation in Kansas oak savannas and associated macroinvertebrates resulting from sericea lespedeza invasion. Vegetative composition, canopy coverage, density of lespedeza stems, yield, and macroinvertebrate numbers in oak savannas clearings infested with sericea lespedeza were compared with uninfested clearings during the summer of 1996. The plant's ability to invade and outcompete the native flora has resulted in a negative effect on the oak savanna ecosystem where it has become established. Reductions in overall species diversity, wildlife habitat and diversity, and quality and quantity of forage were observed in our study.

Study Area

Our study site is located in the Chautaqua Hills, an undulating uplift extending from the Kansas-Oklahoma border to Woodson County, Kansas (Bare 1979). The hills are dissected by deep ravines with occasional sandstone bluffs along the major drainages. Soils are sandy clays and loams with sandstone outcrops of Pennsylvanian age. The tallgrass prairie vegetation is interspersed with groves of blackjack oak (*Quercus velutina* Lam.) and post oak (*Quercus stellata* Wang). Local landowners reported that the infestation of sericea lespedeza on the 295.4 ha study area has occurred within the last 5 to 7 years.

Methods

Grid lines, 150 m in length and set at 25 m intervals on north-south compass lines, were located in the oak savanna clearings in the 295.4 ha study area. Eighty quadrats, each measuring 1 m^2, were randomly placed along the grid lines in clearings infested with sericea lespedeza and 80 quadrats were similarly distributed in clearings that were not infested.

Using McGregor et al. (1986), grass and forb species were identified and recorded in each of the quadrats in the sericea lespedeza infested sites and the uninfested sites during mid-month in June–August 1996. Canopy coverage of forbs and grasses in the infested and uninfested sites were determined by the Daubenmire (1959) method. The density of sericea lespedeza stems in the infested sites was determined by counts of stems in the quadrats. Seedlings less than 6 cm in length were not included.

Yields in g/m^2 of vegetation from the uninfested and infested areas were compared. Vegetation from ten randomly selected 1 m^2 plots from each of the sericea lespedeza infested and uninfested plots was clipped at a height of 6 cm, oven dried for 72 h, and weighed. Samples from the infested plots were pooled and compared to the pooled samples from the uninfested plots.

Macroinvertebrates in the quadrats infested and those not infested were sampled in mid July with 4 sweeps of a 14 inch-diameter insect net through the vegetation of each quadrat in the middle of the day, followed by examination of the quadrats for additional species. Each specimen was identified to family and recorded.

Results

Eight forb species and four species of grasses were identified in the clearings that were infested with sericea lespedeza (Table 1). In the clearings where sericea lespedeza was not present, 24 forb species and 12 species of grasses were identified. Not only did the infested sites have fewer species, but those species identified were of lower forage quality and were generally considered to be weedy.

Canopy coverage measures were found to be in stark contrast in the infested and uninfested areas. While the greatest percent coverage in the uninfested sites was due to grass and forbs other than sericea lespedeza, most of the percent coverage in the infested sites was attributed to sericea lespedeza (Table 2).

Yields of native forbs and grasses differed between the sericea lespedeza infested areas and the uninfested areas. The pooled clippings of native forbs and grasses from the uninfested clearings had a yield of 388.8 g/m^2. The pooled clippings from the infested clearings had a yield of 31.2 g/m^2. The difference between the areas represents a major loss of desirable forage in the infested areas.

Counts of sericea lespedeza stems from infested clearings ranged from densities of $141/m^2$ to $466/m^2$ ($\bar{x} = 352/m^2$). Recruitment was considered high. Beneath each bunch of stems, many new sericea lespedeza plants were emerging.

Macroinvertebrate species identified in the infested and uninfested areas also differed. While 65 total species, representing 30 families, were identified from the uninfested areas, only 24 total species, representing 14 families, were identified in the infested areas (Table 3).

Table 1. Native forbs and grasses identified in clearings infested with sericea lespedeza and clearing not infested with sericea lespedeza June – August 1996.

Species in Uninfested Clearings	*Species in Infested Clearings*
Forbs	
Amorpha canescens Pursh	*Artemisia ludoviciana* Nutt.
Baptisia australis (L.) R. Br.	*Ambrosia psilostachya* DC.
Dalea candida Michx. *ex* Willd.	*Ambrosia trifida* L.
Psoralea tenuiflora Pursh	*Aster ericoides* L.
Schrankia nuttallii (DC.) Standl.	*Solidago missouriensis* Nutt.
Antennaria neglecta Greene	*Vernonia baldwinii* Torr.
Artemisia ludoviciana Nutt.	*Asclepias viridiflora* Raf.
Cacalia atriplicifolia L.	*Linum sulcatum* Ridd.
Circium undulatum (Nutt.) Spreng.	
Echinacea angustifolia D.C.	
Erigeron strigosus Muhl. *ex* Willd.	
Liatris punctata Hook.	
Ratibida columnifera (Nutt.)Woot. & Standl.	
Rudbeckia hirta L.	
Solidago ridiga L.	
Vernonia baldwinii Torr.	
Asclepias viridis Walt.	
Asclepias viridiflora Raf.	
Asclepias syriaca L.	
Allium canadense L.	
Ceanothus americanus L.	
Euphorbia corollata L.	
Ruellia strepens L.	
Salvia azurea Lam.	
Tradescantia bracteata Small.	
Triodanis perfoliata (L.) Nieuw.	
Linum sulcatum Ridd.	
Grasses	
Andropogon gerardii Vitman	*Andropogon gerardii* Vitman
Bouteloua curtipendula (Michx.) Torr.	*Dichanthelium oligosanthes* (Schult.) Gould
Bouteloua gracilis (HBK) Lag. *ex* Griffiths	*Schizachyrium scoparium* Michx.
Bouteloua hirsuta Lag.	*Panicum virgatum* L.
Buchloe dactyloides (Nutt.) Engelm.	
Elymus canadensis L.	
Koeleria pyramidata (Lam.) Beauv.	
Panicum virgatum L.	
Poa pratensis L.	
Schizachyrium scoparium Michx.	
Sorghastrum nutans (L.) Nash	
Sporobolus asper (Michx.) Kunth	

Table 2. Canopy coverage (%) in clearings infested vs not infested with sericea lespedeza, June – August 1996.

	Infested	*Not Infested*
Sericea lespedeza	84	0
Native forbs	10	28
Native grasses	5	79

Discussion

Exotic and native species compete for a variety of resources such as space, water, nutrients, and light. Kalburji and Mosjidis (1993*a*, 1993*b*) have demonstrated that growth inhibitors in sericea lespedeza residues reduce root development in warm- and cool-season grasses. But, there is no data that demonstrate that forbs are also inhibited in this way. An invading species, when it outcompetes the native species present, can alter a variety of ecosystem properties (Hunter 1996). Such is the case with sericea lespedeza in the oak savannas in Kansas. This plant has rapidly invaded the open prairie and oak savanna clearings and altered the composition, density, and vigor of the vegetation. Once established, sericea lespedeza may inhibit or prevent the restoration of native biodiversity. The cost and difficulty of control, as well as other biological issues, combined with limited public understanding, are bound to make control of this invading exotic plant difficult (Westman 1990).

Table 3. Families and numbers of species of macroinvertebrates in uninfested clearings vs. infested clearings.

	# Species of Macroinvertebrates	
Families	*Uninfested*	*Infested*
Acrididae	5	4
Formicidae	2	2
Cicadellidae	4	
Miridae	6	1
Culicidae	1	
Lygaeidae	2	1
Pentatomidae	2	1
Dolichopodidae	1	
Coccinellidae	3	
Curculionidae	2	
Gryllidae	1	
Noctuidae	2	1
Reduviidae	3	
Salticidae	1	
Tetrigidae	1	
Tettigoniidae	1	2
Nymphalidae	5	1
Chrysididae	1	
Chrysomelidae		3
Muscidae		2
Cydnidae	1	
Mycetophillidae	1	
Scarabaeidae	2	1
Tipulidae	1	
Bombyliidae	3	
Cercopidae	5	3
Dysderidae	1	
Geometridae	1	
Lampyridae	1	
Sphecidae	2	1
Tephritidae	1	
Apidae	3	1
Totals	**65**	**24**

The sericea lespedeza infestation has also reduced the quality and quantity of forage available to livestock. Surviving forbs in most infestation areas are of low nutritive value and are associated with tallgrass prairie in fair to poor condition. Because the plant contains 5–12% tannin, sericea lespedeza has proven to be unpalatable to livestock in most cases. When sericea lespedeza is consumed by cattle, it is only at the earliest time in the season, when the plants are succulent and at their lowest tannin content (Scott 1995).

The loss of native plant diversity that occurs when an area becomes infested by sericea lespedeza also results in a loss of invertebrate diversity. Vertebrate diversity is probably affected as well, and further investigation is indicated. Grasses and forbs that are displaced by sericea lespedeza are superior in terms of shelter and food resources, which are of vital importance for wildlife. The native vegetation is home to a rich diversity of invertebrates that may serve as important food sources for prairie wildlife. The high stem density of sericea lespedeza infested areas presents an almost impenetrable barrier to wildlife movement and essentially eliminates the rich diversity of food and cover provided by the native system.

The continued expansion of this exotic species into the tallgrass prairie will profoundly alter the biota and severely damage the region as a source of high quality forage for livestock and as a habitat for wildlife. Although chemical treatments are available, other methods of control must be identified in order to preserve the prairie element of the oak savanna ecosystem.

Acknowledgments

We would like to extend our thanks to the Kansas Department of Wildlife and Park and Scott Barlow for valuable assistance in the field.

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James O. Evrard

Small Mammals of Northwest Wisconsin Pine Barrens

Abstract *Little is known of the small mammals inhabiting the endangered pine barrens ecosystem in northwest Wisconsin. Early small mammal sampling, which began in 1950, was sporadic and at times haphazard. Systematic sampling of small mammal populations using snap traps throughout the pine barrens was initiated by the Wisconsin Department of Natural Resources in 1993. In 1995, the Great Lakes Indian Fish and Wildlife Commission and the U.S. Forest Service joined the Department of Natural Resources in an expanded coordinated effort to sample four management properties, the Crex Meadows, Namekagon Barrens, Douglas County, and Moquah Barrens Wildlife Areas, located on a southwest/northeast gradient in the northwest pine barrens. Nineteen small mammal species and subspecies were captured using snap traps and pitfall and funnel traps associated with drift fences. Relative small mammal densities, expressed as a catch/effort (C/E) index, varied spatially and temporally and by habitat type and capture technique. Responses to variables were masked by problems associated with field identification of* Peromyscus *spp., intrinsic small mammal population fluctuations, and competition/exclusion among small mammal species.*

In the early 1990s, the focus of research conducted by the Wisconsin Department of Natural Resources (WDNR) began shifting from single species to communities to ecosystems (Gomoll et al. 1995). This focus included increased interest in rare and threatened ecosystems such as the pine barrens. Forest succession due to effective wildfire control and primarily red pine *(Pinus resinosa)* plantations have reduced early successional stages of the pine barrens to only about 1% of the original area in Wisconsin (Riegler 1995). Increased interest in this endangered ecosystem was manifested in the sponsorship of a pine barrens workshop by the WDNR in 1993

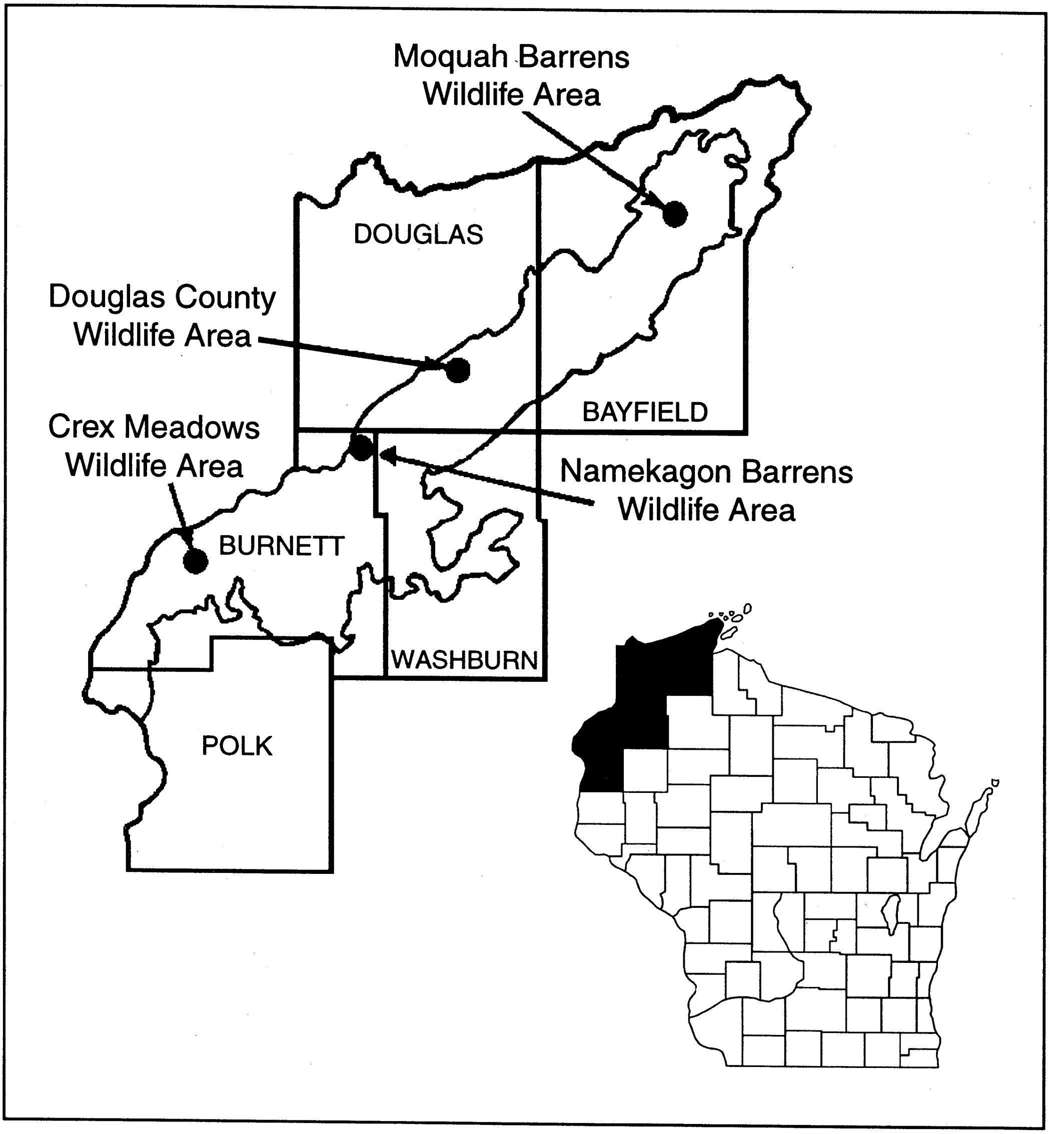

Figure 1. Northwest Wisconsin Pine Barrens showing four properties studied.

(Borgerding et al. 1995). Developing a management plan for the northwest pine barrens was a major workshop recommendation.

Not much is known of the small mammals inhabiting the pine barrens in northwest Wisconsin (Figure 1). During 1950–57, the Wisconsin Conservation Department conducted small mammal surveys throughout the state using snap traps (Bole 1939, Dice 1941, Stickel 1946, Hayne 1949). Two trap lines were in the Crex Meadows Wildlife Area (CMWA) in western Burnett County (N. Stone, Wisconsin Conservation Department, unpublished data). A decade later, Beck and Vogl (1972) reported results from snap-trapping small mammals in the CMWA in August 1967. In 1983, a student intern from the University of Wisconsin-

Stevens Point conducted a survey of small mammals in the CMWA (Brockman 1983). She used snap traps and pitfall traps designed to capture reptiles and amphibians.

In 1978, another student from the University of Wisconsin-Stevens Point used snap traps and pitfall traps to capture small mammals in a variety of habitats on the Namekagon Barrens Wildlife Area (NBWA) in extreme northeast Burnett County (D. Jansen, University of Wisconsin-Stevens Point, unpublished data). In 1986, additional small mammal trapping in the NBWA was conducted by the WDNR using snap and live traps (G. Dunsmoore and J. Riemer, Wisconsin Department of Natural Resources, unpublished data). The methodology and results of the past small mammal trapping was poorly documented and varied considerably.

Part of a WDNR research project I initiated in 1993 involved comparing the effects of clear-cutting and prescribed burning upon pine barrens flora and fauna. In this study, I focused on documenting small mammal populations inhabiting pine barrens, their habitat preferences, and their responses to two major forces that shape the present pine barrens ecosystem: logging and fire.

Study Area

The northwest Wisconsin pine barrens have been described in detail by Curtis (1959), Vogl (1970), Mossman et al. (1991), and Niemuth (1995). Murphy (1931) described the area as "... a long narrow strip of sand where coniferous forest and open expanses of sweet fern and grassy barrens dwarf into insignificance the few evidences of man's present occupancy and use of the land.... The grassy and sweet fern barrens.... are desolate open tracts where only an occasional charred stump, a cluster of jack pines, or a scrub oak bush, breaks the monotonous sweep of rolling, thinly clad ground surface .... Almost every year forest fires sweep sections of the Barrens...."

Today, the effects of man on this landscape are more evident. Much of the pine barrens are managed for wood products in private, county, state, federal, and industrial forests. What remains in early successional stages of the pine barrens is found primarily in four areas managed with controlled fire for sharp-tailed grouse *(Tympanuchus phasianellus)* (Figure 1). The CMWA is owned and managed by the WDNR. The NBWA is managed by the WDNR on lands leased from Burnett County as is the Douglas County Wildlife Area (DCWA), which is mostly leased from Douglas County. The Moquah Barrens Wildlife Area (MBWA) is owned and managed by the U.S. Forest Service. Infrequent wild fires and large clear-cuts resulting from salvage logging due to jack pine budworm *(Choristoneura pinus)* outbreaks temporarily create additional early successional habitat on publicly and privately owned forest lands.

Methods

In a cooperation with the University of Wyoming (Niemuth 1995), the WDNR snap-trapped small mammals in seven study plots in June 1993 and in five study plots in July 1994. These plots were located in burned and clearcut areas in county and industrial forests in Burnett and Douglas counties. Each 0.2-ha plot or grid consisted of 50 snap traps (40 mouse- and 10 rat-size) in 5 rows of 10 traps each. Both the rows and the traps were located 7.6 m apart. The traps were baited with peanut butter and checked daily for 5 days, resulting in a total of 1,750 trap nights in 1993 and 1,250 trap nights in 1994. Results were expressed as an index to the population, the adjusted catch/effort (AC/E) index, (Nelson and Clark 1973), which is corrected for sprung traps. Mammals were identified to species in the field. Due to difficulties in field identification of *Peromyscus* spp. (Hooper 1968, Stromberg 1979, McGowan 1980, Long and Long 1993), deer mice and white-footed mice were generally recorded as one species. These were the same trapping methods I used in earlier research conducted managed grasslands in St. Croix and Polk counties in west-central Wisconsin (Evrard 1993).

Beginning in 1995, I initiated more intensive small mammal trapping in the study area, using the same timing and methodology as in 1993–94. As part of research to determine the impact of prescribed burning and clear-cutting in the NBWA, nine grids were trapped in three areas of jack pine *(Pinus banksiana)*/Hill's oak *(Quercus ellipsoidalis)* forest. Three grids were trapped in an intermediate-aged, uncut forest, and another three grids were trapped in a forest that was clearcut in 1990–91 and 1994–95. The final three grids were trapped in a clearcut forest that was burned in late April 1996.

In 1995–97, I also trapped three grids (forest, old burn, and new burn) in the CMWA. The three areas sampled included a mature Hill's oak forest having a thin shrub understory; an area of brush prairie (Strong 1880) that was burned in the spring one year prior to trapping; and an area of brush prairie that was burned 6–8 weeks prior to trapping. The brush prairie was located within a designated state natural area.

In a 1995 cooperative effort, three grids were trapped in the DCWA (G. Kessler, WDNR, unpublished data) and four grids in the MBWA (P. David, Great Lakes Indian Fish and Wildlife Commission, unpublished data). In 1996, the cooperative effort was repeated with the exception of the DCWA. Both properties were cooperatively trapped in 1997.

The three areas sampled in the DCWA included an open grassland burned in 1993 and dominated by sweetfern *(Comptonia peregrina);* an area containing only hoary puccoon *(Lithospermum canescens)* and a few young aspen (*Populus* spp.) and willow (*Salix* spp.) that survived a fire in the fall of 1996; and an area of tall grass containing shrubby willow and young aspen burned in 1990.

The four areas sampled in the MBWA included an area of young oak trees (oak forest) with little understory had been lightly burned in 1993; an area clearcut (old clearcut) several years prior to 1995 and had thick, brushy ground cover; a third area (old burn) was burned in 1991 and had a well-developed, brushy understory including many berry-bearing species; and the fourth area (new burn) was burned in the spring of 1995 and had a thin ground cover.

Selected captured small mammals were frozen for species identification confirmation by Charles A. Long, Curator of the University of Wisconsin-Stevens Point Zoological Museum and Richard Bautz, WDNR Research, Monona.

In addition to snap-trapping, drift fences (Vogt and Hine 1982) were also operated in the CMWA, NBWA, DCWA, and MBWA in 1996–97 to sample reptiles and amphibians. Small mammals were captured in pitfall and funnel traps (Imler 1945) associated with the drift fences. Drift fences, 15.2 m in length, were constructed of 46 cm high aluminum roof flashing in either a "T" of "I" design adjacent to a wetland. Each drift fence contained from 8–10 pitfall traps and 2–5 wire-mesh funnel traps. The pitfall and funnel traps were opened for four 6-day periods from late April to early June following significant precipitation events. The small mammals drowned in water maintained in the pitfall traps to prevent desiccation of amphibians. Trapping results were expressed as a C/E index since there was no adjustment for "snapped" or unavailable traps.

Thus, small mammals were sampled using two different trapping methods in several habitat types from four core management properties located along a southwest/ northeast gradient in the northwest pine barrens (Figurel).

I compared the 1993–97 pine barrens snap-trapping results with 1989–90 snap-trapping results in seven plots located in managed upland grassland in St. Croix and Polk counties (Evrard 1993). Trapping in terms of timing and effort were equal in both studies, although there were differences in habitat sampled.

I used paired *t*-tests and 2-way and 3-way ANOVA (SAS 1989) to compare AC/E and C/E differences for small mammal species relative abundance between trapping methods, habitat types, and management properties.

Results and Discussion

Species Distribution

Nineteen small mammal species were captured using snap traps and pitfall traps in the CMWA, NBWA, DCWA, and MBWA during the period 1995–97 (Table 1). The masked shrew *(Sorex cinereus),* pigmy shrew *(Microsorex hoyi),* thirteen-lined ground squirrel *(Spermophilus tridecemlineatus),* red-backed vole *(Clethrionomys gapperi),* meadow vole *(Microtus pennsylvanicus),* and the meadow jumping mouse *(Zapus hudsonius)* were trapped in all four properties. In addition, the woodland deer mouse *(Peromyscus maniculatus gracillis)* and the white-footed mouse were trapped on all four properties. The identification of *Peromyscus* spp., including the prairie deer mouse *(Peromyscus maniculatus bairdii)* was verified from

Table 1. Small mammals captured in Wisconsin's northwest pine barrens, 1995–97.

	Crex Meadows	*Namekagon Barrens*	*Douglas County*	*Moquah Barrens*
Masked shrew	X	X	X	X
Arctic shrew				X
Pigmy shrew	X	X	X	X
Shorttail shrew	X	X	X	
Star-nosed mole				X
Longtail weasel		X		
Shorttail weasel	X			
Thirteen-lined ground squirrel	X	X	X	X
Eastern chipmunk		X	X	X
Least chipmunk		X	X	
Red squirrel		X		
Woodland deer mouse	X	X	X	X
Prairie deer mouse		X	X	
White-footed mouse	X	X	X	X
Southern bog lemming			X	
Red-backed vole	X	X	X	X
Meadow vole	X	X	X	X
Meadow jumping mouse	X	X	X	X
Woodland jumping mouse			X	

voucher specimens identified by Charles A. Long.

Some species were captured on only one property. This included the arctic shrew *(Sorex arcticus)* in the NBWA, the southern bog lemming *(Synaptomys cooperi)* and the woodland jumping mouse *(Napaeozapus insignis)* in the DCWA, and the star-nosed mole *(Condylura cristata)* in the MBWA.

Due to the trapping methods used, the red squirrel *(Tamiasciurus hudsonicus)*, shorttail weasel *(Mustela erminea)*, and the longtail weasel *(M. frenata)* were considered accidental captures.

Three additional species, the northern water shrew *(Sorex palustris)*, the Franklin's ground squirrel *(Spermophilus franklinii)*, and the pine vole *(Pitymys pinetorum)*, were recorded in the northwest pine barrens by earlier workers. The northern water shrew was reportedly trapped in the NBWA (D. Jansen, University of Wisconsin-Stevens Point, unpublished data). Brockman (1983) reported capturing the Franklin ground squirrel and pine vole in the CMWA.

Population Indices

Seven species were snap-trapped in the pine barren grids of Burnett and Douglas counties in 1993–94 compared to four species in 1989–90 in the grassland grids in St. Croix and Polk counties (Table 2).

The thirteen-lined ground squirrel and red-backed vole were the most common small mammals trapped in the pine barrens grids while *Microtus* spp. (mostly meadow voles with a few prairie voles, *M. ochrogaster)*, thirteen-lined ground squirrel, and *Peromyscus* spp. were the common species in the more southern grasslands (Table 2). Despite relative densities of small mammals, expressed as AC/E, apparently being 4–6 times higher in the managed grassland grids examined in St. Croix and Polk counties

Table 2. Adjusted Catch/Effort[a] for small mammals captured in snap traps in Burnett and Douglas counties, 1993–94 and St. Croix and Polk counties, 1989–90.

	Burnett/Douglas		*St. Croix/Polk*	
Species	*1993*[b]	*1994*[c]	*1989*[b]	*1990*[b]
Masked shrew	0.00	0.00	0.06	0.06
Shorttail shrew	0.07	0.00	0.00	0.00
Thirteen-lined ground squirrel	0.29	0.66	0.74	1.40
Eastern chipmunk	0.07	0.00	0.00	0.00
Least chipmunk	0.14	0.00	0.00	0.00
Deer and white-footed mice	0.07	0.17	0.80	0.76
Red-backed vole	0.07	0.42	0.00	0.00
Meadow and prairie voles	0.00	0.17	3.21	3.82
Meadow jumping mouse	0.07	0.08	0.00	0.00
Total	0.78	1.50	4.81	6.04
$\bar{x}$	0.09	0.17	0.53	0.67
SD	0.09	0.23	1.06	1.28

[a] Adjusted Catch/Effort = $\dfrac{\text{A (number animals trapped) x 100}}{\text{TU (trapping interval x length of interval x number of traps) – IS (total number of traps snapped)/2}}$
(Nelson and Clark 1973).

[b] 1,750 trap nights (7 grids x 50 traps x 5 nights).

[c] 1,250 trap nights (5 grids x 50 traps x 5 nights).

than in the early successional grids of the pine barrens, the differences were not significant (*F* = 1.528, *P* = 0.25).

Small mammal numbers varied by species between the pine barrens properties trapped during 1995-97 (*F* = 3.201, *P* = 0.005). In 1995, the AC/E for all species from snap-trapping in the DCWA was only half of that for the CMWA, NBWA, and MBWA (Table 3). In 1996, the small mammal index AC/E for the CMWA, NBWA, and MBWA grids declined from the previous year. No trapping was conducted in the DCWA in that year. *Microtus* spp. and *Peromyscus* spp. decreased while thirteen-lined ground squirrels increased. In 1997, the AC/E for all small mammals snap-trapped on the CMWA showed little change from 1996 and increased for the NBWA and MBWA. The 1997 index for the DCWA could be compared only to that from 1995 which was higher.

While intended to capture amphibians and reptiles, the C/E for some small mammal species captured in pitfall traps associated with drift fences was comparable with the AC/E for snap traps. In 1996, the drift fence capture indices showed considerable variation among the four properties (Table 4). From 1996 to 1997, the C/E for all small mammals increased on all four barrens properties. However, some species increased on one property and decreased on another property in the same year. In both years, the C/E index was larger on the NBWA than the other three properties. In 1996, the leading species captured in the NBWA was the red-backed vole and the meadow jumping mouse. In 1997, red-backed voles decreased and jumping mice increased.

Meadow jumping mice were captured in only one year in one pine barrens property using snap traps. In contrast, jumping mice were captured in pitfall traps in all four properties in both years of trapping. Pitfall traps associated with drift fences captured more masked shrews (*t* = 2.332, *P* = 0.06) than snap traps, while snap traps captured significantly (*t* = 2.871, *P* = 0.03) more thirteen-lined ground squirrels than pitfall traps. Differential vulnerability of some small mammal species to different types of traps has been reviewed by McGowan (1980) and reported by Pendleton and Davison (1982).

Since jumping mice prefer wet, grassy habitat (Jackson 1961), the location of drift fences adjacent to wetlands may have been responsible for the large number of jumping mice captured. The shrews may have been attracted to the large numbers of insects trapped in the pitfall traps.

The C/E index derived from drift fence captures probably underestimated changes in relative small mammal population sizes. This is due to the long trapping periods involved (24–56 days) compared to the 5-day trapping period used for capturing small mammals with snap traps. Previous research (Bole 1939, Pelikan and Zejda 1962) has shown that most of the resident small mammal population in the trapped area are captured during the first 3–5 days of trapping.

Habitat Preferences

When snap-trapped small mammals were examined based upon habitat types (burned, clearcut, and forested) across the four barrens properties, differences existed among all small mammal species (*F* = 17.64, *P* = 0.0001), years (*F* = 3.95, *P* = 0.03) and species/habitat interaction (*F* = 3.83, *P* = 0.0003). When only the four most common species, *Peromyscus* spp., thirteen-lined ground squirrel, meadow vole, and red-backed vole, were examined, the same differences of species (*F* = 9.53, *P* = 0.002), years (*F* = 4.57, *P* = 0.03), and species/habitat interaction (*F* = 5.36, *P* = 0.007) existed.

Table 3. Adjusted Catch/Effort[a] for small mammals captured in snap traps in Wisconsin's northwest pine barrens, 1995–97.

	Crex Meadows[b]			*Namekagon Barrens*[c]			*Douglas County*[b]			*Moquah Barrens*[d]		
	1995	*1996*	*1997*	*1995*	*1996*	*1997*	*1995*	*1996*	*1997*	*1995*	*1996*	*1997*
Short-tailed shrew	0.00	0.00	0.00	0.05	0.00	0.00	0.00	—	0.14	0.00	0.00	0.00
Masked shrew	0.00	0.00	0.00	0.00	0.00	0.00	0.28	—	0.00	0.00	0.00	0.11
Arctic shrew	0.00	0.00	0.00	0.00	0.00	0.00	0.00	—	0.00	0.00	0.00	0.11
Thirteen-lined ground squirrel	0.14	0.57	0.00	0.09	0.14	0.33	0.30	—	0.41	0.21	0.44	0.76
Eastern chipmunk	0.00	0.00	0.00	0.05	0.00	0.05	0.15	—	0.00	0.00	0.11	0.00
Least chipmunk	0.00	0.00	0.00	0.62	0.23	0.15	0.00	—	0.00	0.00	0.00	0.00
Red squirrel	0.00	0.00	0.00	0.00	0.05	0.00	0.00	—	0.00	0.00	0.00	0.00
Deer mouse	1.16	0.57	0.14	0.19	0.19	0.79[a]	0.91	—	0.00	1.27	0.22	0.22
White-footed mouse	1.30	0.57	0.00	0.47	0.33	—	—	—	—	—	—	—
Red-backed vole	0.58	0.00	1.70	1.47	0.94	0.98	0.15	—	0.00	0.42	0.00	0.00
Meadow vole	0.00	0.00	0.00	0.19	0.00	0.14	0.00	—	0.00	1.27	0.00	1.95
Meadow jumping mouse	0.00	0.00	0.00	0.00	0.00	0.00	0.00	—	0.00	0.21	0.00	0.00
Total	3.18	1.71	1.84	3.08	1.88	2.44	1.79	—	0.55	3.38	0.77	3.15
$\bar{x}$	0.29	0.16	0.17	0.28	0.17	0.22	0.16	—	0.05	0.31	0.07	0.29
SD	0.74	0.37	0.51	0.46	0.30	0.35	0.27	—	0.13	0.50	0.14	0.60

[a] Adjusted Catch/Effort (Nelson and Clark 1973.

[b] 750 trap nights (3 grids x 50 traps x 5 nights).

[c] 2,250 trap nights (9 grids x 50 traps x 5 nights.

[d] 1,000 trap nights (4 grids x 50 traps x 5 nights).

Table 4. Catch/Effort[a] for small mammals captured in pitfall and funnel traps in Wisconsin's northwest pine barrens, 1996–97.

	Crex Meadows[b]		*Namekagon Barrens*[c]		*Douglas County*[d]		*Moquah Barrens*[e]	
	1996	*1997*	*1996*	*1997*	*1996*	*1997*	*1996*	*1997*
Masked shrew	0.15	0.58	0.87	0.17	0.45	0.91	0.00	0.00
Pigmy shrew	0.05	0.10	0.00	0.75	0.00	0.15	0.51	1.67
Shorttail shrew	0.10	0.10	0.00	0.17	0.00	0.15	0.00	0.00
Star-nosed mole	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Longtail weasel	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
Shorttail weasel	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
Thirteen-lined ground squirrel	0.00	0.00	0.09	0.08	0.15	0.30	0.00	0.00
Least chipmunk	0.00	0.00	0.00	0.08	0.15	0.00	0.00	0.00
Deer/white-footed mice	0.00	0.00	0.35	0.42	0.45	0.00	0.38	0.13
Red-backed vole	0.05	0.05	2.34	1.25	0.00	0.00	0.00	0.00
Meadow vole	0.00	0.20	0.52	0.33	0.00	0.91	0.00	0.64
Southern bog lemming	0.00	0.00	0.00	0.00	1.06	0.45	0.00	0.00
Meadow jumping mouse	0.15	0.58	2.52	5.33	0.45	0.00	0.13	0.00
Woodland jumping mouse	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00
Total	0.50	1.66	6.69	8.66	2.71	3.02	1.02	2.57
$\bar{x}$	0.04	0.12	0.48	0.62	0.19	0.22	0.07	0.18
SD	0.06	0.20	0.87	1.40	0.31	0.32	0.16	0.46

[a] Catch/Effort = $\frac{A \times 100}{TU}$ (Nelson and Clark 1973)

[b] 2,056 trap nights (2 drift fences x 20 traps x 56 nights). Data courtesy of Steve Hoffman, WDNR, Grantsburg.

[c] 1,152 trap nights (3 drift fences x 16 traps x 24 nights).

[d] 660 trap nights (2 drift fences x 10 traps x 33 nights). Data courtesy of Greg Kessler, WDNR, Brule.

[e] 780 trap nights (3 drift fences x 10 traps x 26 nights). Data courtesy of Peter David, Great Lakes Indian Fish and Wildlife Commission, Odanah, Wisconsin.

In 1995, the AC/E for all small mammals captured with snap traps in recently burned areas in the CMWA, DCWA, and MBWA was less than that for clearcut and forested areas in the same areas (Table 5).

The following year, the AC/E for all small mammals decreased somewhat for recently burned areas in the CMWA, DCWA, and MBWA but declined precipitously for the clearcut and forested areas. This decline was due primarily to declines in *Peromyscus* spp. and red-backed voles.

In 1997, the AC/E for numbers of all small mammals continued their decline in the burned areas of all four wildlife areas, but increased in the clearcut and forested areas (Table 5). This increase was primarily due to increased numbers of *Peromyscus* spp., most likely white-footed mice, and red-backed voles. Meadow voles and thirteen-lined ground squirrels also increased in the clearcut areas.

There were several problems that complicated the analysis of information obtained in this study, including the cyclic behavior of voles (*Microtus* spp.) (Krebs and Myers 1974, Birney et al. 1976, Hansson and Henttonen 1988, many others) and fluctuations of white-footed mouse *(Peromyscus leucopus)* populations (Popp et al. 1989). This intrinsic variation in numbers from year to year and from location to location could mask population responses by these species to different habitat types or habitat changes.

Table 5. Adjusted Catch/Effort[a] for small mammals captured in snap traps by habitat type in Wisconsin's northwest pine barrens, 1995–97.

	Burned			*Clearcut*			*Forested*		
Species	*1995*[b]	*1996*[c]	*1997*[d]	*1995*	*1996*	*1997*	*1995*	*1996*	*1997*
Masked shrew	0.12	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Arctic shrew	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00
Thirteen-lined ground squirrel	0.31	0.67	0.61	0.06	0.00	0.42	0.09	0.00	0.00
Red squirrel	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00
Eastern chipmunk	0.06	0.00	0.05	0.06	0.00	0.11	0.00	0.00	0.00
Least chipmunk	0.00	0.18	0.09	0.80	0.21	0.00	0.00	0.00	0.00
Deer/white-footed mice	1.06	0.60	0.23	0.73	0.11	0.85	2.23	0.88	1.48
Red-backed vole	0.12	0.49	0.19	1.35	0.64	0.85	1.38	0.50	1.48
Meadow vole	0.67	0.00	0.37	0.30	0.00	1.27	0.00	0.00	0.07
Meadow jumping mouse	0.06	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Totals	2.40	2.03	1.63	3.30	1.06	3.61	3.70	1.38	3.03
$\bar{x}$	0.24	0.20	0.16	0.38	0.11	0.36	0.37	0.14	0.30
SD	0.35	0.27	0.20	0.47	0.20	0.47	0.78	0.30	0.62

[a] Adjusted Catch/Effort (Nelson and Clark 1973).

[b] Seven burned grids (1,750 trap nights), 7 clearcut grids (1,750 trap nights), and 5 forested grids (1,250 trap nights).

[c] Seven burned grids (1,750 trap nights), 4 clearcut grids (1,000 trap nights), and 5 forested grids (1,250 trap nights)

[d] Nine burned grids (2,250 trap nights, 4 clearcut grids (1,000 trap nights), and 6 forested grids (1,500 trap nights).

There is also a tendency for some small mammal species to compete and displace other species (Kirkland and Griffin 1974, Crowell and Pimm 1976, reviewed by McGowan 1980, Vickery 1981, Adler et al. 1984, Swihart and Slade 1990, Nichols and Conley 1981), also influencing habitat use.

Burning reduces forbs and woody plants and debris, habitat that white-footed mice (M'Closkey and Lajoie 1975, Kitchings and Levy 1981, Kaufman et al. 1983, Clark et al. 1987, McMurry et al. 1996) and red-backed voles prefer (Gunderson 1959, Beck and Vogl 1972, Yahner 1983). Burning also reduces the litter layer that *Microtus* spp. prefer (Moreth and Schramm 1972, Kantak 1981, Snyder and Best 1988). Resprouting of fire-killed woody plants and the accumulation of litter in years following fire apparently improves the habitat for white-footed mice and red-backed and meadow voles.

However, deer mice numbers increase in the year of the burn (Beck and Vogl 1972), then decline to pre-burn levels in years following the burn (reviewed by McGowan 1980, Peterson et al. 1985, Snyder and Best 1988, Garman et al. 1993), a response opposite to that of white-footed mice. Since the two *Peromyscus* species were lumped together as one species in this study, their different responses to fire could not be demonstrated. Thirteen-lined ground squirrels were most numerous in burned areas which agrees with earlier findings of Vogl and Beck (1972) for the northwest Wisconsin pine barrens.

Conclusions

The species composition of the small mammal community sampled within the northwest Wisconsin pine barrens varied by location, habitat type, year, and capture technique. Burning initially reduced the numbers of meadow voles, *Peromyscus* spp., and red-backed voles, but increased the number of thirteen-lined ground squirrels. Small mammal indices in the clearcut and forested areas were overall greater than in the burned areas during the period sampled.

Acknowledgments

I wish to thank J. Hoefler and S. Hoffman, Wisconsin Department of Natural Resources, for trapping assistance and data from the Crex Meadows Wildlife Area, L. Rantala, Wisconsin Department of Natural Resources, for trapping assistance in the Namekagon Barrens Wildlife Area, G. Kessler, Wisconsin Department of Natural Resources, for trapping data from the Douglas County Wildlife Area, P. David, Great Lakes Indian Fish and Wildlife Commission, for trapping data from the Moquah Baarrens Wildlife Area, P. Rasmussen, Wisconsin Department of Natural Resources, for statistical assistance, C. A. Long, University of Wisconsin-Stevens Point and R. Bautz, Wisconsin Department of Natural Resources, for verification of small mammal identifications, and E. Anderson, University of Wisconsin-Stevens Point, and A. Wydeven, WDNR, for review of the manuscript. Partial funding for this study was provided by the Federal Aid to Wildlife Restoration under Pittman-Robertson Wisconsin Project W-141-R.

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Andrew Hipp

A Checklist of Carices for Prairies, Savannas, and Oak Woodlands of Southern Wisconsin

Abstract *Sedges (genus* Carex*) rivaled grasses in diversity and abundance in presettlement prairies and oak woodlands of the midwest, yet there has been relatively little published of the ecology, even the habitat preferences, of southern Wisconsin* Carex *species. Few data are available from presettlement accounts, and modern studies of prairie and oak savanna flora are too often incomplete or inaccurate with regard to sedges, or have limited application to the southern Wisconsin flora. In order to assemble a summary of prairie and oak woodland sedge habitats, I inspected vouchers deposited at the University of Wisconsin-Madison Herbarium for each of the 133 Wisconsin carices occurring south of the tension zone. From this study I identify seventy-four* Carex *species that occur in today's prairies and oak woodlands in Wisconsin. I summarize statewide habitat distributions for each of these from information recorded on labels of herbarium specimens and provide information on associates where such data are available for prairies and oak woodlands. I further identify forty-four carices as relatively certain members of the presettlement prairie and oak woodland flora and recommend them for planting in restorations. This document is especially intended for use by restorationists, whose work may prove indispensable in refining our understanding of midwest* Carex *ecology.*

Wisconsin is home to over a hundred and fifty species of *Carex,* which inhabit a nearly full range of light, moisture, and soil conditions. As is the case in temperate regions worldwide, *Carex* is unquestionably among the state's most "widespread and ecologically important genera of vascular plants" (Reznicek 1990). Yet a lack of publication and field education has contributed to a regrettable paucity of common knowledge about the ecology of this beautiful and pervasive genus.

Carex very likely makes up four to seven percent of the groundlayer diversity in midwest oak savannas (Delong and Hooper 1996, McCarty in press). Workers in adjacent states (Voss 1974, Wheeler and Ownbey 1984, Swink and Wilhelm 1994, Wilhelm 1995) have compiled habitat information on the sedges of their area by reference to herbarium specimens and field research. Others have included sedge species in more comprehensive hypothetical oak savanna or prairie floras derived primarily from bibliographic records (Gould 1941, Bray 1960, Packard 1988*b*, Bowles and McBride 1994, Delong and Hooper 1996, Ladd 1997) or by a combination of bibliography and fieldwork (Curtis 1959, Hujik 1995, Leach 1996, Bader and Fifield-Murray in review). But many of the reports from adjacent states do not completely accord with field observations in Wisconsin, because relatively minor shifts in geology and climate may significantly alter the habitat requirements of the plants studied (see Discussion section below). Moreover, field and bibliographic studies often treat only those sedges with which the workers are already familiar and occasionally report seemingly inaccurate habitat accounts without a satisfying explanation of methods. Regrettably, *The Vegetation of Wisconsin* (Curtis 1959) gives very incomplete information about the role of *Carex* in the communities delimited and studied, and the reports of Wisconsin's presettlement *Carex* flora are practically nonexistent, suggestive though the few direct accounts may be (e.g., Cheney and True 1893).

I have sought to identify *Carex* species of Wisconsin's prairies, oak woodlands, and oak savannas by reference to habitat information recorded on the labels of specimens housed at the University of Wisconsin-Madison Herbarium (WIS). While one cannot directly determine what species were present in Wisconsin's presettlement savannas due to the almost utter loss of habitat (Curtis 1959, Nuzzo 1986, Leach and Ross 1995, Leach 1996), a summary of the known habitats of Wisconsin's carices may illuminate the roles that those species played in the presettlement landscape.

Methods

Unless otherwise indicated, habitats presented in the Results section of this paper are summarized solely from information available on labels of *Carex* specimens housed at WIS. These specimens have been collected from throughout the state, mapped, and inspected by multiple experts. Due to the diligent caricographic work of Theodore S. Cochrane and the late Dr. James H. Zimmerman, which began in the late 1940s, the collection at WIS represents a relatively complete and accurate portrayal of the state's *Carex* flora. I also searched the herbarium of the Milwaukee Public Museum for vouchers of rare species; none of the species of interest were represented in the collection.

I inspected all species known to occur south of and within the tension zone as identified by Curtis (1959) (Table 1), a total of 133 species comprising around 8,000 vouchers; Cochrane's meticulous township maps of WIS collections were

Table 1. Species inspected. These are the specific epithets of carices that were considered for inclusion in this paper. Two of them ('+') are not known to be members of Wisconsin's flora—but were inspected because of their inclusion in the Wisconsin section of Ladd's (1997) tallgrass prairie species list. Six ('*') are introduced or adventive species that probably were not present in Wisconsin before European settlement.

albicans var. _albicans_
albicans var. _emmonsii_
albursina
alopecoidea
aquatilis
arcta
assiniboinensis
atherodes
aurea
backii
bebbii
bicknellii
blanda
brachyglossa
brevior
bromoides
brunnescens
*_bushii_
buxbaumii
canescens
careyana
cephaloidea
cephalophora
chordorrhiza
communis
comosa
+_conjuncta_ – turns out to be a misidentified _stipata_
conoidea
crawei
crawfordii
crinita
cristatella
crus-corvi
cryptolepis
cumulata
davisii
debilis var. _rudgei_
deflexa
deweyana
diandra
digitalis
disperma
eburnea
echinata ssp. _echinata_
emoryi
festucacea
flava
foenea
folliculata
formosa
gracilescens
gracillima
granularis
*_gravida_
grayi
grisea
gynandra
gynocrates
haydenii
*_hirta_
hirtifolia
hitchcockiana
hystericina
interior
intumescens
jamesii
lacustris
laeviconica
laevivaginata
lasiocarpa
laxiflora
*_leavenworthii_
leptalea
leptonervia
limosa
livida var. _radicaulis_
longii
lupuliformis
lupulina
lurida
meadii
merritt-fernaldii
molesta
muhlenbergii
muskingumensis
*_nebrascensis_
normalis
norvegica ssp. _inferalpina_
oligocarpa
oligosperma
paupercula
peckii
pedunculata
pellita
pensylvanica
plantaginea
*_praegracilis_
prairea
prasina
projecta
pseudocyperus
radiata
retrorsa
richardsonii
rosea
rugosperma
sartwellii
scabrata
schweinitzii
scoparia
+_shortiana_ – no acceptable voucher
siccata
sparganioides
*_spicata_
sprengelii
sterilis
stipata
straminea
stricta
suberecta
swanii
tenera
tetanica
tonsa
torreyi
tribuloides
trichocarpa
tuckermanii
typhina
umbellata
utriculata
vesicaria
viridula
vulpinoidea
woodii

invaluable to this selection, and virtually all references to species' geographic distribution are based on these maps. Those species of which at least two specimens are described by their collectors as occurring in prairie, savanna, or oak woodland were inspected with particular care. Habitats and associates information were transcribed directly from herbarium labels, studied, and summarized, then compared with other workers' studies of oak savanna and prairie sedges (cited under habitat descriptions).

I have included in this paper only those sedges that occur within the habitat delimited in the introduction to *The Tallgrass Restoration Handbook* (Packard 1997), excluding species particular to sedge meadows or wetter habitats (thus, for example, *C. stricta*), and including those of oak-dominated forests, which may in some cases harbor savanna species (cf. Packard 1988*a*). I exclude most species that appear to occur only in lowland forests, except where dominance by oaks suggests sites that may once have been lowland savannas (Hujik 1995); because of the difficulty of distinguishing between floodplain forests and savannas in the habitat descriptions on the typical herbarium label, some lowland savanna species may have been overlooked. These delimitations, like any such, are arbitrary, rooted in this case primarily in the research interests of the restorationists with whose work I am most familiar.

In several cases, the habitats of species reputed to occur in oak savanna appear in this study despite their seeming absence from Wisconsin's prairies and oak ecosystems. Such are instances in which another worker (always cited in the habitat description) has made what I judge to be a reasonable case for the species' inclusion; the habitat descriptions are still solely from WIS specimens except as specifically indicated in the text. I have not attempted an exhaustive review of the relevant ecological or taxonomic literature.

Associates are included only for sites that fall within the limits of this study. Associates should not be taken as representative of the full range of a species' habitat tolerance, but rather as examples by which to better understand the species' habitat requirements *within prairies and oak ecosystems*. The absence of associates for a given species in the list generally indicates a lack of good associate lists on WIS labels for that species as it occurs in prairies and oak ecosystems of southern Wisconsin.

Results

I recognize a total of seventy-four species as actual or probable inhabitants of Wisconsin's prairies and oak ecosystems (Checklists 1 and 2). Of these, I recommend forty-four for planting in southern Wisconsin (Table 2); of the remaining thirty, I identify seven as rare (also Checklist 1), three as exotic, and twenty as marginal or speculative denizens of prairies and oak ecosystems (Checklist 2).

The summary of habitat presence of relatively common *Carex* species (Table 2) may serve as a preliminary planting guide for restorationists working in southern Wisconsin. It is remarkable, though perhaps unsurprising, that fully half of these forty-four species may occur in wet prairie (22 species), with lowland savanna (14 species) ranking second and mesic savanna and dry to mesic oak woods tying for third (11 species). While the table is at best a crude summary of almost purely qualitative data, it is most likely a fair representation of the relative sedge diversities of the various habitats, and a confirmation of the mesophytic proclivity of the genus (cf. habitat distributions of carices listed in Curtis 1959, species list at end of book). For caveats regarding use of tables and lists as planting guides, see discussion section.

The habitat descriptions that follow (Checklists 1 and 2) represent the species' habitat distributions throughout the state, both north and south. In cases in which I hazard a prediction of a species' behavior within oak savannas, I set the prediction off clearly from the habitat as derived from herbarium specimens. Species that are rare, markedly restricted in geographic distribution, or adventive in Wisconsin are so indicated in the first line of the habitat description. Associates are presented only as they are recorded for specimens collected in prairies or oak ecosystems of southern Wisconsin.

Nomenclature throughout this paper follows the *Checklist of the vascular plants of Wisconsin* (Wetter et al., in review).

Table 2. Summary of habitats of 44 relatively common species. The following summary of habitats may be taken as a preliminary planting recommendation for restorationists working in southern Wisconsin and adjacent counties. Anyone planting the following species should first read the more complete habitat summaries in Checklist 1 and adhere to any geographic restrictions that apply; while this table does not include rare or highly restricted species, cf. Reinartz' (1997) guidelines to restoring rare or geographically restricted plant species.

Dry lime prairie
eburnea
meadii
pensylvanica – infrequently; tending toward sandier sites
richardsonii
rugosperma
umbellata

Dry sand prairie
brevior
muhlenbergii
pensylvanica
rugosperma
siccata
tonsa

Mesic prairie
bicknellii
brevior
molesta
pensylvanica

Wet prairie
brachyglossa – especially in sand
atherodes – in wet swales or standing water
bebbii
bicknellii
buxbaumii
conoidea
emoryi – alluvial soils only
haydenii
hystericina
interior
laeviconica – alluvial, especially in swales
molesta
normalis
pellita
sartwellii
scoparia – especially in disturbed, sandy soils
stipata – transitions
tenera
tetanica
trichocarpa – alluvial
vesicaria – alluvial
vulpinoidea

Dry to mesic oak woods (sugar maple not dominant)
blanda
brevior – tending toward sandier, more open woods
cephalophora
gracillima – generally on richer soils
normalis
pensylvanica
radiata
rosea
sparganioides – primarily in sugar maple forests
sprengelii – primarily in sugar maple forests

Dry savanna
brevior – not commonly
eburnea – especially *Juniperus* glades
muhlenbergii — sand
pensylvanica
rugosperma
siccata

Mesic savanna
bicknellii
blanda
brevior
cephalophora
debilis var. *rudgei*
normalis
pensylvanica
radiata
rosea
tenera
vulpinoidea

Lowland savanna
atherodes – very open, in swales or standing water
bebbii – minimal shade
bicknellii – minimal shade
emoryi – alluvial soils only
granularis – calcareous soils
laeviconica – alluvial
lupulina – generally alluvial
normalis
projecta
stipata – transitions between woods and openings
tribuloides – alluvial
trichocarpa – alluvial
vesicaria – alluvial
vulpinoidea

CHECKLIST 1

Native species of southern Wisconsin prairies and oak ecosystems

***Carex albicans* Willdenow *ex* Sprengel var. *emmonsii* (Dewey *ex* Torrey) J. Rettig (*C. emmonsii* Dewey *ex* Torrey)**
Restricted to the bed of Glacial Lake Wisconsin. A rare and highly restricted species of low, open, sandy woods, to sphagnous woods, sandstone cliffs, and low prairies. In a sandy jack pine-scrub oak community in Wood County, it was reported as forming 50% of the ground cover, with *Carex pensylvanica, C. siccata, Gaylussacia, Lithospermum caroliniense, Lupinus, Myrica, Oryzopsis pungens, Panicum, Prunus serotina,* and *Vaccinium*. Another population of undescribed proportions was found in a pastured sand prairie/low aspen woodland in Portage County, with *Antennaria, Artemisia campestris, Viola adunca, V. labradorica, Comandra, Vaccinium, Scrophularia, Lupinus,* and *Salix*. Wilhelm characterizes this as a species of sandy woods, often associating with *Quercus velutina,* and to a lesser extent of sandy prairies and beech forests.

***Carex atherodes* Sprengel**
Most common in standing water to two feet deep, ranging into wet, typically unshaded soil without standing water; also in cattail/bur-reed marshes, sedge meadows, willow swamps, tamarack bogs, and occasional upland areas. It was once reported in an upland forest edge and adjacent old field with low areas in Polk County; associates included *Lysimachia quadriflora, Apocynum androsaemifolium, Desmodium glutinosum, Nepeta cataria,* and *Solidago* sp. Hujik includes this in his list of lowland savanna plants, but does not analyze its sun and moisture requirements.

***Carex backii* Boott**
***Fairly rare in Wisconsin*; vouchers are from only Oconto, Florence, Door, Dane, Juneau, and La Crosse counties. Most generally in shady habitats, on sandy soils bordering a river or creek. The species ranges in southern Wisconsin from sandy upland or hilltop oak woods (with *Quercus velutina, Q. alba*) to, less commonly, mesic or bottomland forests. In northern Wisconsin, it is more common in dry, rocky, pine or oak woods, or on rock outcrops in the same. Delong and Hooper hypothesize that the species occurs in Iowa's mesic and clay-loam savannas; in Wisconsin, it seems more likely to range into open sandy woodland or sand savanna, especially adjacent to rivers.

***Carex bebbii* Olney *ex* Fernald**
Wet-mesic to low prairies and other open wet areas, including marshes, ditches, stream edges, lake shores, and old fields; in both peaty and sandy soils; ranges occasionally to fens, marlish sand, or white cedar swamps. At a characteristic site, a low flat prairie in Kenosha County bordering Lake Michigan, the species associates with *Agrostis gigantea, Calamagrostis canadensis, Carex viridula* (common), *Scirpus pendulus, S. atrovirens, Juncus dudleyi, J. nodosus, Salix discolor, Rosa blanda, Phlox glaberrima, Calamintha arkansana, Hypericum kalmianum, Argentina anserina, Lobelia spicata, Aster lanceolatus* var. *simplex,* and *Solidago gigantea.* The species occasionally ranges into upland or, more frequently, wooded areas. It occurs often enough under sparse shade to recommend it as a potential species of very open or moderately shady lowland savanna.

Carex bicknellii **Britton**
Most common in mesic to wet-mesic prairies, but ranging from completely open prairies to moderate shade and from sedge meadows to the tops of sandy moraines. The species grows occasionally in sandy oak-hickory woods, rarely in waste areas. On a low, dry sandy ridge of the Wisconsin River floodplain terrace, dominated by very abundant *Sporobolus heterolepis,* it was found with *Andropogon gerardii, Sorghastrum nutans, Scleria triglomerata, Lepedeza capitata, Polygala verticillata* and *P. sanguinea, Veronicastrum virginicum, Eryngium yuccifolium, Prunus pumila, Euphorbia corollata,* and *Euthamia graminifolia.* It is reported from a foot off of a trail through a Walworth County white and red oak savanna, with *Trifolium pratense, T. repens, Achillea millefolium, Hypoxis hirsuta, Dodecatheon meadia, Rhus glabra.* Hujik's calculations portray it as a species of wet, distinctly shady sites within lowland savannas, though his first year's graphs (Hujik 1995, Appendix B) indicate highest frequency in high light and medium elevation. See Henderson (1995) for recommended seeding rates.

Carex blanda **Dewey**
Most common in wet-mesic, lowland, and mesic deciduous forests, especially on silt loam soils; ranging to mesic or wet-mesic savannas, brushy thickets, prairies, and open or shaded waste areas. It generally associates with such woodland species as *Quercus alba, Q. rubra, Q. macrocarpa, Carya ovata, Desmodium glutinosum, Zanthoxylum americanum, Geranium maculatum, Ceanothus americanus, Festuca subverticillata, Vitis aestivalis, Amphicarpaea bracteata, Juglans cinerea,* and *Carya cordiformis.* The species is identified by Bowles and McBride (1994) as occurring in Illinois' presettlement barrens (defined, for purposes of their work, as more or less brushy prairies on silt loam soils—"rich," "productive," fire-dependent systems grown thick with *Corylus americana* or other shrubs, *Vitis riparia, Quercus,* or other grubs); it is known from such habitats in Wisconsin as well, often with *Zanthoxylum.* This is one of our weediest species, growing in moist or shaded hollows of all kinds, garden beds, sawdust, jig tailings, roadside gravel, and split railroad ties.

Carex brachyglossa **Mackenzie**
(*Carex annectens* Bicknell)
Commonly in wet prairies and other wet sunny areas, especially where sandy; it is generally found with such wet prairie species as *Blephilia ciliata, Lilium michiganense, Phlox pilosa, Prenanthes racemosa, Silphium terebinthinaceum, Scleria triglomerata, Arnoglossum plantagineum,* and *Lobelia spicata.* The species is occasional in shaded or upland sites—collected in wooded dunes in La Crosse County and a partly wooded west slope in Iowa County, as well as a few dry sand prairies and fields—and in marsh or sedge meadow. Tolerant of disturbance.

Carex brevior **(Dewey) Mackenzie *ex* Lunell**
Mostly in sandy, dry to dry-mesic prairies; ranging into pine barrens, cedar glades, open dry to mesic oak savannas (especially with *Quercus macrocarpa,* but also sometimes with *Q. velutina*) and oak woods; occasionally in mesic soils, rarely to marshes or low prairies. The species grows readily in sand blowouts, fallow fields, road edges, suburban shrub beds, fence rows, and other such disturbed areas. Wilhelm (1995) notes that while its habitat "is a little difficult to pin down because wherever it is found there is evidence of disturbance," the species occurs in both sandy prairies and dry woods of the Indiana Dunes area. Associates of an individual collected from a dry sand prairie

in Richland County include *Aristida tuberculosa, Panicum virgatum, Digitaria cognata* var. *cognata, Schizachyrium scoparium, Eragrostis spectabilis, Koeleria macrantha, Froelichia gracilis, Lechea intermedia, Helianthemum bicknellii, Opuntia macrorhiza, Cladonia* spp., *Selaginella rupestris, Rumex acetosella, Mollugo verticillata, Lespedeza capitata, Monarda punctata, Polygala polygama, Asclepias verticillata, Oenothera biennis or parviflora, Euphorbia corollata, Erigeron annuus, Ambrosia psilostachya, Solidago nemoralis, Carex siccata, C. muhlenbergii, C. pensylvanica,* and *Cyperus lupulinus* ssp. *macilentus.* One Dane County collection was made in a dry-mesic hardwood stand under *Quercus macrocarpa* and *Carya ovata,* with *Antennaria plantaginifolia, Hypoxis hirsuta, Sisyrinchium campestre,* and *Poa palustris.*

Carex buxbaumii Wahlenberg
Open wet areas, typically calcareous, though it grows occasionally in bogs as well; most frequently in wet prairies, sedge meadows, and fens. When the species grows in the immediate vicinity of trees, it is nearly always in a boggy or sphagnous substrate (e.g., "black spruce swamp" or "tamarack bog"). One collection is from shallow standing water at the shore of Lake Michigan, in sandy crevices among dolomite gravel. Typical low prairie associates include *Hypoxis hirsuta, Phlox pilosa, P. glaberrima, Packera paupercula, Heuchera richardsonii, Hypericum kalmianum, Pentaphylloides floribunda, Lythrum alatum, Liatris pycnostachya, Solidago ptarmicoides, Solidago riddellii, S. rigida, S. ohioensis, Valeriana edulis, Oxypolis rigidior, Aster ericoides, A. novae-angliae, Thelypteris palustris* var. *pubescens, Dodecatheon meadia, Pycnanthemum virginianum, Galium obtusum* ssp. *obtusum, Krigia biflora* ssp. *biflora.*

***Carex cephalophora* Muhlenberg *ex* Willdenow**
Most common in mesic to dry-mesic or xeric deciduous woods, but also in open areas, prairie and old field alike, and in the partial shade of *Quercus alba, Q. macrocarpa,* and other oaks; often in more disturbed areas of prairies and savannas, when present at all in those habitats (personal observation). Cheney and True (1893) cite habitat as unspecified "dry soil," in which they noticed it to be "rather common." Bowles and McBride (1994) identify this as a species of Illinois' presettlement barrens (cf. *C. blanda*).

Carex conoidea Schkuhr *ex* Willdenow
Most characteristically in wet prairies, occasionally ranging to sedge meadows, sphagnous jack pine woodlands, and wet, ruderal habitats; once collected from dry sand at a Waushara County farm. Hujik identifies this as a sedge of lowland savannas but does not give details on light or elevation tendencies. Wheeler reports that it is found (rarely) in "thinly-wooded areas" in Minnesota. Probably undercollected in Wisconsin. See associates list under *C. buxbaumii.*

***Carex cumulata* (Bailey) Fernald**
***Restricted to the bed of Glacial Lake Wisconsin; rare in Wisconsin.* Generally in wet, sphagnous, sandy jack pine woods. One of our collections is from a dry oak-poplar-paper birch-maple woods atop a Jackson County bluff; another is from moist, sandy, open ground in Monroe County, with *Carex deflexa.* Wilhelm notes that while rare in the Chicago area, the species occurs more frequently in pin oak savannas of Willow Slough, Newton County (Illinois). May have occurred in presettlement lowland or perhaps upland sandy savannas and barrens *in the bed of Glacial Lake Wisconsin.*

Carex davisii **Schweinitz & Torrey**
***Rare in Wisconsin.* Collections have been made only in La Crosse, Trempealeau, Jackson, Columbia, and Dane counties, predominantly in alluvial forest or wet to mesic openings within the same. Of ten vouchers deposited at WIS, eight are from riverside forests or, less commonly, unshaded alluvium. Though primarily of lowland forests, its occasional presence in open or partly shaded areas suggests that this species may have grown in presettlement lowland savannas as well. Delong and Hooper (1996) identify it as frequent in oak savannas of Iowa.

Carex debilis **Michaux var.** ***rudgei*** **Bailey**
Concentrated in central Wisconsin (Jackson, Wood, and Portage counties especially), but ranging north to the Apostle Islands, Douglas, Oneida, and Marinette counties. Only two specimens at WIS were collected south of northern Sauk County, and only one of those from Dane County (in a second- growth oak woods). The species appears to do best under shade, in wet or moist sandy ground with a peaty component. Typical habitats in Wisconsin include sphagnous woods, bog edges, alder thickets, and low, sandy oak or pine woods; occasional in low sandy savanna, but has probably never been common in much of southern Wisconsin. The species was once collected from a sandy to peaty low prairie in Juneau County, on a site that grades to groves of *Quercus velutina* (?), *Pinus banksiana,* and *Acer rubrum,* with *Castilleja coccinea, Sorghastrum nutans, Viola lanceolata, V. sagittata.* One Marquette County collection is from a black oak woodland with *Quercus macrocarpa* and *Populus tremuloides,* in a grassy opening filled with *Rubus idaeus* var. *strigosus* and *Poa pratensis,* with *Potentilla simplex* and *Prunus serotina* seedlings.

Carex eburnea **Boott**
A calciphilic, wiry sedge that forms monotypic mats in open or semi-shade of sandy or limy prairies and savannas, or on exposed limestone. The species is most commonly known from cedar glades (*Juniperus* savannas) in the driftless area, though it is also found in Ashland County, Michigan Island, and in white cedar *(Thuja occidentalis)* swamps on the shore of Lake Michigan (especially Door County). Typical associates in a Pepin County cedar glade include *Amorpha canescens, Andropogon gerardii, Artemisia campestris, Asclepias viridiflora, Aster azureus, A. ericoides, A. oblongifolius, A. sericeus, Bouteloua curtipendula, B. hirsuta, Coreopsis palmata, Euphorbia corollata, Juniperus communis, J. horizontalis, Kuhnia eupatorioides, Liatris aspera, L. cylindracea, Linum sulcatum, Muhlenbergia cuspidata, M. racemosa, Mirabilis hirsuta, Dalea candida, D. purpurea, Prunus pumila, Solidago nemoralis, S. sciaphila.* One population was found atop a boulder under *Juniperus virginiana,* with *Aquilegia canadensis, Arabis lyrata, Campanula rotundifolia, Pellaea glabella,* and *Sporobolus vaginiflorus.* The species is also found in boreal forest in Door County, and occasionally at trail edges in sugar maple-red oak forest.

Carex emoryi **Dewey**
In wet prairies, standing water or muddy sloughs, lowland forests (frequently within openings), and occasionally on stream banks or sandbars, always in alluvial soils; associates with such species as *Calamagrostis canadensis, Glyceria striata, Iris versicolor, Onoclea sensibilis, Packera aurea.*

Carex festucacea Schkuhr *ex* Willdenow
***Extremely rare in Wisconsin.* The only specimen at WIS with useful habitat information is from Avoca prairie, a wet prairie on the Wisconsin river, where it associates with *Liatris pycnostachya, Allium canadense,* and *Thalictrum dasycarpum.* Likewise in Minnesota, the plant is known from only one location, the slightly raised banks of a river running through a lowland forest (Wheeler 1984). Rothrock, without considering individuals growing in Wisconsin, observes that *C. festucacea* "prefers moist, open woods or brush," favoring sites that are shadier than those inhabited by *C. longii,* and "soils with less sand content than typical for *C. albolutescens* and *C. longii*" (Rothrock 1991). Probably this was an uncommon denizen of low prairies and open savannas in presettlement Wisconsin.

Carex gracillima Schweinitz
Most typically in mesic or bottomland forests, often under *Acer saccharum.* Also on apparently drier sites under oak-dominated canopies (e.g., *Quercus alba, Q. velutina*), but these generally with a mesic forest element as well; usual associates include mesic forest species such as *Desmodium glutinosum, Rubus occidentalis, Festuca subverticillata, Brachyeletrum erectum,* and *Phryma leptostachya.* This common species seems to tend toward drier and occasionally more open sites in northern Wisconsin.

Carex granularis Muhlenberg *ex* Willdenow
Primarily in wet forests to moderately shady wet areas, often in disturbed calcareous substrates. The species occasionally grows in gravel roadsides, calcareous wet prairies, and fens or bog-like areas, and very occasionally in upland woods; it is extremely common in a recently disturbed lowland marl at the University of Wisconsin Arboretum in Dane County, under partial shade (personal observation). Hujik esteems this a species of lowland savannas, and it may find its way into very occasional upland savannas as well, especially on calcareous soils. For associates in a typical low prairie, see *Carex bebbii.* It is interesting to note that the type specimen of *Carex granularis* var. *haleana* was collected by T. J. Hale, with no information on the label other than "Madison, Wisconsin—1860."

Carex haydenii Dewey
Typically in marshes, sedge meadows, wet prairies, and wet waste areas; it frequently grows in soils with a sandy component. Associates from a wet prairie remnant in Rock County include *Carex bicknellii, Comandra umbellata, Dodecatheon, Houstonia caerulea, Hypoxis hirsuta, Phlox pilosa, Polemonium reptans, Sisyrinchium campestre, Zizia aurea.* Individuals are occasionally collected in riverbottom or other rich forests, wet areas within otherwise dry woodlands, or alder thickets in the north. Within Dane County, one population was reported as growing in a second-growth oak woods (Aastad et al. s.n). The species ranges mostly south of a line from Milwaukee to Oshkosh to Stevens Point and the Black River.

Carex hystericina Muhlenberg *ex* Willdenow
Very common in a variety of wet, open to barely shaded, calcareous habitats; seems to occur more often on peaty or sandy soils than in loam. Common in fens and sedge meadows, less so in conifer swamps; also on shores and along ditches and streams. Individuals occur occasionally in very wet prairies, perhaps especially those with spring-fed soils or other fresh-water flow (personal observation). Reported associates from a wet prairie in Rock County include *Gentianopsis, Betula* x *sandbergii, Cornus,* and *Larix.*

Carex interior **Bailey**
Almost exclusively in open, calcareous wetlands: sedge meadows, low prairies, fens. Ecology overlaps that of *Carex buxbaumii* and other wetland calciphiles. In northern Wisconsin, forma. *keweenawensis* (Herm.) Fern. may tend toward coniferous bogs and swamps, but limited collections make this difficult to know for certain.

Carex laeviconica **Dewey**
Uncommon in Wisconsin, where it is at the northeast edge of its range (Hujik 1995). Our populations are found in both open and wooded wet areas, slightly more frequently in the former than the latter; probably without exception on alluvial soils. Occasionally it crawls up onto roadsides or railroad embankments, which probably simulate the alluvial shores on which it naturally fares well. At Avoca Prairie on the Wisconsin River, the species is known to hybridize with *Carex trichocarpa.* Hujik describes this species as a specialist on moderately shady swales within lowland savannas.

Carex lupuliformis **Sartwell *ex* Dewey**
***Very rarely collected in Wisconsin*, and difficult to distinguish ecologically from *C. lupulina*, with which it co-occurs.

Carex lupulina **Muhlenberg *ex* Willdenow**
A species of wet to (less frequently) wet-mesic forest, rarely in adjacent wet open areas. Sometimes found in extremely wet shrubby areas, in shallow standing water, or on unshaded riverbanks; rarely in shaded uplands. The species generally grows on alluvial soils. It is known from "wet thickets" in turn-of-the-century Dane county (Cheney and True 1893). The species' occasional presence in lowland forest openings suggests that it would probably do well in shady microenvironments of lowland savannas or in wet microenvironments within drier, oak-dominated woods.

Carex meadii **Dewey**
Most typical of dry lime prairies, but sometimes occurs in low prairies as well, where it is easily confused with *Carex tetanica.* Occasionally found in shrubby prairies or beneath sparse oaks, and occasionally averred to grow in sandy soil as well. A typical Crawford County dry prairie collection, from the upper quarter of a steep, west-northwest-facing dolomitic hillside lists as associates: *Poa pratensis* (dominant), *Amorpha canescens, Aster ericoides, Carex richardsonii, Celastrus scandens, Comandra umbellata, Cornus racemosa, Hypoxis hirsuta, Lithospermum canescens, Pycnanthemum virginianum, Malus ioensis* var. *ioensis, Ratibida pinnata, Ribes cf. hirtellum, Sporobolus heterolepis.* The species was once collected from a shallow ditch, where it grew with *Typha latifolia, Juncus* spp., etc. See Henderson (1995) for suggested seeding rates.

Carex molesta **Mackenzie *ex* Bright**
Primarily in low to wet-mesic prairie, where it may be found with *Carex pellita, C. scoparia,* etc.; also in sedge meadows, wet road edges, shaded river banks, and virtually any other wet, unshaded, or moderately shady area. Grows in sandy to clay soils. Wilhelm notes that it occurs in swamps in upland woods with *Asclepias incarnata, Glyceria striata, Quercus bicolor,* and *Packera pauperculus.* While primarily of open areas in southern Wisconsin, the species probably reaches into open lowland savanna.

Carex muhlenbergii **Schkuhr *ex* Willdenow**
One of the most typical sedges of sand barrens, dry sand prairies, and black oak savannas; less frequently on sandstone outcrops,

sand beaches, dunes, and dry (especially sandy) oak woodlands. Tolerant of disturbance. Associates on a typical sand prairie in Richland County include *Tephrosia virginiana, Koeleria macrantha, Danthonia spicata, Monarda punctata, Achillea millefolium, Poa compressa, Ambrosia psilostachya,* and *Plantago aristata.* The species occurs rarely on lime prairies with Carex meadii. Two collectors report having found the plant in marshes, and two others report it in prairies with darker, siltier soil.

Carex normalis Mackenzie
Generally in moist, wooded places, though ranging to dry oak woods or wet prairies; like many species, will grade to drier locations in the shade than it will in the sun. Voss describes its usual habitat as "moist ground, damp fields, thickets, woods," with plants sometimes growing in "dry open ground." Wilhelm declares that it is "often found in mesic savannas" with associates including (among a greater number of species more typical of closed woodlands) *Rosa blanda, Veronicastrum virginicum,* and *Zizia aurea.*

Carex pellita Muhlenberg
(*C. lanuginosa* auct. non Michaux)
Common in wet, open or slightly wooded areas throughout southeastern Wisconsin, especially in sandy or disturbed soils; sporadic to the north and west borders of the state. The species frequently forms rhizomatous clones in wet prairies, low fields, sedge meadows and marshes, spreading readily to adjacent upland areas (as at road edges, railroad embankments, slopes leading up from lakeshores), where its vegetative shoots are frequently noticed if not usually recognized. While it is more frequently found in unshaded habitats, the species tolerates moderate shade, and reaches into upland and lowland savanna and forests; it very occasionally grows in a shady woodland. One Marquette County collection was made in a dry sand, scrubby black oak savanna, the sedge undoubtedly slowly invading from the adjacent extensive fen at the base of the slope, with *Equisetum hyemale, E. laevigatum, Carex pensylvanica, Arabis lyrata, Smilacina racemosa, Amorpha canescens, Asclepias syriaca, Galium boreale, Aster oolentangiensis, Monarda fistulosa,* and *Gaylussacia baccata.*

Carex pensylvanica Lamark
Most typical in dry to dry-mesic woods and prairies, especially in sand, though it ranges into sugar maple or bottomland forests as well, and very occasionally into lime prairies; one of our commonest species. In a Richland County sand prairie and thin jack pine-black oak woods, it is reported growing with *Vulpia octoflora* var. *octoflora, Hudsonia tomentosa, Koeleria macrantha, Opuntia compressa, Panicum virgatum, Rhus glabra, Selaginella rupestris,* and *Tephrosia virginiana.* Wilhelm describes this as "a common species of morainic savannas. . . . May well have been one of the principal fuel species in our timbered lands." Zimmerman similarly describes it as a species of dry prairies, barrens, and oak savannas. No effort is made here to discuss the segregate species or varieties that have been proposed for this species.

Carex projecta Mackenzie
Most typically in lowland or rich sugar maple forests as well as swampy thickets and shaded borders. Occasionally in lowland savanna or unshaded wet areas, though perhaps just the edges of these. Frequently in sandy soils. This species is common northward, where it occasionally strays from conifer swamps or mesic forest into bogs,

moist depressions in sand dunes, shallow standing water, or, rarely, sunny uplands. Much collected in the Apostle Islands, where it seems disproportionately frequent in open areas, perhaps due to higher humidity near the lake.

***Carex radiata* (Wahlenberg) Small**
(*Carex rosea* Schkuhr *ex* Willd., misapplied)
In a variety of wooded stands, from bottomland forests to dry oak woods, most often in relatively mesic or wet microsites; ranges to forest edges, sparsely wooded or open fields, and, infrequently, wet or dry prairie. It is frequent under white oaks and butternuts in the University of Wisconsin Arboretum's Noe Woods, with *Carex pensylvanica, Galium triflorum, Liparis lilifolia, Circaea lutetiana* ssp. *canadensis.* The species occurs not uncommonly in shady or wet microsites of mesic oak savannas (personal observation).

***Carex richardsonii* R. Brown**
Almost exclusively of dry, thin-soiled lime prairies, though ranging to dry sandy prairies and occasionally to calcareous wetlands. Cochrane notes that the species is "not rare, as previously thought, but undercollected due to early seasonality, poor fruiting, and resemblance to *C. pensylvanica.* L. J. Musselman and [Cochrane] have taken it on almost every dry prairie, dolomite or gravel, as well as on some sand prairies, that either has visited during the appropriate season. Like *Spiranthes magnicamporum, Solidago ptarmicoides,* and *Lithospermum canescens,* also calciphiles, this sedge is occasionally found in fens, not the type of habitat usually ascribed to it" (personal communication plus note on label of Cochrane & Cochrane #5989). See *Carex umbellata* for associates.

***Carex rosea* Schkuhr *ex* Willdenow**
(*Carex convoluta* Mackenzie)
Very common in deciduous woods, primarily in sugar maple forests, throughout the state; also in oak woods, damp to dry, and occasionally in prairies or wet pastures; leans toward drier habitats than does the closely related *Carex radiata.* Probably both species were found in shady microsites in presettlement savannas. Associates in its typical habitat, a white oak-shagbark hickory woods in Iowa County, include *Carex hirtifolia* (abundant), *Arisaema triphyllum, Crataegus* sp., *Cynoglossum officinale, Lithospermum latifolium, Muhlenbergia schreberi, Parietaria pensylvanica, Podophyllum peltatum, Ranunculus abortivus, R. hispidus* var. *nitidus, Ribes missouriense, Sanicula canadensis, Zanthoxylum americanum.*

***Carex rugosperma* Mackenzie**
(*C. umbellata* var. *umbellata* sensu Fernald)
Primarily of open or partly shaded sandy soils, especially dry; appears more shade tolerant than the closely related *Carex tonsa.* Usually in jack pine barrens, sand prairies, beaches and granitic outcrops, uncommon in moist hemlock woods and white cedar swamps.

***Carex sartwellii* Dewey**
Most frequently in sedge meadow and other wet, organic soil, including bogs; more generally in alkaline than acid soils. It grows invariably in open sun or barely shaded sites, and ranges from wet prairie to standing water in marshes, ditches, lake edges. The species may be more common in wet prairies than is suggested by the infrequency of collections, as the closely studied prairies of the University of Wisconsin Arboretum have yielded the species in abundance, growing with *Stachys palustris, Anemone canadensis, Calamagrostis canadensis, Liatris pycnostachya,* and *Hierochloe odorata.*

Carex scoparia **Schkuhr *ex* Willdenow**
Most common in open, wet, sandy soil, occasionally in microsites that are more or less bare of other vegetation. The species ranges from shallow water (base of plant submerged) to, rarely, dry sandy uplands, and from sun to partial shade. Typical habitat includes marshes, sedge meadows, lake shores, ditches, wet prairies, sphagnum bogs; aberrant on bluffs and in upland woods. One collection was made in Iowa County in moist loamy sand, from the bottom of a disturbed moist depression in a *Quercus velutina-Pinus banksiana* woodland, with *Carex tribuloides, Cyperus strigosus, Fimbristylis autumnalis, Scirpus cyperinus, Calamagrostis canadensis, Juncus effusus, J. tenuis, Onoclea sensibilis, Thelypteris palustris, Ranunculus pensylvanicus, Potentilla simplex, Spiraea alba, Verbena hastata, Hypericum majus, Viola* sp., *Penthorum sedoides, Lycopus americanus, Lobelia inflata, Conyza canadensis* var. *canadensis, Eupatorium perfoliatum, Euthamia gymnospermoides, Bidens cernuus, Erechtites hieraciifolia, Galium tinctorium.*

Carex siccata **Dewey**
(*C. foenea,* misapplied)
Prominently rhizomatous; most frequent in dry sand prairies, sandy savannas (including black oak and pine barrens) or sandy woods, with such species as *Stipa spartea, Comandra umbellata, Lupinus perennis, Asclepias tuberosa, Arabis hirsuta, Lithospermum caroliniense, Coreopsis palmata, Artemisia campestris, Antennaria palinii* ssp. *fallax,* and *Lespedeza capitata.* The species ranges to mesic to wet prairie or even, very occasionally, sedge meadow. It is, for the most part, limited to the southern half of the state, with scattered individuals as far north as Douglas and Marinette counties.

Carex sparganioides **Muhlenberg *ex* Willdenow**
Almost exclusively in rich sugar maple and associated forests, though occasionally in slightly lower, wet forests or dry to mesic oak-dominated forests. Once found with *Poa pratensis* in an open fallow field west of Madison's University Bay, seventy feet from an oak wood. Found as well in oak leaf litter in the "Bud" Jackson School Forest, a dry-mesic southern oak forest on rolling topography, under *Quercus alba, Q. velutina,* with *Prunus serotina, Carya ovata, Q. macrocarpa, Ulmus rubra* and *Malus ioensis;* associated herbs include *Smilacina racemosa, Geum canadense, Rubus rosa, Amphicarpaea bracteata, Desmodium glutinosum, Geranium maculatum, Parthenocissus vitacea, Vitis riparia, Osmorhiza claytonii, Prunella vulgaris* ssp. *lanceolata, Circea lutetiana* ssp. *canadensis, Galium concinnum, G. circaezans* var. *hypomalacum,* and *Phryma leptostachya.*

Carex sprengelii **Dewey *ex* Sprengel**
Like *Carex sparganioides, C. sprengelii* grows almost exclusively in rich upland or lowland forest, with occasional individuals on rocky outcrops; rarely in full sun. Once collected in a dry-mesic forest with *Quercus alba, Populus grandidentata,* and once in a white oak-black oak-ash-shagbark hickory forest in Brown County; the latter site is perhaps drier than one in which I would expect to find *C. sprengelii* growing in southern Wisconsin. Delong and Hooper report that this species occurs infrequently in the savanna region of Iowa, where it ranges from upland woods to wet-mesic and dry-mesic prairie.

Carex stipata **Muhlenberg *ex* Willdenow**
Common throughout Wisconsin in a variety of moist, often shaded habitats, such as river or pond edges (especially at woodland borders), transition zones between forest and

open wetland, and the edges of logging roads or trails through low moist woods; tolerant of disturbance. Also in sedge meadows, sand flats, and transitions between open upland and open wetland. The species likely occurs at the edges of ponds, streams, and open wetlands enclosed by or abutting oak savannas. Typical associates include *Carex pellita, C. trichocarpa, Allium canadense, Ranunculus hispidus* var. *nitidus, Thalictrum dasycarpum,* and many lowland weeds.

Carex tenera Dewey
Probably most common in wet prairies with *Sporobolus heterolepis, Calamagrostis canadensis,* etc., though collections derive from a diversity of sites, ranging from mesic and dry forest to mesic or, less frequently, dry sand prairie. From a single site in Rock County, the species was collected in both a rich, wet-mesic prairie, with *Andropogon gerardii, Asclepias hirtella, A. purpurascens, Carex bicknellii, C. buxbaumii, C. umbellata, Cirsium discolor, Gentiana andrewsii, Silphium integrifolium, S. laciniatum, S. terebinthinaceum, Sorghastrum nutans*; and the mesic transition to an adjacent upland woods, with *Equisetum arvense, Poa pratensis, Carex pellita, Geranium maculatum, Helianthus grosseserratus,* and *Solidago canadensis.* Wilhelm refers to this species as one of wet to mesic savannas and their associated prairies.

Carex tetanica Schkuhr
A species of sedge meadows, wet prairies, fens, and other open wet areas, typically marly or calcareous, with such associates as *Equisetum arvense, Thalictrum dasycarpum, Pycnanthemum virginianum, Veronicastrum virginianum, Helianthus grosseseratus.* According to Theodore Cochrane, the species is frequent but undercollected. More or less limited to the southern two-thirds of eastern Wisconsin, with one collection from Trempealeau County.

***Carex tonsa* (Fernald) Bicknell**
(*Carex umbellata* var. *tonsa, C. rugosperma* var. *tonsa*)
In predominantly dry, sandy, unshaded or only slightly shady habitats; apparently more restricted in habitat than the less frequently collected *Carex rugosperma.* Typical sand prairie associates, from two Sauk County collections are *Liatris aspera, Aster ericoides, A. sericeus, A. oblongifolius, Kuhnia eupatorioides, Cyperus lupulinus* ssp. *macilentus, Hudsonia tomentosa* (rare), *Krigia virginica, Solidago nemoralis, Antennaria plantaginifolia, Opuntia macrorhiza, Panicum villosissimum, P. oligosanthes* var. *scribnerianum, Koeleria macrantha, Stipa spartea, Carex muhlenbergii, Sisyrinchium campestre, Arenaria stricta* ssp. *stricta, Viola pedatifida, V. sagittata, Calystegia sepium, Polygala polygama* var. *obtusata, Triodanis perfoliata.*

Carex torreyi Tuckerman
***This extremely rare and restricted species* is near the east edge of its range here. Specimens from far western Wisconsin and other states (from the southeast to the Rockies) come from open to shady deciduous hardwood stands. One Trempealeau County collection is from an open deciduous woods of *Quercus macrocarpa, Carya ovata,* and *Populus tremuloides* atop a high limestone hill. Another is from a rich oak forest on the slope of an esker in Waukesha County, with *Carex cephalophora, Liparis lilifolia,* and *L. loeselii.*

Carex tribuloides Wahlenberg
Primarily in riverbottom or floodplain forests, but ranging occasionally to prairie sloughs, wet fields, sedge meadows, sandbars of the Wisconsin River, and upland woodlots; rarely to dry sand. The species is most common in southwest Wisconsin (only two specimens from Dane County at WIS) and

probably more or less restricted to alluvial soils. Cheney and True (1893) note that the species was "rather common" in "low, wet places" of Dane county at the turn of the century. It may be that they confused this species with the very similar *C. projecta,* which is not restricted to floodplains; for it seems unlikely that *C. tribuloides* would be so undercollected in the low, wet places of modern Dane county. *Carex tribuloides* appears rarely in oak openings bordering marshy ground and seems a likely resident of alluvial lowland savanna.

Carex trichocarpa **Muhlenberg** ***ex*** **Willdenow**

Generally in open or partly shaded alluvial soils, ranging occasionally to lowland forest edges or interior. The species often forms large vegetative colonies in marshes, sedge meadows, the wettest of alluvial prairies or low weedy fields, and on the banks of streams and springs. In the transition between a marsh and wet prairie in Rock County, it is reported as associating with *Carex stricta, Salix* spp., *Phlox pilosa, Angelica atropurpurea, Cornus racemosa, Zizia aurea, Caltha palustris, Galium obtusum,* and *Silphium terebinthinaceum.* Some collections have been identified as hybrids with *Carex atherodes* (most often in cattail marshes (*fide* Cochrane) or *C. laeviconica,* the latter occupying habitats similar to those of *C. trichocarpa.*

Carex umbellata **Schkuhr** ***ex*** **Willdenow**
(*Carex abdita* Bicknell)

Predominantly of dry lime prairies, but also on sandstone or dolomite bluffs, sand dunes, barrens, and related sites (e.g., trail edges in dry pine stands). Like other calciphiles (c.f. discussion under *C. richardsonii*), the species is occasional in calcareous wetlands (e.g., fens, sedge meadows, low prairies). Rarely in deep soil prairie. Associates from a dry prairie in Crawford County, two-thirds of the way up a steep west-northwest-facing hillside, on thin silt loam soil over Prairie du Chien (Ordovician) dolomite, are *Carex richardsonii* and *C. meadii* (both present nearby on same hillside), *Hypoxis hirsuta, Heuchera richardsonii, Comandra umbellata, Oxalis violacea, Lithospermum canescens, Hypericum* sp., *Erigeron pulchellus, Dalea candida, Rubus idaeus, Solidago missouriensis, Cirsium hillii* (many plants, generally distributed), *Triosteum aurantiacum.* See Henderson (1995) for recommended seeding rates.

Carex vesicaria **Linnaeus**

Sunny, wet areas, usually somewhat wetter than wet prairie—common in swales of Avoca Prairie, Iowa county—and usually on alluvial soils, these ranging from peat to sand; typically grows with such sedges as *Carex haydenii* and *C. sartwellii,* though often in wetter habitats than these two species require. Other typical habitats include lake shores, standing water, bogs and sedge meadows, ditches. Occasionally found in lowland forest edges or openings, sometimes in alluvial forests. Hujik includes this in his list of lowland savanna species.

Carex vulpinoidea **Michaux**

In marshes, wet forest edges, alluvial woods, lake and stream edges, and wet areas generally; often in sand, but less so than is the closely related *Carex brachyglossa.* Occasionally found in wet prairies, and once found on a sandy hillside. Infrequent in bogs and standing water.

CHECKLIST 2
Exotic, marginal, or speculative species

The following species are not native to Wisconsin, barely fall within the range of habitats delimited in the Methods section of this paper, or appear to have a proper place within these habitats despite a lack of examples among WIS specimens. In the interests of space, habitat descriptions may be cursory.

Carex albicans Willdenow *ex* Sprengel var. *albicans*
(*C. artitecta* Mackenzie)
***A very rare sedge in Wisconsin,* the only collections being from the immediate Devil's Lake area; more common south and east of us. Fernald accounts it a sedge of "dry woods and clearings." Wilhelm describes the typical locale as "dry, sandy woods, mostly in the dune region [of the Chicago region];" and Voss, similarly: "Deciduous woods of all kinds except the wettest, especially on sandy soils, in disturbed areas, along roads, and in clearings." In Wisconsin, known from dry rocky woods on the west bluff of Devil's Lake, where still extant along a path in the pines (Cochrane, personal communication), and on talus slopes around the lake.

Carex alopecoidea Tuckerman
A species of floodplain forests and open alluvium. Perhaps occasional in presettlement alluvial prairies and lowland savannas, though not represented from these habitats among recent collections. Wilhelm (1995) and Wheeler and Ownbey (1984) both describe this as a species of wet forests and meadows/fields.

Carex bromoides Schkuhr *ex* Willdenow
Primarily wet to mesic forests, occasionally to open fields, closed oak forests and, most likely, lowland savannas.

Carex bushii Mackenzie
*** Exceedingly rare, north of its historic range.* There is one known station in Wisconsin for this species; the north edge of its range passes through central Illinois. Wilhelm recognizes this as "evidently recently introduced [to Cook County] from farther south," the first collection being in 1978 and all collections being from eroded soils grown over with "weeds and non-conservative natives." According to *Flora of the Great Plains,* the species is "most common in ungrazed prairies, occasional in ditches and margins of wooded areas." This accords with our only documented site, in Iowa County: undulating terrain near a small stream course, originally high lime prairie on Dodgeville silt loam soil, actively grazed, with closest associates being *Antennaria neglecta, Cirsium hillii* (200 plants), *Erigeron strigosus, Daucus carota, Medicago lupulina, Phleum pratense, Trifolium pratense, Solidago rigida, S. speciosa,* and *Verbena stricta.*

Carex communis Bailey
Primarily a northern species, with a few populations in southern Wisconsin. Most generally of sugar maple or other mesic forests, but found once in a goat prairie, and once in what the collector considered a dry/dry-mesic forest with oaks.

Carex crinita **Lamark;** ***C. gynandra*** **Schweinitz**
Both primarily in bottomland forests, often alluvial. *C. gynandra* was once found at the edge of a pool in an upland oak woods, and *C. crinita* once found at the edge of a lowland woods with *Quercus bicolor*. Possibly these widespread species were formerly found in lowland savannas.

Carex cristatella **Britton**
Bottomland forests, marshy cornfields, sedge meadows, swales adjacent to wet prairies, one or two erratics in upland forest—but not a specimen from within good quality low prairie. The species' presence in what appears to be degraded low prairies suggests that it could easily occur in wet alluvial prairies.

Carex deweyana **Schweinitz;** ***Carex digitalis*** **Willdenow;** ***Carex hirtifolia*** **Mackenzie**
All three are found primarily in sugar maple forest, and range only rarely into oak-dominated forests.

Carex gravida **Bailey**
***Apparently adventive from the west.* This species is considered by Cochrane and Zimmerman to be adventive from prairies of the Great Plains, where it is common (Cochrane, personal communication). There is one record—no habitat information, label reading only "Madison, Wisconsin"—from 1861; the next specimens were collected in the 1930s. The species is most frequently found in open disturbed habitats —roadsides, railroad beds, ditches, etc.—but is very occasionally found in prairies as well, especially dry, ranging very infrequently to wet prairies, marshes, fens and lake edges, and forest edges.

Carex grisea **Wahlenberg**
(*C. amphibola* Steud. var. *turgida* Fernald, misapplied)
Primarily of mesic to lowland, often alluvial forests. Some specimens occur in open deciduous forests or lowland forest with *Quercus bicolor*, perhaps supporting McCarty's observation that in Missouri this is a relatively conservative species on closed and usually mesic fire-dependent sites (McCarty in press). Perhaps a lowland savanna species in Wisconsin.

Carex intumescens **Rudge**
Most typical of moist to wet woodlands. Collected once in a dry oak-hickory woods in Columbia County.

Carex lacustris **Willdenow**
Appears not to grade into wet prairies (more typical of sedge meadows, marshes, and other such wet habitats), but certainly in sloughs within wet prairies.

Carex lasiocarpa **Ehrhart**
Typically found in sedge meadows, sphagnum bogs, marshes, and lake edges, often in shallow water. Very rarely in the wettest of prairies.

Carex leavenworthii **Dewey**
***Very local in Wisconsin, where apparently adventive*, its native range being to the south. The bulk of Wisconsin collections come from a single location, a "weedy lawn" at the base of Science Hall on the UW-Madison campus's Bascom Hill, where the first collection of the species from the state was made in 1957; the population there is now extirpated. This site, in a region of former oak savanna, and a second collection from a lawn shaded partly by *Quercus macrocarpa* accord with Delong and Hooper's assessment of the species as a denizen of "prairie, woodlands, wooded bluffs" and mesic/clay loam oak savanna.

Carex merritt-fernaldii Mackenzie
Infrequent in Wisconsin, slightly more common northward. Usually in low, sandy, open disturbed areas, rarely in open woodlands. This species might have been present in disturbed areas of low sand prairies before settlement.

Carex muskingumensis Schweinitz
Always on alluvial soils, chiefly along the Wolf, Wisconsin, and Mississippi Rivers; primarily of lowland forests and transition zones. Once recorded from a "*Carex* spp. bog or marsh" at the edge of a bottomland woods with *Quercus bicolor* (Iltis #6058). Other than this, it apparently has been found only in shade, but it might occasionally grade into shady lowland savanna.

Carex swanii (Fernald) Mackenzie
*** This is one of Wisconsin's rarest sedges* (four collections at WIS, three of which are from the southeast corner of the state), probably at the northwest extent of its range here. Wilhelm describes it as "a characteristic species of black oak savannas in our eastern and southern sectors," but WIS specimens are from a Waushara County alder thicket, a sandy roadside in Kenosha County, and a sugar maple forest in Waukesha County. In other prairie-province states, *C. swanii* has been found in rich, rocky soil beneath a thick oak-hickory canopy (LeFlore County, Oklahoma), in a prairie slough (Winnebago County, Illinois), and in a dry, sandy logging road through a forest clearing (St. Joseph County, Indiana). This species may have occasionally found its way into sandy oak savannas before settlement, though its seeming absence from sand savanna remnants and its extreme rarity in Wisconsin render this doubtful.

Carex tuckermanii Dewey
Primarily in wet shaded woods, generally on alluvial soils, occasionally in unshaded sloughs, river banks, and wet pastures as well, and at the edges of pools in alluvial or otherwise wet woodlands. In the north, often ranges to wet hardwood forests, and sometimes to conifer bogs, alder thickets, cedar swamps, marshes and wet grasslands. This species may be occasional in very shady lowland savannas, though such placement is not strictly supported by vouchers inspected.

Carex typhina Michaux
A plant of floodplain forests, frequently growing with *Quercus bicolor.* This species may occasionally move into lowland savanna.

Carex viridula Michaux
Primarily of wet sandy or rocky shores, calcareous wetlands, and adjacent communities. Thus collected once in a wet prairie adjacent to Lake Michigan (Kenosha County, Cochrane et al. #11,279). Schneider (1994) found this in a quarter of the Ohio fens that he studied, and he accounts it, with *Carex interior,* an obligate calciphile.

Discussion

Those who plan to utilize these checklists and Table 2 as planting guidelines should interpret the data with some care. The portrayals of species' environmental requirements in this paper generally do not adequately represent the full range of their tolerance and preferences across the range of environments present in Wisconsin; *Carex richardsonii* and *C. tetanica,* for instance, are sufficiently undercollected that the breadth of their behavior in Wisconsin prairies may not be well understood. Conversely, the ecology of some species pairs with markedly overlapping habitats, such as Carex meadii and C. richardsonii, tend to resemble one another less than the habitat narratives in this paper suggest. As is the case worldwide, work on Wisconsin carices suffers from a lack of knowledge of the species' autecology (Catling et al. 1990). Experimental plantings and more sophisticated empirical studies are required to both differentiate and sufficiently represent the habitat requirements within this genus (cf. Jordan et al. 1987, Leach 1996).

The distributions of a few species in this study seem to support Bray's hypothesis (1958) that species of wet to wet-mesic prairies may move into shady sites of somewhat drier uplands; *Carex bicknellii, C. normalis, C. tenera,* and *C. vulpinoidea,* for example, all occur in both wet (open) prairies and mesic to dry oak woods and savannas. On a larger scale, a few species exhibit trends in habitat requirements that support the observation that several forest species of south-central Illinois grade into more open savanna toward the north and east, particularly in Wisconsin (Delong and Hooper 1996). In particular, *Carex gracillima, C. pedunculata,* and *C. sprengelii* appear to gravitate toward more open and perhaps drier habitats as they move northward. Such geographic and habitat shifts surely affect other species as well. Restorationists, many of whom are already fully conscious of these trends, can contribute greatly to the fine discrimination of species habitats through experimental plantings and close observation.

Acknowledgments

This project would not have been possible without continual help from the staff, curators and director of the University of Wisconsin Herbarium, who have been forebearing and supportive since I first got interested in Carex and started clogging their already busy tables. Most especially, I thank Ted Cochrane for his patience and expertise in helping to identify prairie and oak woodland carices at the onset of this project, for access to his impeccable maps, for invaluable feedback on a draft of this paper, and for graciousness and generosity with his time and knowledge. I thank Mark Leach for taking time to look at an early draft of this report, both him and Brian Bader for insight on the nature of this work, Dr. Robert Freckmann for valuable suggestions on format and content, and Ken Wood for combing over the final draft. Thanks to Libby Zimmerman for an advance copy of her Carex keys and comments on the paper, and the University of Wisconsin Arboretum for funding an initial portion of this work. And I am most grateful to my wife Rachel, both for comments on the presentation that preceded this paper and for encouraging me to sit down and write.

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Richard S. King

Dispersal of Karner Blue Butterflies (Lycaeides melissa samuelis *Nabokov) at Necedah National Wildlife Refuge*

Abstract *Mark-release-recapture research was conducted to determine dispersal ability and patterns of the Karner blue butterfly* (Lycaeides melissa samuelis *Nabokov). Karner blue butterflies were marked during the first and second flights of the 1995 field season. Two hundred and three individuals were marked during the first flight, and 1,236 were marked during the second flight. The mean distance traveled by males between locations was 456.9 m and 214.7 m during the first and second flights, respectively. The mean distance traveled by females between locations was 69.8 m during the first flight and 359.2 m during the second flight. Inter-site dispersers (those individuals dispersing ≥ 1,150 m to new sites) represented 7.4% and 11.2% of the recaptures during the first and second flights respectively. Only one individual (0.07%) was located on a road corridor between suitable habitat patches. The percentage of individuals making inter-site dispersals was markedly different between sexes and among individual sites. Wind direction had no detectable effect on emigration rates for any of the sites, although significant differences in immigration rates were detected among wind directions. The observed dispersal trends indicate that Karner blue butterflies were able to disperse substantial distances (> 1,150 m) frequently and that they rarely use corridors to do so.*

Range-wide population declines of the Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) led to its listing as an endangered species in December 1992 (Clough 1992). Despite being one of the most studied butterflies of North America (Dirig 1994), many information gaps exist regarding the ecology of the Karner blue butterfly (Andow et al. 1994). One of the most fundamental information gaps concerns movements and dispersal of individual butterflies within and among populations. Karner blue butterfly populations are generally assumed to have metapopulation dynamics (Givnish et al. 1988). However, reviews of metapopulation literature reveal that data supporting critical assumptions of metapopulation theory are lacking for any species (Harrison 1991). Central to metapopulation dynamics theory is dispersal of organisms between patches (Hanski 1991).

Few studies focusing on the dispersal of Karner blue butterflies have been conducted. A limitation common to all insect dispersal research to date is the issue of decreasing probability of detection with increasing dispersal distances (Premo et al. 1994). All Karner blue butterfly dispersal studies to date fall into two major categories: studies conducted on corridors (Lawrence and Cook 1989, Sfera et al. 1993, Bidwell, unpublished data) and studies conducted in forested landscapes with Karner blue butterfly habitat patches (Fried 1987, Packer 1987, Welch 1993). Without knowledge of individual Karner blue butterfly movements and dispersal, development of management plans aimed at safeguarding this species will lack an important foundation.

Methods

This study was conducted during June, July, and August (the Karner blue butterfly's first and second flight periods) of 1995 on three populations on the Necedah National Wildlife Refuge (NNWR) in south-central Wisconsin (48°83′N, 90°10′W) (Figure 1). All populations are on restored oak barrens habitat (Curtis 1959) and are separated from each other by 1,150, 1,550, and 2,250 m of unsuitable habitat. Unsuitable habitat included water impoundments and wetlands void of nectar sources and wild lupine *(Lupinus perennis)* (the Karner blue butterfly's only known larval food source). The populations all lie within an area dominated by an open landscape with oak barrens and wet meadow habitats abutting large water impoundments.

Mark-release-recapture (MRR) was conducted throughout the entire study site every day of the first and second flight periods regardless of weather conditions. MRR began at 0800 and ended at 1530. The study area was staked with 50 m x 50 m grids that provided a reference to geographic location. The grid system also was used to keep search effort equal throughout the study area. Equal time was spent in each 50 m x 50 m cell every day. This decreased the number of butterflies that were captured but reduced bias toward what observers considered suitable habitat. Butterflies were captured with standard aerial butterfly nets, and individuals were given a unique three digit number on their hind-wing with an ultra-fine point "Sharpy" marker. Individuals were released immediately after marking was completed. The entire procedure usually took approximately 15 seconds, and no mortalities were observed during the study. The location, condition, and sex of each individual were recorded as well as date and time.

Data Analysis

Mean-distance-per-move (MDM) (average of all distances between locations), mean-distance-moved-per-day (MDD) (distance moved, divided by the number of days since the last location), total-distance-moved (TDM) (the sum of all linear distances between locations) and range-length (RL) (linear distance between the two most distant locations) were determined for male and female Karner blue butterflies during the first and second flights.

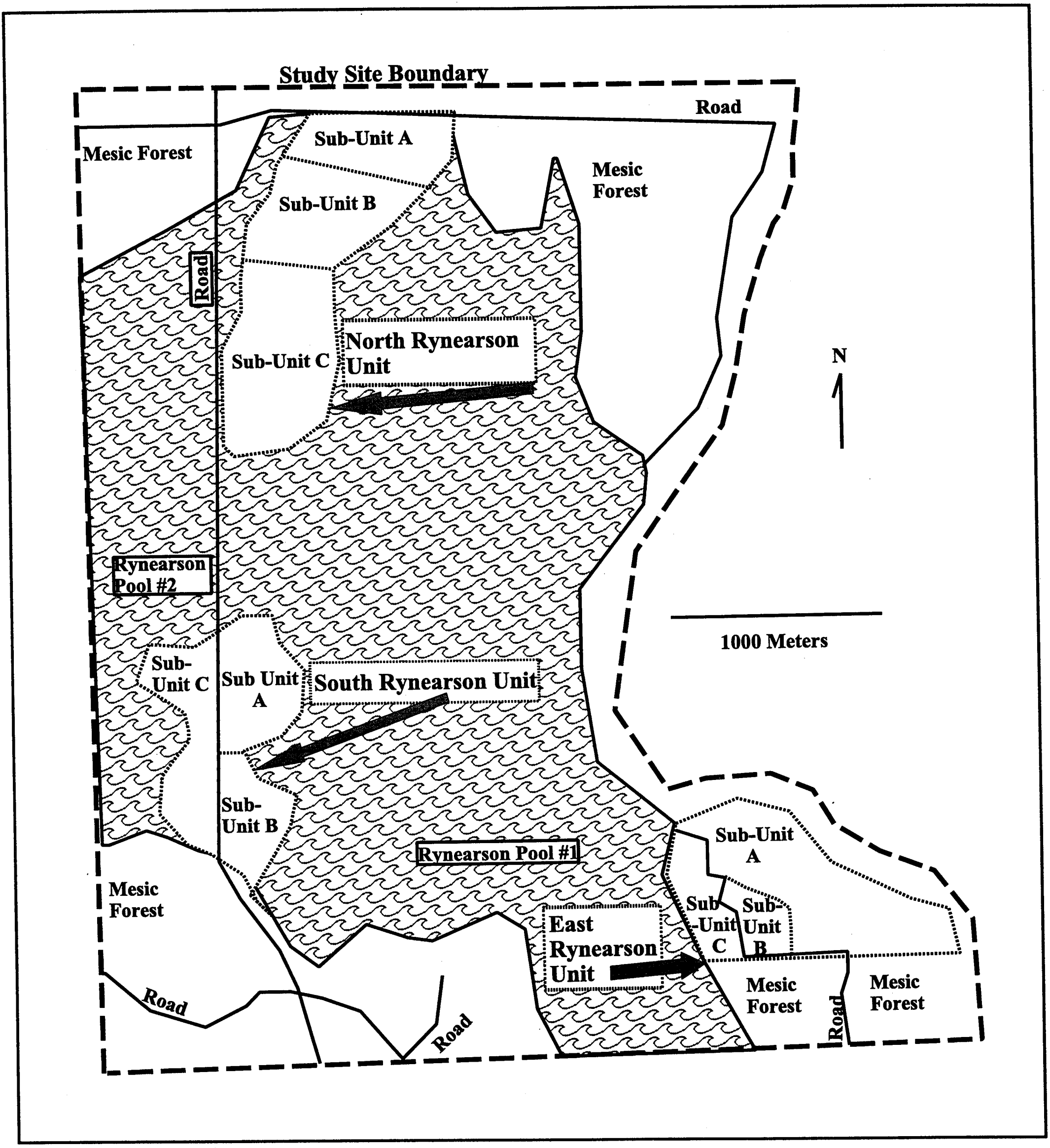

Figure 1. Location of units and sub-units within study area boundary on Necedah National Wildlife Refuge, Juneau County, Wisconsin.

All population parameters were estimated using mark-release-recapture data. Population size (P_i), total number of new animals entering the population (B_i), and survival probability (F) were determined as outlined by Pollock et al. (1990) using the using the software "Jolly." The total number of individuals emigrating (E_i) and immigrating (I_i) was determined from the dispersal data. The total number of emigrating individuals dispersing from a site was estimated as:

$$E_i = \frac{m'_{i+1}}{m_i} P_i$$

where m_i is the number of animals marked in the ith sample and m'_{i+1} is the number of those individuals that disperse out of the unit by the I + 1th sample. Individuals were assumed to have emigrated on the I - 1th sample that they were observed on a different site. The number of individuals immigrating into a unit was estimated as:

$$I_i = Ea_{(I-1)} + Eb_{(I-1)}$$

where Ea_{i-1} and Eb_{i-1} are the number of individuals dispersing to that site from the two other sites in the study area.

Wind direction was determined daily at 1300 (generally when maximum winds occurred) with a weather station (Forest Technology Systems, Bellingham, Washington). The weather station recorded wind direction in degrees. These data where then converted into eight classes (N, NW, W, SW, S, SE, E, NE) for analysis.

A chi-square analysis was used to test for differences in the proportion of individuals making inter-site dispersals (dispersal > 1,500 m) between sexes and among units. A Kruskal-Wallis test was used to test for differences in the distributions of dispersal between the sexes and flights. A Kruskal-Wallis test was also used to test for differences in the distributions of the emigration and immigration data among wind directions. Means are reported ± SE. The results of statistical procedures were regarded significant at $P \leq 0.1$.

Results

Two hundred and three individuals were marked during the first flight and 1,236 were marked during the second flight. Recapture rates with data pooled by sex were 11.7% and 25.7% for the first and second flights respectively, which were significantly different ($\chi^2 = 21.64$, df = 1, $P = 0.0012$). The male recapture rate (25.8%) was significantly greater ($\chi^2 = 3.91$, df = 1, $P = 0.05$) than that for females (21.9%) with data pooled over the flights.

Inter-site dispersal (movements between sites) (ISD) represented 7.4% and 11.2% of the recaptures on the entire study area during the first and second flights respectively. Individuals first located on the East Rynearson site had the highest proportion of individuals making ISD (40.0%). The proportion of Karner blue butterflies making ISD was 22.4% and 6.1% for individuals first located on the South and North Rynearson Sites respectively (Figure 2). The proportions of individuals making ISD from the three sites were significantly different ($\chi^2 = 41.21$, df = 2, $P = 0.001$). Of all females, 15.3% made at least one ISD, which was significantly more ($\chi^2 = 5.46$, df = 1, $P = 0.02$) than for males (7.9%) (Table 1).

When pooling data by flight, males moved significantly less between locations than females ($\chi^2 = 6.99$, df = 1, $P = 0.008$). Mean-distance-per-move (MDM) for first flight males (456.9 ± 261.7 m) was not significantly more ($\chi^2 = 0.61$, df = 1, $P = 0.44$) than that for second flight males ($\bar{x} = 214.7$

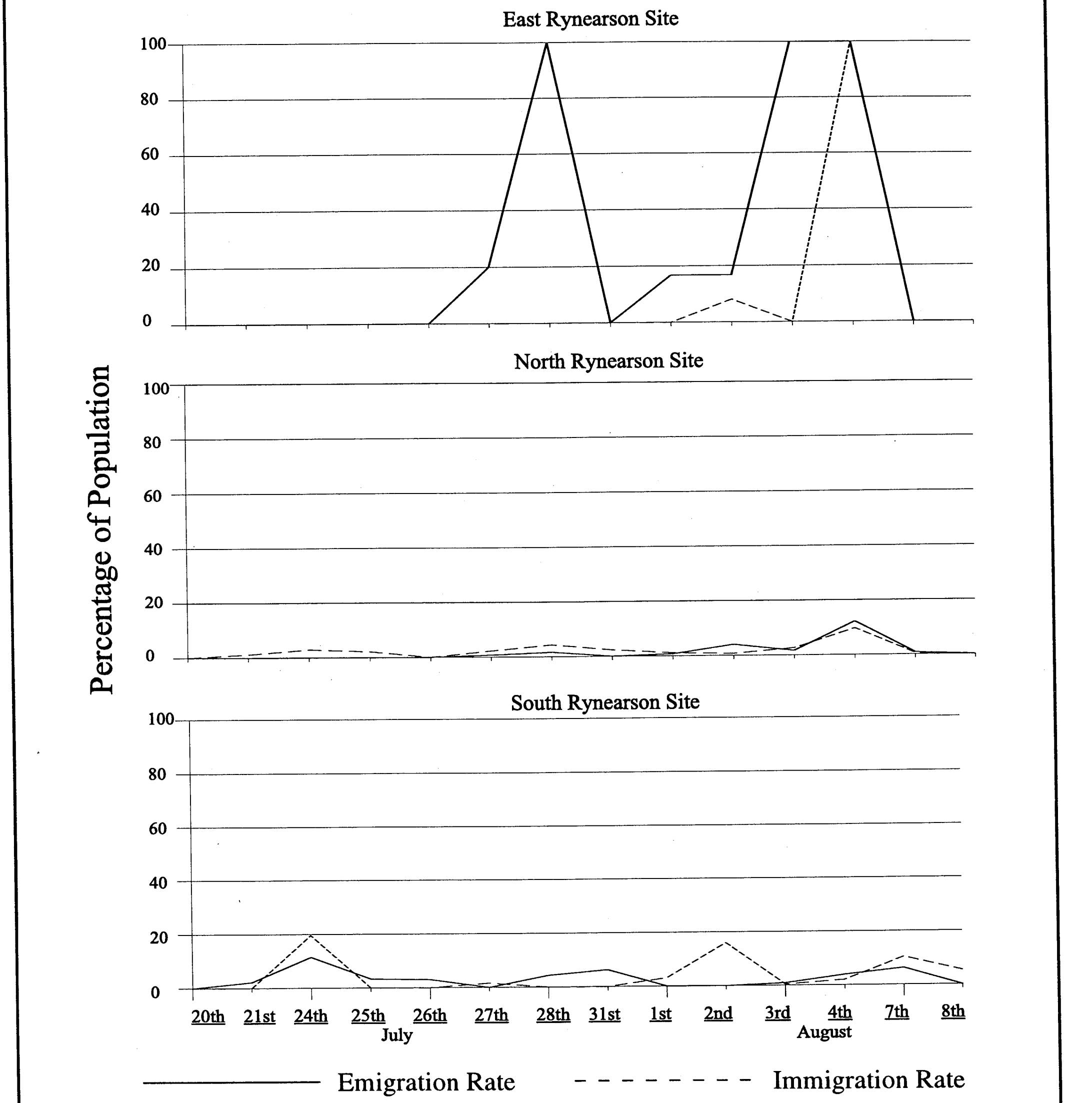

Figure 2. Emigration and immigration rates by day on the three populations studies during the second flight of 1995, on Necedah National Wildlife Refuge, Juneau County, Wisconsin.

Table 1. Summary of the number of individuals captured and recaptured by sex and flight during 1995 on Necedah National Wildlife Refuge, Juneau County, Wisconsin.

	♀	♂	*First Flight*	*Second Flight*
Number of individuals marked	674	765	203	1,236
Number of indivuduals recaptured	189	266	27	428
Recapture percentage	21.9	25.8	11.7	25.7
ISD	15.3	7.9	7.4	11.2

Recapture percentage represents the precent of individuals reptured on at least one occasion.
ISD = the percentage of individuals making at least one inter-site dispersal (≥ 1,500 m).

Table 2. Summary of dispersal statistics ($\bar{x}$ ± SE) for Karner blue butterflies during the first and second flights of 1995 on Necedah National Wildlife Refuge, Juneau County, Wisconsin.

	♀	♂
First flight		
MDM	69.8 ± 17.5	456.9 ± 261.7
TDM	74.4 ± 5.0	456.9 ± 261.9
DBR	1.4 ± 0.3	2.6 ± 0.1
MDD	48.2 ± 12.1	108.6 ± 32.7
RL	73.3 ± 13.8	457.0 ± 261.9
Second flight		
MDM	359.2 ± 27.3	214.7 ± 30.8
TDM	433.1 ± 72.8	277.1 ± 39.7
DBR	3.3 ± 0.3	2.5 ± 0.2
MDD	173.2 ± 13.1	119.5 ± 7.5
RL	613.7 ± 167.1	373.6 ± 98.6

MDM = mean distance between all locations.
TDM = sum of all distance between locations.
DBR = days between recapture.
MDD = mean distance traveled divided by the number of days between locations.
RL = maximum distance between any two locations.

± 30.8 m). MDM for first flight females (69.8 ± 17.5 m) was significantly less (χ^2 = 3.28, df = 1, P = 0.07) than that for second flight females (359.2 ± 27.3 m) (Table 2).

Taking elapsed time into consideration (mean-distance-moved-per-day), females did not move significantly (χ^2 = 1.55, df = 1, P = 0.21) further than males when pooling data by flight. MDD was 108.6 ± 32.7 m and 119.5 ± 7.5 m for males during the first and second flight, respectively, which was not significantly different (χ^2 = 1.97, df = 1, P = 0.16). Female MDD was also not significantly different (χ^2 = 0.26, df = 1, P = 0.61) between the first ($\bar{x}$ = 48.2 ± 12.1 m) and second ($\bar{x}$ = 173.2 ± 13.1 m) flights (Table 2).

Days-between-recapture (DBR) (the days between original and subsequent recaptures) was significantly different (χ^2 = 3.50, df = 1, P = 0.06) for males and females, which explains the discrepancies that were observed between the MDM and MDD data. First flight male DBR ($\bar{x}$ = 2.6 ± 0.1) was nearly identical to the second flight male DBR ($\bar{x}$ = 2.5 ± 0.2) with no significant difference

(χ^2 = 0.001, df = 1, P = 0.98). Spacing between recaptures was significantly (χ^2 = 6.27, df = 1, P = 0.01) greater for second flight females ($\bar{x}$ = 3.3 ± 0.3) than first flight females ($\bar{x}$ = 1.4 ± 0.3). Unlike the MDM and MDD data, a significant difference (χ^2 = 3.26, df = 1, P = 0.07) in the DBR data was detected between the flights with data pooled by sex (Table 2).

The maximum distance between any two locations (range-length) was also significantly different between the flights (χ^2 = 5.03, df = 1, P = 0.03) with data pooled by sex. RL was not significantly different (χ^2 = 0.02, df = 1, P = 0.90) between the sexes when the flights were pooled. Mean RL was 73.3 ± 13.8 m and 613.7 ± 167.1 for first and second flight females respectively, which was significantly different (χ^2 = 5.17, df = 1, P = 0.02). First flight male RL ($\bar{x}$ = 457.0 ± 261.9 m) was not significantly different (χ^2 = 0.40, df = 1, P = 0.53) than the second flight male RL ($\bar{x}$ =373.6 ± 98.6 m) (Table 2).

The total-distance-moved (TDM) was not significantly different between the sexes and flights. TDM was significantly shorter (χ^2 = 4.67, df = 1, P = 0.03) between the first ($\bar{x}$ =74.4 ± 5.0 m) and second ($\bar{x}$ = 433.1 ± 72.8 m) flights for females. First flight male TDM ($\bar{x}$ = 456.9 ± 261.9 m) was not significantly greater (χ^2 = 0.001, df = 1, P = 0.92) than second flight male TDM ($\bar{x}$ = 277.1 ± 39.7 m) (Table 2).

Emigration rates were not significantly different among wind directions for any site, but immigration rates differed significantly (χ^2 = 9.55, df = 4, P = 0.05) among wind directions on the South Rynearson Site. Similar results were seen on the North Rynearson Site with immigration rates being significantly different (χ^2 = 8.05, df = 4, P = 0.09) among wind directions. Immigration to the North and South Rynearson sites peaked on days with a west wind (Table 3). Sample size was too small for analysis of the East Rynearson immigration data.

Discussion

Karner blue butterflies studied on the NNWR were able to move large distances (>1,150 m), and exchange of individuals among the populations was frequent. Approximately 11% of all individuals marked during the second flight were eventually recaptured at sites other than their original capture site (Table 1). Distances between locations in excess of 1,500 m were common (7.5%, n = 429). Limitations in the study design necessitate viewing these figures as minimums. Although particular effort was given to detect the long-range dispersers during this study, Karner blue butterflies could have dispersed outside of the study area boundary. If detected, these long range dispersers would

Table 3. Immigration rates (reported as percent ($\bar{x}$ ± SE) of population estimated to have originated at a different site) for Karner blue butterflies during the second flight of 1995 on Necedah National Wildlife Refuge, Juneau County, Wisconsin.

	Wind Direction				
Population	*Northwest*	*South*	*West*	*Northeast*	*Southeast*
South Rynearson	0.0 ± 0.0	0.1 ± 0.1	10.8 ± 7.6	1.5 ± 1.1	8.3 ± 4.2
North Rynearson	1.2 ± 0.7	2.0 ± 1.2	6.3 ± 4.5	0.6 ± 0.4	0.8 ± 0.4

Sample size was too small for the East Rynearson site to permit analysis of immigration rate data.

have increased the means of all the summary statistics. Also, limitations of the study design may have lowered the percentage of individuals observed making movements in excess of 1,500 m. MRR was conducted over a large study area to make the study sensitive to long distance dispersals. The cost of this approach was that most individuals were relocated only once. If MRR had been conducted only in the areas of highest concentration, the recapture rate and summary statistics may have been higher. Of the individuals that were located greater than three times, movements in excess of 1,500 m were even more common (8.5%, n = 354).

Exchange of individuals among populations required that individuals crossed ≥ 1,150 m of unsuitable (nectarless) habitat. How this exchange occurred is unknown. Of the 1,439 individuals that were marked during the first and second flights, only one (0.07%) was located on a road corridor connecting the populations while a full 11.0% of the individuals made at least one inter-site dispersal. Use of roadsides as corridors can be assumed to be negligible given that the roadsides received as much search effort as any other part of the study area. Prevailing wind does not provide an answer either. Wind direction was a poor indicator of emigration rates. Immigration rates, the rate of individuals dispersing to a site, appeared to be related to wind direction for the South and North Rynearson sites (Figure 1). However, it can be assumed that butterflies were not passively carried by wind to these sites. Neither the North nor South Rynearson sites had a population source to the immediate west, and yet immigration to both those sites peaked on days with a west wind. Therefore, most of the immigration occurred against prevailing winds.

All summary statistics indicate females travel greater distances than males during the second flight. The opposite was true for the first flight, which could be a function of small sample size. When pooling data by flight, females (15.3%) were more likely to make one inter-site dispersal of 1,150 m or more than were males (7.9%) (Table 1). The recapture ratio (1:1.2 females to males) and the significant difference between the sexes in days-between-recapture (DBR) data suggest that catchability and/or detectability between the sexes may vary greatly with Karner blue butterflies. Therefore, as with many invertebrate species (Carothers 1973; Begon 1979; Tabashnik 1980; Gall 1984*a*, 1984*b*; Murphy et al. 1986), it would be advisable to determine population estimates separately for each sex when using mark-release-recapture methods. Differences in detectability also could affect population estimates of Karner blue butterflies when using methods other than mark-release-recapture.

All butterflies, regardless of sex, flight, and population source, were able to move around the study site easily. The study site is atypical of Wisconsin's Karner blue butterfly habitat. Open canopy uplands and wetlands comprised the entire study site. Typically, Karner blue butterfly populations are separated by closed canopy forests. Although road corridors did not enhance dispersal during this study, they could aid dispersal through closed canopy forests. During this study, all dispersals between sites occurred across unsuitable habitat that had no nectar sources. The presence of nectar sources between the sites could have enhanced inter-site dispersal. Further research is needed to determine how Karner blue butterfly dispersal is affected by nectar sources between sites and the presence of corridors in closed canopy landscapes.

Acknowledgments

I thank the field technicians who worked on this project: Chris Bosley, Jillene Summers, Joyell Wilber, Heather Lambert, Jeffery Berry, Patrick Molitor, Jeffery Johnson, Ramona Berger, and Joseph Black. Thanks to the National Fish and Wildlife Foundation, U.S. Fish and Wildlife Service, and the Forest Industry for funding of this research. My special thanks are extended to Dr. Gene Wood, Dr. Mark Boyce, Jenny Brown, and the anonymous reviewers of this manuscript who provided so many helpful comments.

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and John E. Ebinger

Woody Vegetation Survey of Sibley Burr Oak Grove Nature Preserve, Ford County, Illinois

Abstract *Densities, basal areas, and average diameters were determined for the woody overstory at Sibley Burr Oak Grove, Ford County, Illinois. Consisting of two groves originally separated by a lake and a sedge meadow, the woods consisted almost entirely of bur oaks; only two other species with a total of 10 individuals entered the canopy. In the largest area (13.75 ha) the bur oaks averaged 69.9 cm dbh, had a density of 38.8 stems/ha, and a basal area of 16.33 m^2/ha. Most trees had broad, open-grown crowns characterized by 2–7 main branches and low branches or branch scars within a few meters of the ground. More than 60 bur oaks exceeded 100 cm dbh. The structure, size, and open-grown nature of the trees indicates that the grove was a savanna or open woodland prior to European settlement in the 1860s.*

Prairie groves on morainal ridges were common in the Grand Prairie Division of central Illinois in early settlement times (Schwegman 1973). These groves were particularly common in the headwaters region of east-central Illinois in Ford County, (Headwaters Region Map 1871), where five river systems have their origins (Figure 1). Numerous ponds, sloughs, sedge meadows, and other wetland communities occurred between the morainal ridges. Some of these ridges supported small groves dominated by *Quercus macrocarpa* Michx. (bur oak). These "bur oak openings" existed because fires would not carry across these wetlands in most years (Stout 1946). High intensity fires undoubtedly burned through these wetlands and groves in drought years.

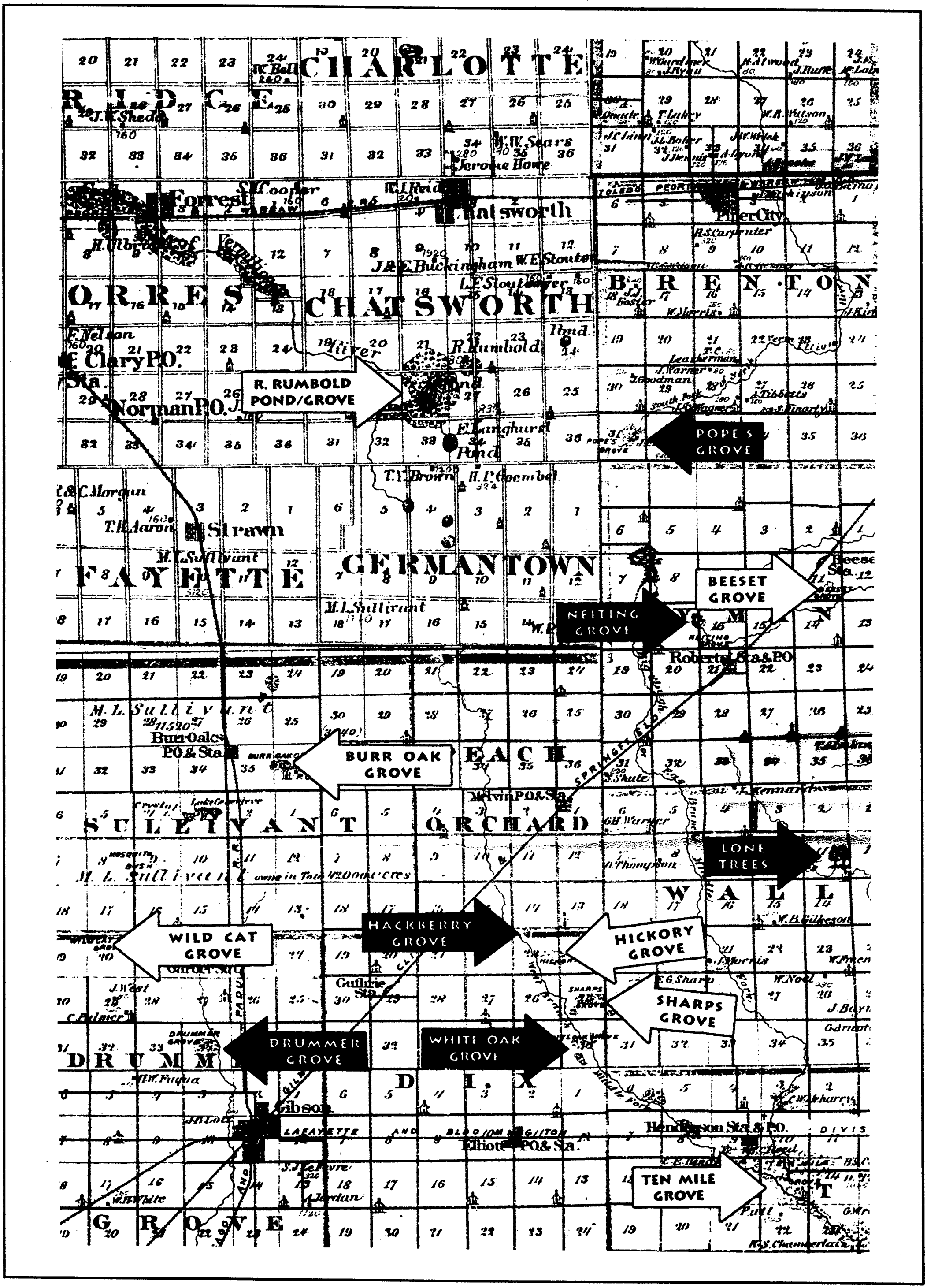

Figure 1. Prairie groves of the headwaters region of central Illinois in 1871 (Headwaters Region Map 1871).

Much of the prairie in Illinois, Indiana and Ohio probably would have been replaced by forest if not for the extensive fires that regularly burned across these states (Gleason 1912, 1913; McClain and Elzinga 1994). Most grasses and forbs were not adversely affected by these fires, which occurred mostly in late fall and sometimes in early spring. In contrast, most woody species, particularly young individuals and species with thin bark, were easily killed (Anderson 1983, Ebinger 1986, Ebinger and McClain 1991). Resprouting of top-killed individuals was common, but sprouts and damaged individuals were also more susceptible to future fires and predator damage (Hruska and Ebinger 1995).

Most of the prairie groves associated with morainal ridges have been destroyed. One of the few remaining examples is located near Sibley, Ford County, Illinois. This study was undertaken to determine the composition and structure of the overstory vegetation at the Sibley Burr Oak Grove.

Description of the Study Area

Located 1.5 km southeast of Sibley in western Ford County, Illinois, Sibley Burr Oak Grove Nature Preserve lies within the Grand Prairie Section of the Grand Prairie Division (Schwegman 1973). This grove (S 35 & 36 T25N R7E), located on a ridge and not associated with any stream, was described on November 29, 1823, by Elias Rector, a Government Land Office (GLO) surveyor, as an oak-hickory forest with an undergrowth of hazel (GLO field notes Vols. 231, 243 and 343).

The grove is 252 m above sea level with a local relief of 4 m. The soils of the grove have developed on shallow loess (less than 1 m thick) on calcareous glacial till of Wisconsin age. These Blount Silt Loams, which occur on nearly level ground, are somewhat poorly drained and occur as irregular areas at higher elevations on moraines. The available water holding capacity and organic content are both moderate, while the depth of the seasonal water table is more than 1 m (Fehrenbacher 1990).

European settlement of the Sibley area began in 1860 when Michael Sullivant purchased 40,000 acres around the grove and started a farming operation. Originally, the village of Burr Oak was located in the grove, but it was moved about 1.5 km to the northwest in 1868 to be adjacent to the Illinois Central Railroad. During Sullivant's occupancy, Burr Oak Farms was the world's largest farm and was featured in *Harper's Weekly Magazine* in 1871. Due to two consecutive droughts Michael Sullivant was forced to sell, and by 1879 Hiram Sibley owned the farm. At that time the town's name was changed to Sibley. From the 1860s until 1930 the grove was used as a staging area for farming operations and for the grazing of livestock. From 1930 until 1960 the grove was part of a hog farm operation, hogs being allowed to roam throughout the woods. After 1960 the grove was not grazed, resulting in the development of a dense understory of *Crataegus mollis* (Torrey & Gray) Scheele (red haw), *Prunus serotina* Ehrh. (black cherry), *Maclura pomifera* (Raf.) Schneider, and *Celtis occidentalis* L. (hackberry). In the fall of 1995 the grove was donated to The Nature Conservancy, and restoration efforts were started.

At the present time the grove consisted of two tracts, an eastern tract of 13.75 ha (34 acres), and a small western tract of 1.62 ha (4 acres). Between the two was a cultivated field about 50 m wide, that, according to early records, was originally a small pond and sedge meadow. Presently the exotic and weedy woody understory species have been removed from the grove, and parts of the grove have been subjected to ground fires. The small pond and sedge meadow that originally existed between the two tracts have been restored. This involved the removal of 65 cm of mineral soil that had accumulated over the original Houghton Muck.

Materials and Methods

The number, size, and species of all living and dead standing canopy and subcanopy species (25 cm dbh and above) were recorded during the summer of 1996. From these data the relative dominance, relative density, importance value (IV), average diameter (cm), density (stems/ha) in broad diameter classes, and the basal area (m^2/ha) were calculated for each species. The IV determination is the sum of the relative values for each species with a total possible of 200 (McIntosh 1957). The percent cover was determined by photographing the canopy from below (16 points) and calculating the percent of the area covered using a 100 point dot matrix. Nomenclature follows Mohlenbrock (1986).

Results and Discussion

Of the 661 canopy and subcanopy trees recorded in the grove, 651 were bur oaks (*Quercus macrocarpa* Michx.), nine were black walnut (*Juglans nigra* L.), and one was a white oak (*Q. alba* L.) (Table 1). Bur oaks, which dominated all diameter classes, were characterized by open-grown crowns having 2–7 main crown branches (Table 2). Most individuals had low branches or branch scars; the first branch or large branch scar averaged 3.3 m above the ground. Bur oak diameters ranged from 30.0 to 139.9 cm dbh. There were 170 bur oaks that had diameters greater than 80 cm, and 61 that had diameters in excess of 100 cm dbh. No attempt was made to age the living bur oaks, but one dead individual, with a dbh of 96 cm, was aged at 330 years.

The data on the two separate tracts of the grove (east and west areas) were kept separate (Table 1). The 13.75 ha eastern tract had an average of 39.34 stems/ha, and a basal area of 16.59 m^2/ha. The average diameter of bur oaks was nearly 70 cm, with 2.4 stems/ha less than 40 cm dbh, and 4.07 stems/ha above 100 cm dbh. The small western tract (1.61 ha in size) had a average of 74.08 stems/ha, and a basal area of 24.75 m^2/ha. Here the average diameter of bur oaks was nearly 63 cm dbh, with over 71 stems/ha being less than 80 cm dbh. In this section the canopy was essentially closed with 85% cover, while the eastern section was more open with 67% cover.

The dense understory of red haw, black cherry, and hackberry was removed during the past two years. Tree rings of cut stumps indicate that both red haw and osage orange were present in the preserve more than 90 years ago. In contrast, the other understory exotic and weedy woody species have only been present for the past 35 years, after the hog operation ceased. Bur oak seedlings were occasionally encountered in unburned parts of the grove, but very few saplings of this species were found.

Most of the prairie groves found in central Illinois are associated with streams and rivers. These streamside groves are usually large; many are more than 5 square miles in size. They also have a high woody species diversity with more than 20 species reaching the canopy. Most of these groves have high densities of *Acer saccharum* Marsh. (sugar maple) and other thin-barked, fire-sensitive species. Oak and hickories are present, and except for white oak, have low

Table 1. Diameter classes, relative values, importance values and average diameters of the woody overstory species at the Sibley Burr Oak Grove Nature Preserve, Ford County, Illinois.

	Stems/ha by Diameter Classes (cm)							*Basal Area*				*Average Diameter*
Species	*<40*	*40–59*	*60–79*	*80–99*	*100–119*	*120+*	*Total*	*m²/ha*	*Relative Density*	*Relative Dom.*	*IV*	*(cm)*
East area— 13.75 ha (34 acres)												
Bur oak	2.40	13.60	11.71	6.98	2.76	1.31	38.76	16.33	98.5	98.5	197.0	69.9
Black walnut	—	0.15	0.07	0.29	—	—	0.51	0.24	1.3	1.4	2.7	75.3
White oak	—	0.07	—	—	—	—	0.07	0.02	0.2	0.1	0.3	51.3
Totals	2.40	13.82	11.78	7.27	2.76	1.31	39.34	16.59	100.0	100.0	200.0	
West area— 1.62 ha (4 acres)												
Bur oak	5.56	30.86	25.31	8.03	1.85	1.23	72.84	24.37	98.3	98.5	196.8	62.9
Black walnut	—	0.62	0.62	—	—	—	1.24	0.38	1.7	1.5	3.2	62.3
Totals	5.56	31.48	25.93	8.03	1.85	1.23	74.08	24.75	100.0	100.0	200.0	

Table 2. Average crown diameters (m) by broad diameter classes of the bur oaks at the Sibley Burr Oak Grove Nature Preserve, Ford County, Illinois.

Diameter Classes (cm)	*Number Examined*	*Average Crown Diameter (m)*
40.0–59.9	20	13.03
60.0–79.9	24	19.07
80.0–99.9	40	20.14
100.0–119.9	17	21.91
120.0–139.9	8	23.20

IV's, bur oak being a minor component (Boggess 1964, Boggess and Bailey 1964, Boggess and Geis 1966). In contrast, Sibley Burr Oak Grove has only three canopy species with bur oak being, by far, the leading dominant (Table 1). Its overstory closely resembles that of the bur oak openings of Wisconsin, Minnesota, and Michigan (Stout 1946, Curtis 1959).

Sibley Grove is but one of the many groves, consisting primarily of bur oak, that were common in Ford County at the time of European settlement. Some contained an occasional white oak and *Carya ovata* (Mill.) K. Koch (shagbark hickory), but bur oak dominated according to the GLO survey notes. Presently most of these groves have been destroyed, and the few that remain have been highly modified by grazing, cutting, exotic species invasion and fire suppression.

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Identifying Highly Restorable Savanna Remnants

Abstract *The restoration of Wisconsin's native oak savannas has become a conservation priority. It is our opinion, however, that thousands of acres of highly restorable oak savannas have been overlooked because of flawed ideas regarding their structure and composition. Commonly, savannas are defined as having a specified "percent canopy" and a prairie-like groundlayer. Percent canopy is a flawed indicator of restorable oak savanna because it does not account for canopy dynamics nor spatial heterogeneity and because, by itself, percent canopy is a poor measure of light penetration to the groundlayer—the home of most plant species. Likewise, the presence of prairie-like groundlayers is not a good indicator of species-rich savanna remnants, especially on more productive soils. We suggest two elements that are both characteristic and diagnostic of highly restorable oak savannas: the presence of historic open-grown oaks and a groundlayer vegetation rich in native plant species in both sunny and shadier locations.*

Land survey records from the 1830s indicate that Wisconsin oak savannas occupied 42% of the land below the Tension Zone (Curtis 1959, Hole 1976). Oak savannas with intact groundlayer vegetation are now considered extremely rare in Wisconsin and the Midwest (Curtis 1959, Nuzzo 1986, Leach and Ross 1995). Oak savanna undoubtedly occurred on a wide range of soil and moisture conditions, on sites with varying fire frequency, and with a concomitant variation in species composition and structure (Curtis 1959, Will-Wolf and Montague 1994, Leach and Givnish in press). John Curtis (1959) in *The Vegetation of Wisconsin* recognized three primary kinds of oak savanna, based on canopy composition and soil conditions. Oak barrens occupied sandy or gravely substrates on upland sites and were dominated by shrubby, multi-stemmed Hill's oak *(Quercus ellipsoidalis)* or black oak *(Q. velutina).* Oak openings occupied mesic, loamy soils on upland sites and were dominated by large, single-stemmed bur oaks *(Q. macrocarpa),* although white oak (*Q. alba*) and black oak were sometimes common. Lowland oak openings occupied flood plains and glacial lake beds and were dominated by swamp white oak (*Q. bicolor*), although bur oak may have also been common.

In recent years the ecological restoration of oak savanna has become a conservation priority of many public and private land managers (e.g., Kline 1992, Henderson 1995, Leach and Ross 1995, Ross 1997). In Wisconsin, the Fish and Wildlife Service, the Forest Service, the Army, the Department of Natural Resources, the Nature Conservancy, and many local governments are, in many cases, doing a wonderful job protecting and restoring degraded savanna remnants. Ecological restoration is the practice of reconstructing damaged or degraded ecological systems. However, ecologists often lack detailed information on the historic nature of these systems prior to their degradation. Oak savannas, especially on more productive sites, presumably changed rapidly after settlement (Curtis 1959), well before modern ecologists could study them (Packard 1988*a*). The geographic extent of savannas and the paucity of ecological information set the stage for lively disagreements on the nature of savanna vegetation (Leach and Givnish in press). Although conservation agencies for many years have been aware of the recovery potential of degraded savannas, in our view the opportunity for savanna recovery may be much greater than generally recognized.

We contend that many highly restorable oak savannas have not been conserved because their recovery potential has gone unrecognized. Perhaps hundreds of thousands of acres have been overlooked. This probably was due to several factors. The early heritage inventories relied too strongly on Curtis's overly simple models of intact savannas. For many years, little was known about how to "set back" succession in overgrown savannas, which were often valued as forests. Grazed savannas were assumed to be of little conservation value. Thus degraded, but in many cases retrievable, sites were not considered for conservation or were conserved as forests. More recently, we suspect that commonly used search images missed highly recoverable sites, because such search images find some kinds of recoverable savannas but not all.

In this paper we critique commonly used definitions of oak savanna that are based on tree canopy measurements and the presence of prairie-like groundlayers. We suggest conservationists consider alternative search images when inventorying for savanna preserves. We hope this discussion provokes interest in savanna ecology and accelerates the identification and recovery of savanna remnants. Evaluation of both the tree and groundlayer strata is important; however, for convenience we discuss the two separately.

Canopy

Curtis (1959) viewed savanna as transitional between prairie and forest. To classify stands into vegetation types, Curtis made arbitrary (and he clearly called these arbitrary) distinctions among prairie, savanna, and forest. By his definition prairie has less than one mature tree per acre, forest has greater than 50% canopy cover, and savanna lies between. Canopy cover is the portion of sky over an area intercepted by canopy projected downward from above (Nuttle 1997).

Classification of continuously spatially variable vegetation requires setting arbitrary cut-off points (Klijn 1994). In addition to Curtis's definitions, several classification schemes used in the Midwest rely on percent canopy (e.g., United Nations Educational, Scientific and Cultural Organization 1973, White and Madany 1978, Faber-Langendoen 1995). Classification aids communication but can cause problems when arbitrary definitions are used, not to describe, but to prescribe.

In our view, using percent canopy to identify remnant savannas presents at least four serious problems:

1. Percent canopy can be a misleading measure of direct sunlight reaching the groundlayer (Chan et al. 1986, Nuttle 1997), which houses the bulk of plant diversity. Light penetration greatly influences the composition, diversity, and reproduction of plants in the groundlayer (Bray 1955, 1958, 1960; Curtis 1959; Pruka 1994, Hujik 1995, Leach 1996, Leach and Givnish in press). Used alone, percent canopy ignores the influence of canopy height on light penetration (Figure 1). Measuring percent canopy by outlining a tree crown perimeter—its drip line—also neglects the variable amount of light passing through tree crowns. In contrast to the relatively dense shade of oaks grown on productive sites, an oak growing on a drought-prone, nutrient-poor, or otherwise stressful site allows 20% or more of direct sunlight through its sparser foliage (Leach, unpublished data). In contrast to measuring canopy cover, several recent savanna studies (Pruka 1994, Hujik 1995, Leach 1996, Leach and Givnish in press) have used computer analysis of hemispherical photographs, which more appropriately estimate light penetration (Chazdon and Field 1987, Nuttle 1997, Valladares et al. 1997).

2. Savanna trees have long been noted for their spatial heterogeneity, with trees arranged in clusters, groves, peninsulas, or transitions (Gleason 1913, Bray 1955, Curtis 1959, Pruka 1994). Percent canopy is a kind of average spatial description for a stand. Like other averages, percent canopy loses meaning in heterogeneous stands (Figure 2).

3. The percent canopy of a stand describes the present condition, but not past conditions. The suppression of once-common wildfires (Leach and Givnish 1996) allowed many oak savannas to rapidly change into thickets, woodlands, or forests (Ellarson 1949, Curtis 1959, McCune and Cottam 1985, Pruka 1994).

4. Generally, the systems for classification using percent canopy fail to give operational definitions. We assume that those using percent canopy measures are making visual estimates in the field or by inspection of aerial photographs.

For the above reasons, percent canopy is a flawed measure and therefore is of questionable value as a criterion for identifying highly restorable oak savannas. In our experience, a much simpler and much more effective clue to the presence of historic oak savannas is simply the presence of open-grown oak trees. (The inspection of old air photos is also useful.) An oak tree grown in an open, fire-maintained, and therefore high-light environment develops a characteristic form with large horizontal branches (Bray 1955). Such open-grown oaks are still common in pastures, fields, urban parks, and other places where a fresh growth of trees has been kept in check. However, in most such sites (with the occasional exception of those on steep slopes), much of the native groundlayer flora has been lost. Relict, open-grown trees are common in our southern-Wisconsin woodlands and forests where many younger trees have filled in the canopy. Increased shade has caused lower branches to die, leaving dead limbs or trunk scars as evidence.

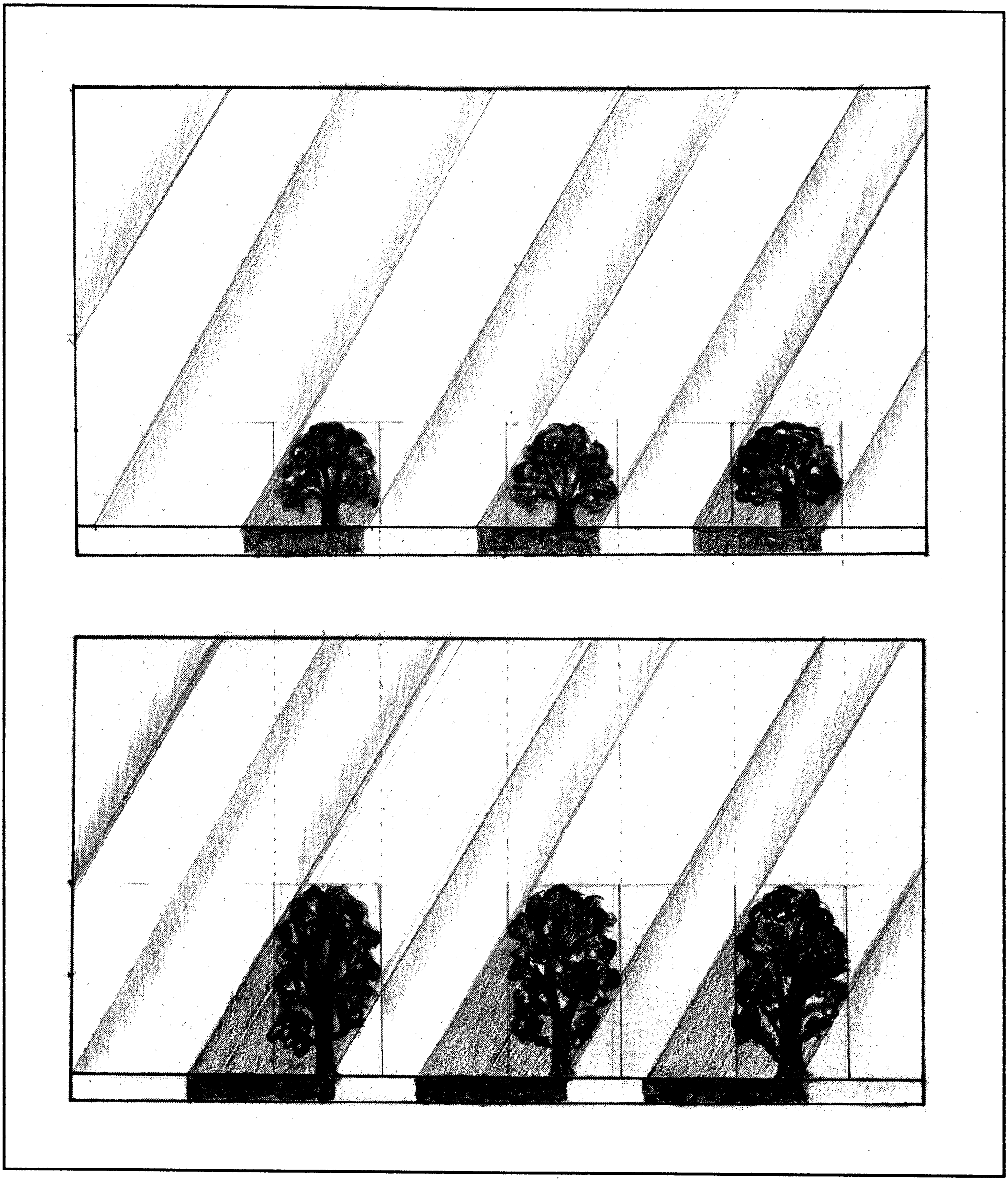

Figure 1. The often-used measure "percent-canopy" does not adequately describe light penetration to savannas groundlayers. By vertical projection, both stands A and B have percent-canopies of 40%. The trees in A are half the height of those in B. At noon on a clear August day the groundlayer in A receives 55% of the potential direct sunlight, while the groundlayer in B receives 40%.

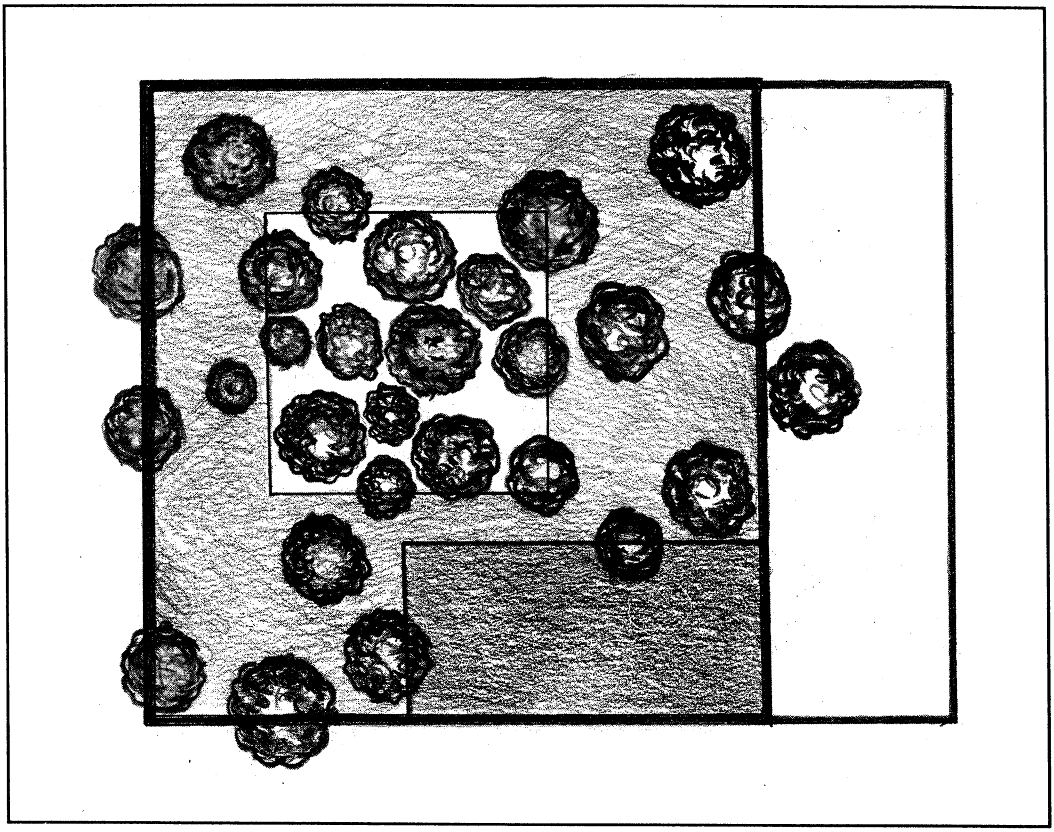

Figure 2. This plan view shows a typical aggregation of savanna trees. The percent-canopy for the area shown is 30%, but varies among sub-areas: A - 36%, B - 72%, C - 5%, and D - 9%. Obviously, the benefits of using percent-canopy as an objective ecological parameter must be weighed against the capriciousness of the areas' boundary.

Groundlayer

While there has been little argument over the canopy composition of historic oak savannas, there has been considerable debate regarding the nature of savanna groundlayers (Packard 1988*a*, 1988*b*, 1993; Anderson 1991; Pruka 1994; Leach 1996; Leach and Givnish in press). Bray and Curtis emphasized the similarity of the savanna flora to that of the prairies. This emphasis is commonly echoed in the description of savanna as "prairie with trees" (e.g., Tester 1995). Specifically, Curtis described the groundlayers of oak barrens as "largely dry-mesic prairie or sand barrens grassland." Similarly he described oak openings as usually a mixture of "bur oak and mesic prairie" or, for the lowland types, a mixture of "swamp white oak and wet-mesic prairies" (p. 326). Curiously, having described the nature of lowland savanna groundlayers, a page later Curtis wrote, "no stands on either wet or wet-mesic sites were found which were not pastured; hence no information is available on these types, except for their tree compositions."

In the 1940s and 50s other researchers working in Curtis's Plant Ecology Laboratory had learned that cattle grazing severely altered the composition of native prairie vegetation, including the loss of certain grasses and forbs (Dix 1955, Neiland and Curtis 1956, Curtis 1959). To avoid sites that were damaged by cattle grazing, Bray (1955, 1958, 1960) selected study sites based on their abundance of warm-season grasses and other prairie plants. Leach and Givnish (in press, Leach 1996) have suggested that Bray's site-selection criteria—his search image—were responsible for his failure to locate savannas "with intact groundlayers" on moister, more productive sites and for Curtis's statement that none could be located to study. Leach and Givnish (in press) used three site-selection criteria that were unbiased regarding the presence of prairie plants: (1) a canopy of open-grown oaks, (2) a groundlayer dominated by native species in both sunny and shaded microsites, and (3) a history of fire during the past 10 years. They found on moist, productive sites, except in the brightest microsites away from trees, that the groundlayer vegetation lacked the warm-season grass and other characteristic prairie plants sought by Bray.

In recent years other conservationists looking closely at the groundlayer have found savanna remnants with a great potential for recovery in lightly grazed oak groves (Martin 1981, Bronny 1989, Rich Henderson, pers. comm.).

Alternate Search Image

We suggest that conservationists seeking highly restorable savannas abandon concern with present canopy conditions and the abundance of prairie species. They should seek evidence of past (and restorable) savanna physiognomy, either by the presence of historic open-grown trees or from old air photographs. They should seek an abundance and diversity of native plants of any kind. There are now several lists of plants associated with savannas to help the field biologist become familiar with this flora (Packard 1988*a*, 1988*b*; Pruka 1994, 1995; Leach 1996; Packard and Ross 1997; Hipp 1998).

By using these simple search images we have located dozens of savanna remnants that are rich in plant species. Several of these sites contained regionally rare species including wild hyacinth *(Camassia scilloides),* late corral-root *(Corallorhiza odontorhiza),* oval ladies'-tresses *(Spiranthes ovalis),* cream gentian *(Gentiana alba),* and little grape-fern *(Botrychium simplex).* In fact, in just 22 sites totaling 42 ha, we found 507 native vascular plant species (Leach and Givnish in press), 27% of the total vascular floral diversity of Wisconsin.

Of course, not all sites are equally rich in species, and the species that are present vary in their rarity and, hence, in their contribution to conservation goals. Many sites dominated by native plants are populated primarily of Pennsylvania sedge *(Carex pensylvanica),* poison ivy *(Toxicodendron radicans),* or other outbreak species. Our assumption is that such sites are not easily restorable without extensive plantings (see Glass 1988, 1989; McCarty 1998), but this is an area requiring new research.

Our recommended search image is admittedly simplistic. However, there is not enough information on the composition of the various kinds of oak savanna to justify a more complex search image at this time. One may be tempted to speculate that high quality savannas should contain mixtures of plants from the prairie and the forest along with savanna specialists. However, the composition of any savanna is most likely dependent on its landscape context: greater diversity of prairie species in savannas surrounded by prairies, greater diversity of forest species in savannas surrounded by forests. The number of true savanna specialists is probably low in any case. As conservationists become more experienced in locating species-rich savanna remnants and more information becomes available on their constituent flora, we may develop search images using indicator species. Pruka (1995) provides a tentative list of indicators for Wisconsin.

Conclusion

The ability to locate species-rich savanna remnants for conservation can be considered a test of our ecological ideas. Many species-rich, restorable savanna remnants have been overlooked because of the wide acceptance of two flawed ideas: (1) that savannas fit neatly into a range of canopy percentages and (2) that savanna vegetation is essentially prairie with trees. Re-setting our search images to seek historic open-grown trees with native-plant groundlayers (regardless of the abundance of prairie plants) is helping identify important stands for conservation. We hope new search images will spark greater interest in locating additional sites before their restoration become too costly if not impossible.

Acknowledgments

Research contributing to this paper was supported in part by NSF grant DEB-9107379 to T.J.G., and by a grant from the Friends of the (University of Wisconsin-Madison) Arboretum to Thomas J. Givnish and Mark K. Leach. We thank Bill Jordan, Andrew Hipp, Steve Packard, and Roger Anderson for their comments on other versions of this paper, two anonymous reviewers for their useful suggestions, and Vickie Lynn Vander for the illustrations.

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Black Soil Prairie Groves of the Headwaters Region of East-Central Illinois

Abstract *Prairie groves associated with morainal ridges were relatively common plant communities within the Grand Prairie Division of Illinois. The composition and structure of the overstory of four groves were examined during this study. All were on morainal ridges with depressions to the north and west that originally contained wetland communities. The few remaining groves are dominated by open-grown* Quercus macrocarpa *Michx. (bur oak), sometimes along with* Carya ovata *(Mill.) K. Koch (shagbark hickory), and rarely a few other species. Heavily grazed until the middle of the twentieth century, these groves lack the herbaceous and woody understory of presettlement times.*

At the time of European settlement the most prominent landscape feature of Illinois was extensive tallgrass prairie that covered 61% of the state (Iverson et al. 1989). Within this grassland of the Grand Prairie Division were scattered prairie groves along with extensive tracts of timber along rivers and streams (Schwegman 1973). The species composition and structure of these forested tracts was determined by topography, climate, soils, and extensive fires that regularly burned across the region (Gleason 1912, 1913; Ebinger and McClain 1991; McClain and Elzinga 1994).

During pioneer times, two common types of prairie groves were found in the Grand Prairie Division of Illinois: (1) streamside groves associated with water courses and (2) isolated groves on morainal ridges that were somewhat protected from fires by sloughs. The streamside groves were usually extremely large, some extending over an area of five or more square miles (Boggess and Bailey 1964, Boggess and Geis 1966). Gleason (1913) suggested that these groves had been cut off from larger forest areas by attrition from repeated fires. In contrast, based on Government Land Office (GLO) survey notes, the prairie groves on morainal ridges were much smaller and rarely exceeded one square mile in size.

Large remnants of these extensive streamside groves, modified by disturbance and fire suppression, still exist. A few have been studied, including the Funks Grove Natural Area along Timber Creek, McLean County (Boggess and Geis 1966, Cox et al. 1972), Trelease Woods (Pelz and Rolfe 1977), and Brownfield Woods (Boggess and Bailey 1964), the last two being remnants of the "Big Grove" along the Salt Fork River in Champaign County. In these forests 20 or more tree species entered the canopy, the majority being thin-barked, fire-sensitive species such as *Acer saccharum* Marsh. (sugar maple), *Ulmus* spp. (slippery and American elms), *Tilia americana* L. (linden), and *Celtis occidentalis* L. (hackberry). Oaks were important components, *Quercus alba* L. (white oak) being common, *Q. macrocarpa* Michx. (bur oak), and *Q. velutina* Lam. (black oak) usually present as scattered, large-diameter trees. The presence of the thin-barked, fire-sensitive species suggests that the interiors of these large groves only occasionally burned. Based on GLO survey notes, presettlement forest vegetation along the Mackinaw River valley in central Illinois was highly diverse (16 species) with many thin-barked species (Thomas and Anderson 1990). White, bur, and black oaks were important on the terraces where fires were more intense.

In contrast, the isolated prairie groves on morainal ridges were small, closely resembling the "bur oak openings" of Wisconsin, Minnesota, and Michigan (Stout 1946, Curtis 1959). Sometimes described as natural parks (Curtis 1959), these groves were composed almost exclusively of bur oaks that were "all broad-topped and so spaced that seldom are the branches of two trees interlocked" (Stout 1946). These communities were probably subjected to occasional, intense fires, as the dominant bur oaks were mostly open-grown. Thin-barked, fire-sensitive trees seldom occurred here.

In Illinois the vegetation of the prairie groves on morainal ridges has rarely been studied. The few groves that remain have been extensively degraded by grazing, cutting, exotic species invasion, and fire suppression. This study was undertaken to determine the present composition and structure of the overstory of some of these groves and to determine their similarity to other forests of the Grand Prairie Division of Illinois.

Description of the Study Areas

The groves studied are located within what is referred to as the "headwaters region" of Ford County, Illinois (Anonymous 1871). Five rivers have their origins here: the Mackinaw, Vermilion, Sangamon, and Middle Fork Rivers, and Spring Creek, a tributary of the Iroquois River. None of the groves were located next to a stream, all being on morainal ridges with depressions to the north or west that originally contained sloughs and sedge meadows. Presently these depressions are cultivated fields, but soil cores show that two to six feet of top soil covers the Houghton muck that was present in the wetlands at the time of settlement. The soils of these groves are silt loams that developed in shallow loess on calcareous glacial tills of Wisconsin age (Fehrenbacher 1990). Surrounding are dark clay loams to silty clays that developed under prairie vegetation. Except for one section corner, where two bur oaks were listed as witness trees, the GLO survey notes give little indication of species composition or structure of these groves.

Beeset Bur Oak Grove. About 2 km northeast of Roberts, Illinois (S 11 T25N R9E), this grove is located on a long morainal ridge with an extensive lowland to the west and northwest. About 7 ha in size, sections of the grove had been recently disturbed by cutting, and a house with out-buildings was located in the eastern quarter. A part of the grove, 4.61 ha in size, was relatively undisturbed and was surveyed during this study. According to the headwaters map (Anonymous 1871), the grove covered about one-quarter of a section.

Sibley Burr Oak Grove Nature Preserve. Located 1 km southeast of Sibley, Illinois (S 35 & 36 T25N R7E), this grove is on a broad morainal ridge with wetlands to the north and west. It was described in the GLO survey notes as an oak-hickory forest with an undergrowth of hazel approximately one-third of a section in size. The grove is divided into two parts separated by a slough: an eastern section of 13.75 ha, and a western section of 1.62 ha.

Wildcat Bur Oak Grove. Located about 4 km southwest of Sibley, Illinois (S 8 & 17 T24N R7E), the grove is on a narrow morainal ridge with wetland depressions to the north and west. Presently the grove is 4.78 ha in size with an east/west county road traversing the southern quarter. A farm house is located within the southeastern part of the grove, the yard dominated by large bur oaks. According to the headwaters map (Anonymous 1871) the grove covered nearly one-fifth of a section.

Materials and Methods

All of the remaining isolated groves in Ford County were visited, and those that showed the least evidence of recent cutting or other major disturbance were selected for study. The size of each grove was determined by measuring the area using aerial photographs to determine the number of hectares present.

During the summer of 1997 the number, size, and species of all living canopy and subcanopy trees 25 cm dbh and above were recorded at each grove. From these data the density (stems/ha) in broad diameter classes, basal area (m^2/ha), relative density, relative dominance, importance value (IV), and average diameter (cm), were calculated for each species. The IV determination is the sum of the relative density and relative dominance for each species with a total possible of 200 (McIntosh 1957). Nomenclature follows Mohlenbrock (1986).

Results

In the groves listed below, bur oak was, by far, the dominant species, accounting for most of the density and basal area (Table 1). Most of the trees had broad, open-grown crowns, characterized by 2–7 major crown branches rather than a single trunk. Most also had low branches or branch scars within 1–4 m of the ground.

Beeset Bur Oak Grove. The overstory of this grove averaged 75.4 stems/ha with a basal area of 18.55 m^2/ha (Table 1). Bur oak and shagbark hickory were the important components with IV's of 162 and 32 respectively. Bur oak averaged 59.4 stems/ha, a basal area of 15.54 m^2/ha, and averaged 56.7 cm dbh. Of the 274 individuals of this species in the grove, all but 12 had diameters less than 80 cm dbh, suggesting past cutting. Coppice bur oaks averaged 2.4 trees/ha. Individuals of shagbark hickory were scattered throughout the grove, averaged 14.5 stems/ha, a basal area of 2.45 m^2/ha, and no coppice individuals.

Table 1. Diameter classes, relative values, importance values and average diameters of the woody overstory species in the bur oak groves of Ford County, Illinois.

	Diameter Classes (cm)							*Basal*				*Average*
							Total	*Area*	*Relative*	*Relative*		*Diameter*
Species	*25–40*	*40–59*	*60–79*	*80–99*	*100–119*	*120+*	*#/ha*	*m²/ha*	*Density*	*Dom.*	*IV*	*(cm)*
Beeset Grove — 4.61 ha (11.4 acres)												
Bur oak	5.0	33.6	18.2	2.6	--	--	59.4	15.54	78.7	83.8	162.5	56.7
Shagbark	4.3	9.3	0.7	0.2	--	--	14.5	2.45	19.3	13.2	32.5	45.2
Hackberry	0.9	--	0.2	--	--	0.2	1.3	0.48	1.7	2.6	4.3	55.9
White oak	--	--	0.2	--	--	--	0.2	0.08	0.3	0.4	0.7	66.7
Totals	10.2	42.9	19.3	2.8	--	0.2	75.4	18.55	100.0	100.0	200.0	
Sibley Grove (East Section) — 13.75 ha (34 acres)												
Bur oak	2.4	13.6	11.7	7.0	2.8	1.3	38.8	16.33	98.5	98.5	197.0	69.9
Black walnut	--	0.2	0.1	0.3	--	--	0.6	0.24	1.3	1.4	2.7	75.3
White oak	--	0.1	--	--	--	--	0.1	0.02	0.2	0.1	0.3	51.3
Totals	2.4	13.9	11.8	7.3	2.8	1.3	39.5	16.59	100.0	100.0	200.0	
Sibley Grove (West Section) — 1.62 ha (4 acres)												
Bur oak	5.6	30.9	25.3	8.0	1.9	1.2	72.9	24.37	98.3	98.5	196.8	62.9
Black walnut	--	0.6	0.6	--	--	--	1.2	0.38	1.7	1.5	3.2	62.3
Totals	5.6	31.5	25.9	8.0	1.9	1.2	74.1	24.75	100.0	100.0	200.0	
Wildcat Grove — 4.78 ha (11.8 acres)												
Bur oak	5.7	17.2	19.5	8.6	2.3	1.3	54.6	20.48	98.5	97.4	195.9	65.7
Hackberry	--	--	--	0.2	0.4	--	0.6	0.50	1.1	2.4	3.5	100.8
Black cherry	--	0.2	--	--	--	--	0.2	0.04	0.4	0.2	0.6	46.2
Totals	5.7	17.4	19.5	8.8	2.7	1.3	55.4	21.02	100.0	100.0	200.0	

Sibley Burr Oak Grove Nature Preserve. In the large eastern grove the woody overstory averaged 39.5 stems/ha with a basal area of 16.59 m^2/ha (Table 1). Of the 540 canopy and subcanopy trees recorded, all but eight were bur oaks. The average diameter for bur oak was 69.9 cm dbh, and 170 individuals had diameters greater than 80 cm. Of these, 61 had diameters in excess of 100 cm dbh. Coppice individuals were extremely rare. In the small western grove, overstory density averaged 74.1 stems/ha with a basal area of 24.75 m^2/ha (Table 1). Bur oak dominated, accounting for nearly all of the IV; of the 120 individuals encountered, 118 were bur oaks. Bur oaks averaged 63 cm dbh, with over 71 stems/ha being less than 80 cm dbh. No coppice stems were encountered.

Wildcat Bur Oak Grove. Overstory density averaged 55.4 stems/ha with a basal area of 21.02 m^2/ha (Table 1). Bur oak accounted for nearly all of the IV. Of the 260 individuals of bur oak encountered, 202 were less than 80 cm dbh, and only 17 exceeded 100 cm dbh. Coppice bur oaks averaged 5.6 trees/ha, with an average of 2.19 stems/tree.

Discussion

All of the groves studied had relatively high tree densities, ranging from 39.5 stems/ha in the eastern section of Sibley Grove to 75.4 stems/ha in Beeset Grove. Except for scattered openings where trees had recently died, these groves were closed forests where individual tree crowns usually overlapped. These tree densities are low compared to streamside groves of central Illinois (Boggess and Bailey 1964, Boggess and Geis 1966, Cox et al. 1973, Pelz and Rolfe 1977) where densities averaged 300 stems/ha. Before European settlement these groves on morainal ridges were probably more open. As these groves had wetland communities to the north and west (sloughs and sedge meadows) some prairie fires did not reach the groves, allowing for high litter loads. Fires that crossed these wetlands during drought years resulted in the death of many small diameter bur oaks as well as any thin-barked trees that were present.

Most of Ford County was described in the GLO survey notes of 1823 as "2nd rate prairie, land gently rolling." The occasional grove was usually described as an oak-hickory forest. Other than the mention of an "undergrowth of hazel," no information was given on the understory of these groves. Presently the understory contains many weedy and exotic woody species, the most common being *Prunus serotina* Ehrh. (black cherry), *Crataegus mollis* (Torrey & Gray) Scheele (red haw), hackberry and *Lonicera maackii* (Rupr.) Maxim. (Amur honeysuckle). Sometimes bur oak and hickory reproduction occurs, particularly in canopy openings and at the grove margins. The herbaceous layer is dominated by Eurasian, cool-season grasses along with numerous introduced and weedy annuals and perennials. Occasionally a few native woodland grasses and sedges are encountered, and rarely a few perennial prairie species.

Many of the trees in these groves were established long before European man settled the area. The settlement of Ford County did not begin until the railroads came in the 1860s. The numerous sloughs and sedge meadows of the region presented major drainage and transportation problems, and human diseases helped to make this area very unattractive to settlers. A few dead bur oaks in the groves were cut, and individuals between 85 and 145 cm dbh had from 225 to 330 growth rings.

Conclusions

These bur oak-dominated groves are open, averaging between 39 and 75 trees/ha. Most of the bur oaks have branches or branch scars within 4 m of the ground. In the past fire was undoubtedly responsible for maintaining the open conditions of these groves, as well as the very low species diversity of the canopy. This community type is distinct from the streamside forests and groves of the Grand Prairie Natural Division of Illinois. In the streamside forests and groves, tree species diversity is high, tree densities usually exceed 300 stems/ha, and many thin-bark, fire-sensitive species are important forest components.

Only a few of the groves associated with morainal ridges remain, and these have been highly modified by cutting, fire suppression, and exotic species invasion. Due to the ease of clearing these sites, as well as the very productive soil, 14 groves in Ford County have been cleared since the early 1960s (Robert Reber, personal communication).

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Jon Mendelson

Restoration from the Perspective of Recent Forest History

The woodlands of northeastern Illinois, particularly those associated with the Valparaiso, Tinley, and Lake Border Moraines that encircle Chicago and extend northward through Kenosha and Racine counties in Wisconsin, are extensive, constituting substantial remnants of the original forests of the area.[1] Oak dominated, they are similar in species composition from north to south. The soils that developed under them, principally the alfisols Morley and Blount silt loam, are also widespread, extending from Indiana well into southern Wisconsin (Hole 1976, Mapes 1979). These woodlands typically occupy north- and east-facing morainic slopes, and, as has often been noted, they are best developed on the east sides of streams (Gleason 1909, Woodard 1925, Bowles et al. 1994). Perhaps the large amount of forest in the area is related to the north-south orientation of many of its rivers, including the DuPage, the DesPlaines and the North Branch of the Chicago.

As Cowles (1901) pointed out almost a century ago, the landscapes occupied by these woodlands are among the most dynamic in the region. It is here that post-glacial stream dissection and the consequent maturation of drainage basins is most advanced. This maturation is expressed in the ravine topography characteristic of these woodlands, the "broken" lands of the Public Land Survey notes, and is largely a function of the interplay of forest and stream in these landscapes. The forest, once established, provides a land surface more conducive to stream development than does prairie sod. Resulting channel

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[1] I am using the terms "woodland" and "forest" interchangeably, not as distinct community types separated on the basis of density, canopy closure, basal area, etc. There is some question as to the value of making this distinction for northeastern Illinois woodlands.

lengthening and valley widening provide not only avenues for forest advance, but an increasingly diverse set of interior forest habitats, ranging from floodplain and terrace, to mesic ravine slopes, to dry uplands and wet depressions as yet unaffected by stream dissection.

It is this assemblage of woodlands, all recognizably similar in physiognomy and composition but each subtly different from the others, that has become the principal target of restoration efforts during the last decade.

Forest History

Because forested landscapes, alone among terrestrial communities, have a readable history, we have the unique opportunity to place ecosystem processes in an historical context. This history can be read not only in Public Land Survey descriptions, but in tree rings, in fire scars, in changing species composition between canopy and understory, in size and age distributions. The meticulous reconstruction of Henry and Swann (1974) is an example of what can be done in this regard. Other studies in forest history are reviewed in Peterken (1996). Beyond the inherent value of such studies, it is critical for those of us interested in the morainic forests of northeastern Illinois to devote more time to their history, to understanding the forces that shaped them, and to the expression of these forces in the present-day forest. I say this because I believe the existing assumptions about forest history, the assumptions that are presently guiding restoration activities in these woodlands, are simplified at best, badly flawed at worst.

Pre-settlement History

First, I think we need to reevaluate some of our assumptions about historic disturbance patterns in northeastern Illinois. To begin with, we need to analyze critically the idea that these woodlands have some evolutionary relationship to fire, that they have "evolved [with fire] over the eons" (Packard 1993:8). As Hunter (1996) has pointed out, the time period since deglaciation, ~12,000 years, is not long enough for the evolution of species, no less the community-level evolutionary response to fire that has been suggested. Griffin (1994) makes the same point in reference to the origin and development of savannas about which similar evolutionary claims have been made. Moreover, the data that supports the frequent recurrence of fire is entirely anecdotal. We have no information on fire scars from the few pre-settlement trees still present in these woods. Fire or its effects are rarely mentioned in the Public Land Surveys, even though most were conducted in pre-settlement times in this region. Perhaps we need to approach the question of disturbance regimes from the perspective of the pre-settlement forest itself. For example, unpublished data on the size distribution of witness and line trees, 79 in all, from the 1834 Survey of Thorn Creek Woods in Will County, one of these morainic woodlands, includes individuals ranging in size from 7" (17.5 cm) to 24" (60 cm) in dbh, with all intermediate sizes represented. This distribution suggests an all-aged forest existing on the site prior to settlement. Anderson and Anderson (1975) found the same pattern in the forests of Williamson County in far southern Illinois. The implication of an all-aged structure is continuous recruitment, and this, in turn, suggests low levels of disturbance during what appears to be a relatively long period of forest establishment. Clearly, these results are preliminary, but I think they are sufficiently at variance with established conceptions of pre-settlement fire-frequency, conceptions that are driving present day restorations in these same woodlands, that the whole subject might profitably be revisited.

Although we have much to learn about pre-settlement conditions, I believe we should focus most of our attention on post-settlement forest history, agricultural history, patterns of land use in the forest in the 160–170 years since settlement. These topics are more mundane perhaps than the romance of a pre-settlement Eden, but they are, at the same time, more germane to the organization of the forest we now see. The post-settlement agricultural period in northeastern Illinois has in recent years come to be characterized as nothing more than a misguided era of fire suppression (Packard 1993). By doing so, we have ignored two other factors—logging and grazing—whose impact on these forests was of equal or greater significance during the same period and whose long-enduring effects explain much about the structure of today's woodlands.

Logging

The trees of the pre-settlement forest, with few exceptions, are gone from northeastern Illinois woodlands. Most have been logged off, probably within the first eighty years or so of settlement. The principal legacy of logging, presumably in concert with early fire suppression, has been the emergence of the even-aged canopy we see in these woodlands today, a canopy composed almost exclusively of post-settlement trees or those of immediately pre-settlement origin. Cowles' (1901) photographs of typical morainic woodlands show two of these even-aged, second-growth stands as they appeared almost 100 years ago (Figures 1 and 2). At the present time, this canopy, whose success was made possible by the removal of the original forest, is now in full maturity region wide, approaching old-growth status in age.

Early plats show that many of the larger woodlands—Thorn Creek, Plum Creek and Messenger Woods in Will County, for example—were subdivided into numerous small (10–25 acre) woodlots owned by prairie farmers (Figure 3). A similar pattern was found in La Salle County, Illinois (Fuller 1923). Differences in the degree to which these woodlots were harvested created a mosaic of disturbance in these forests. Adjacent woodlots, for example, may have had wholly different histories of exploitation. The imprint of these differences are still detectable in present-day forests.

The implications of the post-settlement origin of our woodlands goes beyond simply the replacement of one generation of trees by another. There has most certainly been an increase in tree density, for example, even in the larger size classes, and with that, a change in tree form, individuals developing a straighter, more forest-grown shape. Restoring the pre-settlement woodland is impossible: the pre-settlement forest is gone. It is not there to be restored. The real management issue is whether it is desireable, or even possible, to recreate a pre-settlement facsimile from the existing forest, given the changes that have occurred.

Grazing

The effects of grazing on these woodlands have been equally profound and equally overlooked. Dairy farming in northeastern Illinois was restricted to morainic landscapes, the very same landscapes that supported extensive tracts of forest (Duddy 1929). I think we have underestimated the ubiquity of grazing in these woodlands. In 1925, for example, just prior to the period of rapid

Figure 1. An even-aged post-settlement stand in 1901. The trees appear to be about 40 to 50 years old. Only the stump in the foreground and possibly the larger tree in the upper left remain from pre-settlement times. Beverly Hills is in southwestern Cook County. Photo courtesy of the University of Chicago Press.

decline in regional agriculture, 92% of 23,000 acres of woodland in Cook County had been or was being grazed; similar percentages were recorded for DuPage, Lake, and Will Counties (Telford 1926, Duddy 1929). A survey of 430 northern Illinois farmers taken during this same period revealed that over 90% grazed their woods (Telford 1926).

The effects of livestock grazing in woodlands are varied, depending on the intensity and duration of the practice. These include soil compaction, which in extreme conditions results in stag-headed trees, and the replacement of the woodland herbaceous layer by bluegrass sod, Canada thistle, and other alien invaders. The stages of forest degradation under increasingly severe grazing pressure were outlined by DenUyl and Day (1939). The subject was recently revisited by Dennis (1997). One result emerges above all others: protracted grazing results in the elimination of the existing woody understory (Figures 4 and 5) and in the cessation of woody plant recruitment (Marks 1942, Dambach 1944, DenUyl 1962). Fuller and Strasburgh (1919:271) concluded that, as a result of grazing "... not over 5% of the oak and bottom forests show reproduction in progress" in La Salle County, Illinois. In the present-day forests of northeastern Illinois the most striking imprint of past grazing is the gap in the size distribution of virtually every species of tree in these woodlands (Men-

Figure 2. Another even-aged stand in 1901. Note the high stem density and the straight, slender forest-grown form of the trees. The tree on the left with the crooked trunk may be the only pre-settlement survivor. Photo courtesy of the University of Chicago Press.

delson 1994). The gap represents the period when, as a result of grazing, tree recruitment essentially ceased.

Recovery of the forest presumably also depends on the previous duration and intensity of utilization. Complete recovery may be slow. Curtis (1959:154-5), who suggests that soil compaction might be the most damaging and the most permanent effect, mentions a lightly grazed red oak stand protected from cattle in 1932 whose recovery was still incomplete 25 years later. It is in this recovery phase that the woodlands of northeastern Illinois are today, and the degree to which they have recovered is inversely proportional to the severity of past disturbance.

Recovery

The most direct response to the cessation of grazing has been the explosive growth of the understory of these woods, beginning in the 1920s with the regional decline in agriculture. The understory that has emerged is clearly delimited from the older, canopy generation by a spatial gap: middle-sized trees of middle-age are largely absent from these woods. The regeneration of the forest which this understory represents may, at first glance, appear chaotic. We have been made all too aware of its less desirable aspects, particularly the inclusion of non-native, sometimes aggressive elements like buckthorn, multiflora rose, honeysuckle,

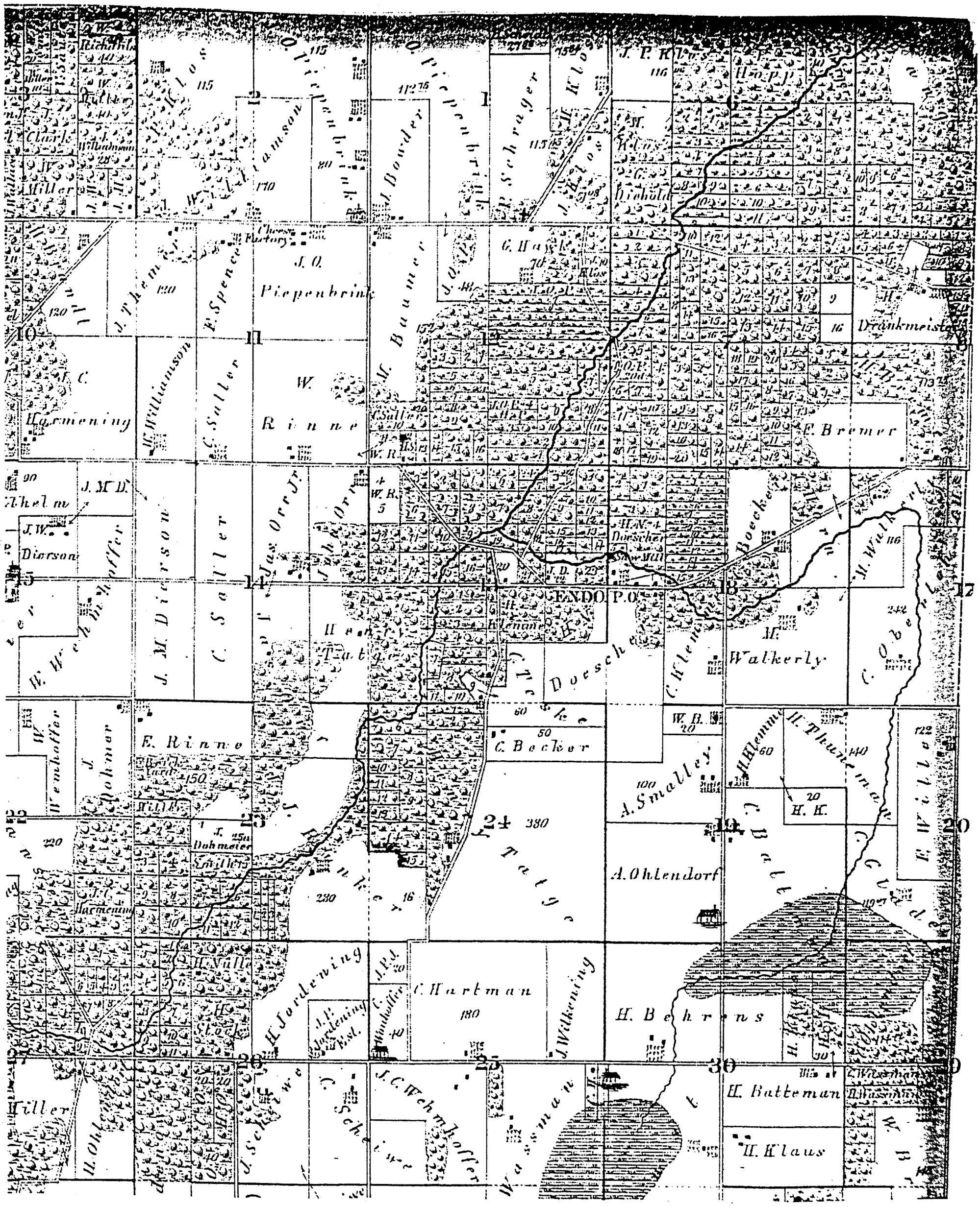

Figure 3. 1873 plat of the northeastern portion of Crete Township, Will County, Illinois, showing the forest along Plum Creek subdivided into many small woodlots. Note the sawmill in the northwest quarter of section 18. The map is from the Atlas of Will county published in 1873 by Thompson Bros. and Burr.

Figure 4. This photo is from "A Manual of Woodlot Management" by C. J. Telford, published in 1926. The woodlot is located in northern Illinois. Photo courtesy of the Illinois Natural History Survey.

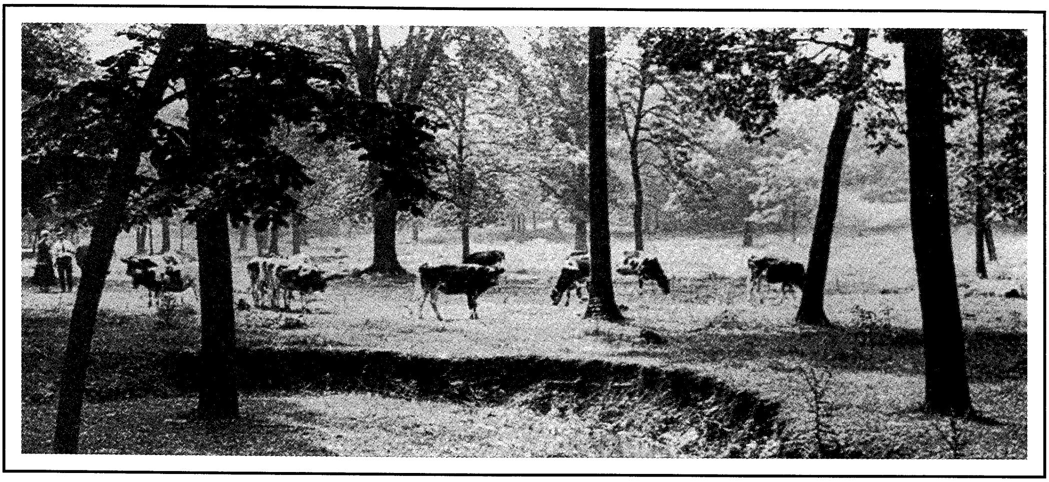

Figure 5. Grazing continued in some forest preserves even after acquisition. This photo is from 1921. Deer Grove Preserve is located in northwestern Cook County. Note the browse line in the background and the virtual absense of understory. The plants in the right foreground appear to be Canada thistle. Photo courtesy of the Cook County Forest Preserve District.

and others in the emerging community. The distribution of most of these alien species, however, seems closely associated with the degree of past disturbance: to a large extent, they have invaded the most disturbed sites, those which are also slowest to recover. Moreover, most of the aliens are shrubs or small trees. None have the capacity to become part of the upper canopy. Species having canopy-forming potential in these woodlands are all native, and all are participating to various degrees in forest regeneration. The early stages in the recovery from grazing are, first, the spread of existing thorny or unpalatable species, of which hawthorn is usually most prominent, which is followed by the arrival of light-seeded and bird-disseminated tree species: ash, slippery elm, sugar maple, basswood, and black cherry, among others. Oaks generally appear later in the process (Den Uyl and Day 1939, DenUyl 1962). This sequence seems to describe very well the pattern of species appearance in northeastern Illinois woodlands, where white ash, slippery elm, and black cherry are frequently found beneath a much older, oak-dominated canopy, and where once vigorous stands of hawthorn are already in decline. The spread of sugar maple from ravine enclaves onto the more mesic of upland sites has been widely commented upon. Maples are still largely absent from dry uplands, which are equally open to invasion, suggesting that edaphic factors, particularly available soil moisture, may be limiting. A recent reexamination of Illinois Natural Areas Inventory sites originally sampled in 1976 indicates an increase in sugar maple in the smallest size class on oak-dominated sites, but virtually no growth into larger size classes during the last 20 years (Bowles et al. 1998*a*).

Why oaks are slow to reestablish in previously grazed settings is not clear. It would seem to be related in part to soil compaction, the most persistent legacy of grazing, and its effects on germination and seedling establishment. Certainly the extreme sensitivity of mature oaks in northeastern Illinois to soil compaction, as witnessed by their high mortality rates around construction sites, has been ajmply demonstrated (Ware and Howe 1974).

There seems to be fairly general agreement that oak populations can be self-sustaining on dry sites (Clark et al. 1996, Fralish, 1997). This seems to hold true for northeastern Illinois woodlands as well, especially where grazing appears to have been light. For example, at the Illinois Natural Areas Inventory (INAI) site in Thorn Creek Woods (Bowles et al. 1998*b*), an area that was apparently lightly grazed and has no history of fire, oak seedlings were present in numbers estimated between 2,500 and 6,500/ha.

In places we see the beginnings of an all-aged structure in these woodlands, with the establishment of a variety of canopy species, including oaks, beginning perhaps 60–70 years ago and continuing today.

These are only a few of the many changes that have come about since the cessation of grazing, changes that are still unfolding, and about which we still have much to learn. To dismiss these complex developments as nothing more than forest deterioration due to fire suppression is a misreading of the past.

Restoration

Such a misreading would be of only academic interest were it not the main justification for restoration efforts in these woodlands, efforts aimed almost exclusively at altering or removing the understory, at reversing the degradation that this outpouring of vegetational energy is supposed to represent. At first, reintroducing fire, the process under which these woodlands allegedly evolved, was the principal method employed. Now, woody species in the understory are routinely cut or girdled first, and then treated with herbicide, usually prior to the application of fire. The latest device to come into use is the Seppi mower, a variant of the brush hog, which leaves a litter of wood chips, and almost certainly compacts the soil of the forest floor, mimicking, in an ironic way, the hooves of cattle. Lack of a sufficient fuel load, and hence the inability of these woodlands to carry a fire hot enough to do its job, is usually offered as the explanation for employing these increasingly severe methods of control. Species that are removed include not only aliens like buckthorn and honeysuckle, but many natives as well: ash, elm, black cherry, sugar maple, and basswood. Most of these are early colonizers after the cessation of grazing.

Reintroducing chronic disturbance into these woodlands has had some unpleasant results. One is the reappearance of species that thrived under heavy grazing. White snakeroot, which can form virtual monocultures in restored woodlands, is an example (Marks 1942). More alarming is the recurrence in restored woods of some of the most pernicious agricultural weeds: Canada thistle, burdock, and mullein among others. This is particularly evident in parts of Swallow Cliff Forest Preserve, Cook County's currently most ambitious restoration. These species are found only in the most degraded of woodland pastures and are eventually eliminated as the forest recovers. They are never part of a healthy woodland flora. Thus in many cases, we appear to be replacing what have been deemed aggressive woody species, including many natives, with equally aggressive herbaceous ones. This is not surprising: with disturbance-based management come disturbance-adapted species, and many of these are aggressive competitors.

It has been suggested that garlic mustard, the latest scourge of our woodlands, also may be favored by disturbance-based management (Anderson et al 1996). Frequency of garlic mustard was significantly higher in burned INAI sites than in those that had not experienced fire management (Bowles et al. 1998*a*). Fire may open seed beds, thus facilitating the spread of this species.

More dangerous than the spread of undesirable species, a process which presumably would be reversed with the cessation of disturbance, is the permanent effect restoration is having on forest structure. Under current management practices, we continue to widen the age gap between an increasingly elderly canopy and what will forever be an immature understory. We are, in other words, prolonging the even-aged condition which itself is an artifact of post-settlement logging and grazing. This takes on particular significance when we consider that some canopy species, notably red and black oak, may be approaching, at 150–180 years of age, the end of their life span. If oak reproduction is not enhanced by current management—there is yet little evidence that it has been—and we continue to remove almost every other native tree species, we may be having impacts on these woodlands more damaging and more permanent than those of the preceding agricultural period. These unexpected effects are the result of our one-dimensional interpretation of recent forest history, and our failure to take into account the sequence of changes that follow the removal of livestock from the land.

I think it is fair to ask, therefore, whether it is wise to continue to impose disturbance-based management on woodlands that have so recently emerged from a long post-settlement period of disturbance. After all, in their entire post-glacial history, these woodlands had never before been cut. Nor had they experienced as intense a period of grazing as they have since settlement. Given this history, might it not be equally appropriate to let biotic interactions, particularly interspecific competition, in this emerging forest determine ultimate forest structure? If so, then management should emphasize stability and reduce chronic abiotic disturbance. The successional trajectory under these conditions may never return us to pre-settlement structure or composition. But then, neither will current management practices: these forests have gone too far down a different road. What we will have, if we manage for stability, are all-aged woodlands, woodlands with greater species diversity in the canopy than we see at present, woodlands that have developed under the natural disturbance regime of this time and place.

Acknowledgments

I would particularly like to thank Judith Dolan Mendelson for sharing her many insights into forest ecology. Thanks also to John Yunger and Nina Mendelson for helpful comments on this manuscript, to Marlin Bowles for graciously providing unpublished data, and to Steve Aultz, Dave Mauger, Tim Bell, and Jim Marzuki, all of whom have influenced my thinking about northeastern Illinois woodlands. Thanks, too, to Dick Burd, Larry Lewis, and Suzanne Oliver for preparing the figures, and to Nancy Shlaes for guiding me through the intricacies of modern literature searches.

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Gradient Responses for Understory Species in a Bracken Grassland and Northern Dry Forest Ecosystem of Northeast Wisconsin

Abstract *Spread Eagle Barrens, located in Northeastern Wisconsin, occupies an area of pitted outwash created during the late Wisconsin glaciation. This irregular topography forms a heterogeneous landscape influencing both site characteristics and associated plant communities. Today the dominant plant communities, which often occur in a mosaic pattern, consist of both bracken-grasslands and northern dry forests. It is in this landscape that we investigated the distribution and position of 35 groundlayer species along six environmental gradients and one competitive gradient. These include slope position, site severity index, canopy, soil nutrient index, organic matter, pH, and bracken fern frond densities. The presence or absence of each species, along with environmental data, were recorded in random 1 m² quadrats placed throughout the Sand Lake Region. Probability responses of individual species along measured gradients were then determined through logistic regression. Response shapes of species across gradients were often non-linear, with both quadratic and cubic functions being common. Results indicate that topoedaphic factors, canopy and bracken fern all influence species distributions. Overall, however, canopy was the single most important gradient examined. Bracken fern frond densities also showed strong significance for many species indicating the important role it plays on the landscape. Additionally, as predicted by competition theory, bracken fern was also found in the center of environmental gradients where the strongest competitors are thought to dominate.*

Savannas are one of the most extensive and socioeconomically important ecosystems on the planet, covering over 18 million km^2 or 14% of the earth's surface (Botkin et al. 1984, Perry 1994). In Wisconsin one type of savanna, called pine barrens, once occupied a large portion of the state covering over 947,000 ha at the time of European settlement (Curtis 1959). Today, however, many of our native Midwestern savanna communities are rare (Nuzzo 1986) due to fire suppression and associated woody encroachment (Abrams 1992). The situation for pine barrens in Wisconsin is no different. Only about 20,000 ha currently remain of both oak and pine barrens (Mossman et al. 1991).

Two distinct forms of pine barrens can be recognized based on the groundlayer composition, perhaps reflecting soils, topography, and location to tension zone (Vogl 1970). The first type, prairie-like barrens, tend to occur in coarse sands, gentle topography, and are geographically close to prairies. The second type, non-prairie barrens, tend to occur in loamy sands and sandy loams, have more topographic variability, and are relatively isolated from prairies or the tension zone. The latter community, which rarely has received attention, also includes that which has been referred to as depauperate bracken-grasslands (Vogl 1964*a*). These bracken-grasslands were initially assumed to be secondary communities in Wisconsin resulting from logging and fire. However, based on both ecological studies of northern Wisconsin (Curtis 1959, Vogl 1964*a*) and European records, it appears that the bracken-grassland community was indeed part of the state prior to settlement, although in relatively small coverage. It since has expanded due to anthropogenic causes.

Today, these bracken-grassland communities are often integrated into a mosaic of other communities in northern Wisconsin, particularly northern dry forests. In some instances, many can even attain the appearance of an aspen parkland, with the dominant woody species being aspen (*Populus tremuloides* and *P. grandidentata*). Once bracken-grasslands are established, they are fairly resilient and do not appear to require fire for their maintenance (Vogl 1964*a*), unlike other savanna communities of the Midwest (Bray 1955; Curtis 1959; Vogl 1964*b*, 1970; Kline and Cottam 1979; Grimm 1984; Haney and Apfelbaum 1990; Leitner et al. 1991; Abrams 1992). Possible mechanisms responsible for this maintenance are competition and microclimate.

Competition between tree seedlings and bracken fern may inhibit or limit succession (Curtis 1959, Vogl 1964*a*). Bracken fern (*Pteridium aquilinum* L. Kuhn), which is the most widely distributed plant in the world (Page 1982), has an excellent ability to compete for moisture, nutrients, and light. In addition to direct competition for resources, bracken fern can also inhibit plant establishment and growth through allelopathy (Ferguson and Boyd 1988). Bracken fern rhizomes also quickly invade or re-establish following disturbance (Conway 1952). Many of the bracken-dominated systems of the world today are associated with disturbances such as fire, timber harvesting, or grazing. In Finland, Oinonen (1967) was able to positively correlate clone sizes of bracken fern to time of last fire, with ages of clones going back to the years of 1300 (old fortress at Sulkava) and 1318 (Turku raided) and clone sizes exceeding 200 m in diameter.

The second factor potentially influencing the stability of bracken-grasslands, at least in Wisconsin, is the microclimate (Curtis 1959, Vogl 1964*a*). In many areas where bracken-grasslands dominate, the landscape (pitted outwash) promotes drastic changes in temperature, including the frequent frost formation as a result of cold air drainage and re-radiation (Figure 1, Table 1). These frosts

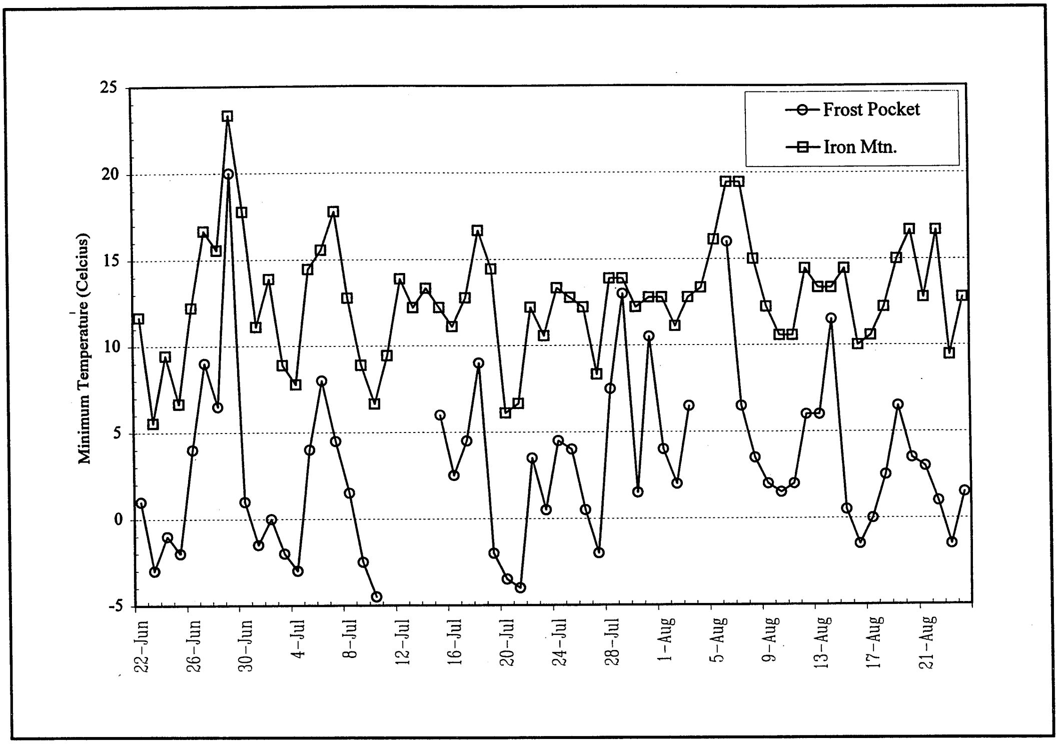


Figure 1. Minimum temperature patterns between a kettle (frost pocket) at the study site and nearest (*c.* 6 km) weather station (Iron Mountain) for the summer of 1996.

may then be referred to as a form of disturbance, which restricts recruitment of woody species in low areas of the landscape. Interestingly, bracken fern is also frost sensitive and restricted from the low kettles and valleys (Nielsen 1997). Therefore, bracken fern itself cannot influence the relative openness and stability of frost pockets (Vogl 1964*a*). It is likely that both competition and extremes in temperature exert an influence, with bracken fern competition acting according to an inhibition model of succession (Connell and Slayter 1977) and the microclimate functioning as a factor influencing recruitment based on frost sensitivity.

Because bracken-grasslands have rarely been studied (however, see Vogl 1964*a*), particularly in relations to the surrounding communities, first understanding which species are present to an area and why, may prove essential in understanding the communities' origins, ecology, and possible future management. In other Midwest savannas, variables such as soils, topography, and canopy have been found to be important determinants of species distributions (Bray 1958, Ware et al. 1992, Leach 1994, Pruka 1994, Hujik 1995). It is our objective here to determine patterns of plant species distributions along the major environmental gradients of canopy, soil organic matter, pH, soil nutrient index, slope position, and site severity index. Additionally, since the importance of bracken fern in this system may be quite substantial, responses of plants to densities of bracken fern fronds are examined.

Table 1. Minimum temperature (°C) patterns for Iron Mountain Weather Station and two data loggers located in a frost pocket and ridge top at approximately a 30 m difference in elevation. Data loggers were located at a 0.5 m height and placed out between 22 June and 24 August of 1996 (n = 58).

Statistic	*Frost Pocket*	*Ridge Top*	*Iron Mtn. Weather Sta.*
Mean*	3.1 [a]	8.3 [b]	12.7 [c]
Standard Error	0.7	0.6	0.6
Median	2.3	8.5	12.8
Minimum	- 4.5	- 0.5	5.6
Maximum	20	22	23.3
Number frosts	16	3	0

*Means ±SE are not significantly different if labeled with the same letter

Methods

Study Site

Field research was conducted at Spread Eagle Barrens State Natural Area, located c. 7 km southeast of Florence, Wisconsin (45°52′N, 85°10′W). This landscape size Natural Area occupies 3,580 ha, being bordered by the Menominee River to the east and approximately dissected in half by the Pine River. An ecological classification of the site in *Ecoregions of North America* (Bailey and Cushwa 1981) identifies Spread Eagle Barrens as a humid temperate domain, humid warm-summer continental division, and Laurentian mixed-forest province. The climate of the area is intermediate between lake moderated and continental, with a mean annual temperature of 5.2°C and a median frost-free period of 113 days. Mean annual precipitation is 739 mm with an average annual snowfall of 1,595 mm.

Elevations of the study area range from 385 to 320 m and form a distinct hummocky appearance. This topographic variation, called pitted outwash, was caused by collapsing sediment of proglacial streams deposited on stagnant glacial ice (Hadley 1976, Clayton 1986). The glacial advance responsible for this formation has been aged at approximately 12,300 years ago and is called the Early Athelstane Advance. This is a Silver Cliff member of the Kewaunee Formation of the late Wisconsin glaciation (Clayton 1986). The depths of these Pleistocene sediments vary from 76 m around Sand Lake to 16 m near the Menominee River. Soils are Spodosols with textures varying from sandy loams to loamy sands and characterized by a low pH (μ = 4.87 SE ± 0.02).

Historically, prior to European settlement, Spread Eagle Barrens was dominated by *Populus tremuloides* (quaking aspen), *Pinus banksiana* (jack pine), and *Betula papyrifera* (white birch) (Table 2) (Nielsen 1997). Today, however, many of the sites have been converted through management (logging and prescribed burning) to large homogenous bracken-grasslands, originally intended to optimize habitat for sharp-tail grouse. One region that escaped much of this management is the area surrounding Sand Lake. This area still maintains a rich mosaic of northern dry forests and bracken grasslands, perhaps because a wildfire swept the area in the late 40s or early 50s. Research was concentrated in the area surrounding Sand Lake because the existence of bracken-grasslands was not a function of management and because of the large variability there in site characteristics and competition across the landscape. In that vicinity we could investigate species responses to the landscape variables without having to account for recent management related effects.

Table 2. Numbers and frequencies of witness trees for Spread Eagle Barrens, listed by common names and Linnaean taxanomic equivalents.

Common Name	*Scientific Name*	*Total Witness Trees*	*# Survey Points*	*Survey Point Frequency*[a]
Aspen	*Populus tremuloides* or *Populus grandidentata*	40	25	44.6
White birch	*Betula paperifera*	26	17	30.4
Jack pine	*Pinus banksiana*	28	16	28.6
Red pine	*Pinus resinosa*	9	8	14.3
White pine	*Pinus strobus*	9	6	10.7
Spruce[b]	*Picea glauca* or *Picea mariana*	8	3	5.4
Maple[c]	*Acer saccharum* or *Acer rubrum*	1	1	1.8
White cedar	*Thuja occidentalis*	1	1	1.8
Oak	*Quercus ellipsoidalis*	1	1	1.8
Total		**123**		

[a] Survey point frequency represents the frequency of tree species to survey point. Since the survey points had between 2 and 4 witness trees, the sum of the frequencies exceed 100%.

[b] It appears that the surveyor did not distinguish between *Picea glauca* and *Picea mariana.*

[c] It appears that the surveyor did not distinguish between *Acer saccharum* and *Acer rubrum.*

Field Methods

In investigations dealing with distribution patterns of populations, a systematic grid design may allow for greater precision in analyses (Brown and Ruthery 1993). Therefore, in the summer of 1996, within the Sand Lake region of Spread Eagle Barrens, six 250 m^2 cells were randomly selected from an overlaying grid on a United States Geological Service 7.5 minute quadrangle. Within each of these six cells, 50 random observation points were chosen for sampling, producing a sample size of 300. Sites were sampled once between the dates of July 10th and August 20th of 1996. Each sample consists of a 1 m^2 circular herbaceous quadrat centered over the random position previously determined. Within this quadrat all living ground-layer plant species (<1 m height) were recorded for presence or absence based on taxonomy following E. G. Voss (1972, 1985, 1996). Along with plant presence or absence, the number of live bracken fern fronds was counted within each quadrat. To determine canopy coverage of a site, the line intercept method was used over a 10 m transect, which was centered over each quadrat (Haney and Apfelbaum 1994). In this method, a vertical plane was projected from the transect with the starting and stopping positions of tree species recorded.

Soil characteristics of each sample point were based on a composite soil sample from around each quadrat by combining four soil cores, each being 2 cm x 15 cm in size, from the major cardinal sectors of the quadrat. Samples were analyzed by the University of Wisconsin-Marshfield Soil and Forage Analysis Laboratory for organic matter, pH, P, K, Ca, and Mg. For the cations (P, K, Ca, and Mg), an index (nutrient index, NI) was created in order to reduce both the number of variables and the multi-collinearity between variables. This was done by ranking (ascending) each soil variable and summing the rank values.

The influence of topography was addressed by two complex gradients. The first is an index relating aspect and slope to incoming solar radiation. In both temperate and boreal zones, both aspect and slope combine to influence vegetation patterns caused by differences in solar radiation. Solar radiation has not only been found to influence vegetation patterns (Haase 1970, Fralish 1988, Bonan and Shugart 1989), but also soil moisture and forest productivity (Beers et al. 1966). Therefore, an index was created for this study called "site severity index" (SSI), which takes into consideration both aspect and slope, thereby representing the amount of direct solar radiation and heating of a site in relation to flat surface.

This index was modified from one created by Beers et al. (1966), which is based on a sine wave varying according to aspect. This gave maximum values for northeast slopes (productive forests) and minimum values for southwest slopes (unproductive forests). Other studies within the Midwest (Ware et al. 1992, Thomas and Anderson 1993) have used this function to investigate the influence of aspect on vegetation. In this study, however, the Beers' equation was modified so that a southwest slope received the highest value and a northeast slope the lowest, while being scaled between +1 and -1, representing xeric to mesic sites respectively. In addition, the function was scaled to take into account the amount of slope. As slope decreases from a high of 45%, the wave dampens toward zero, representing a flat surface. In the field, slope was recorded with a clinometer, while aspect was determined with a compass. Using these values, the site severity index was determined through the equation $SSI = \sin(A + 225) \times (\%\ slope/45)$, where A represents degrees from polar north and % slope from horizontal.

The second topographic variable examined was slope position. For this, each sample location was placed into one of six slope positions based on a visual inspection of the landscape. Slope position categories were as follows: frost pockets and valley bottoms (5), lower one third of slopes (4), middle one third of slopes (3), upper one third of slopes (2), narrow ridge (< 50 m wide) (1), and lastly a broad ridge or plain (> 50 m wide) (0).

Statistical Analyses

To determine species responses along examined gradients, logistic regression was used on presence/absence data of common (>10% frequency) ground-layer species in 1 m^2 quadrats (Appendix A). The logistic regression statistic is similar to linear regression except that the dependent variable (Y) is binary (1 or 0, hence present or absent) instead of continuous (Sokal and Rohlf 1995). Logistic regression then relates the proportions of a dependent variable to an independent variable. This independent variable can be continuous or discontinuous. Significance was considered at the level of $P < 0.10$ for the chi-square statistic. The modeling technique used here is one variant of GLM (general linear modeling) and is similar to analyses of *Eucalyptus* species in Australia by Austin et al. (1990).

For logistic regression modeling, a total of 34 species were tested in order across all six gradients of interest (canopy, NI, soil organic matter, pH, slope position, and SSI). In addition to the standard linear responses, which represent an increase or decrease in probability of that species across a variable, additional combinations were tested by adding quadratic and cubic functions. The quadratic function would indicate a Gaussian or Normal distribution, which is expected in ordination analyses. This type of response has been called Gaussian logistic

Table 3. Gradient partitions used for determining patterns of species optimal responses across examined gradients of topoedaphic factors, bracken fern (a), and canopy (b).

[a] Gradient Variable	Low	Mid	High	[b] Community Classification	Canopy Interval (%)
Soil O.M.	<2.6	2.6–4.0	>4.0	Forest	>85
Soil pH	<4.9	4.9–5.6	>5.6	Woodland	<85–>50
NI	<28	28–46	>46	Savanna	<50–>1
SSI	<-0.34	-0.34–0.34	>0.34	Grassland	<1
Slope position	4,5	2,3	0,1		
Bracken density	<9	9–18	>18		

regression (GLR) by ter Braak (et al. 1986). The cubic function would verify a more complex response, such as bimodal distributions. All gradients were examined for each species in histograms, in order to determine if these higher order functions were appropriate in the logistic model.

After modeling, probability responses for every significant species were plotted across the selected gradient. These gradients were then subjectively divided into sections to determine guilds of species (Table 3a). For these divisions, canopy was the only variable that was not segmented into equal proportions, in order to correspond to existing abstract community definitions based on canopy amounts (Table 3b). Since species are responding across gradients in a continuum fashion, these segmented divisions are to be used only for generalizations.

Results

Canopy

The canopy variable examined was the most important gradient overall, as determined by chi-square significance tests. All 34 species examined showed significant responses to this inferred light gradient. The majority of species response models were linear, followed by quadratic, and finally cubic functions (Table 4, Figure 2a). Along this gradient, four main segments were arbitrarily stratified for determination of optimal position according to community classifications following canopy amounts. Most species modeled were forest species, followed by the grassland guild, woodland guild, and savanna guild. The species that optimized their probabilities in the canopy range associated with the savanna classification include *Apocynum androsaemifolium, Comandra umbellata, Comptonia peregrina, Prunus pumila,* and *Vaccinium pallidum* (Table 5).

Nutrient Index (NI)

Nutrient Index represents the combinations of the relative ranks of available nutrients P, K, Ca, and Mg. This was the least predictive gradient in describing species responses; only 14 species were significantly related to it (Table 4). Of the significant models, most were linear, followed by a few quadratic, and only one cubic function (Figure 2b). Optimal positions tended to occur at the high end of the nutrient index, with a few in the middle and a few at the low end (Table 5). One of the species that optimized low nutrient sites, *Comptonia peregrina,* is a non-Leguminosae nitrogen fixer and perhaps an important early

Table 4. Functions used in logistic regression analyses of species along each gradient. Significance of each model is indicated as a subscript in each function.

Species	Canopy	Nutrient Index	Organic Matter	pH	Topographic Position	Severity Index	Bracken Densities
Acer rubrum	^{c}C	^{a}N		$^{a}P+P^{2}$	$^{c}T+T^{2}$		$^{c}B+B^{2}+B^{3}$
Agropyron trachycaulum	^{c}C			^{c}P	$^{c}T+T^{2}$		$^{c}B+B^{2}+B^{3}$
Amelanchier spp.	^{a}C	$^{a}N+N^{2}$					
Anemone quinquefolia	^{c}C		$^{b}O+O^{2}$		$^{b}T+T^{2}$	^{a}S	^{b}B
Apocynum androsaemifolium	$^{c}C+C^{2}+C^{3}$			^{b}P	$^{b}T+T^{2}+T^{3}$	^{a}S	^{c}B
Aster ciliolatous	^{c}C	^{a}N	$^{a}O+O^{2}$	^{c}P	$^{b}T+T^{2}$	^{a}S	
Aster macrophyllus	^{c}C	^{c}N	^{a}O	$^{a}P+P^{2}$	$^{c}T+T^{2}$		$^{b}B+B^{2}+B^{3}$
Bromus kalmii	^{c}C		$^{a}O+O^{2}$	^{c}P	^{c}T		$^{c}B+B^{2}+B^{3}$
Calystegia spithamaea	^{c}C				$^{b}T+T^{2}+T^{3}$	$^{b}S+S^{2}+S^{3}$	^{b}B
Campanula rotundifolia	^{c}C		^{a}O	^{c}P	$^{c}T+T^{2}+T^{3}$	$^{a}S+S^{2}+S^{3}$	$^{c}B+B^{2}+B^{3}$
Carex pensylvanica	$^{a}C+C^{2}+C^{3}$			^{b}P			
Comandra umbellata	$^{c}C+C^{2}$			^{a}P		^{a}S	$^{b}B+B^{2}+B^{3}$
Comptonia peregrina	$^{c}C+C^{2}$	^{c}N			$^{a}T+T^{2}+T^{3}$	^{a}S	^{c}B
Corylus cornuta	^{c}C		^{c}O	$^{b}P+P^{2}$	$^{c}T+T^{2}$	$^{c}S+S^{2}$	$^{b}B+B^{2}+B^{3}$
Danthonia spicata	^{c}C		^{a}O	$^{b}P+P^{2}+P^{3}$	^{c}T	^{c}S	^{c}B
Diervilla lonicera	^{a}C				$^{c}T+T^{2}$		$^{b}B+B^{2}$
Gaultheria procumbens	$^{c}C+C^{2}$		$^{a}O+O^{2}$	$^{b}P+P^{2}+P^{3}$	$^{c}T+T^{2}$	$^{b}S+S^{2}$	$^{c}B+B^{2}+B^{3}$
Hieracium aurantiacum	^{c}C		$^{a}O+O^{2}$	^{c}P	^{c}T	$^{a}S+S^{2}+S^{3}$	$^{c}B+B^{2}+B^{3}$
Lysimachia quadrifolia	$^{a}C+C^{2}$				$^{a}T+T^{2}$	$^{a}S+S^{2}+S^{3}$	
Maianthemum canadense	^{c}C	$^{b}N+N^{2}$	^{a}O	$^{a}P+P^{2}$	^{c}T	^{b}S	$^{b}B+B^{2}+B^{3}$
Melampyrum lineare	$^{c}C+C^{2}$			$^{a}P+P^{2}$			
Oryzopsis asperifolia	^{c}C	^{a}N	$^{b}O+O^{2}$	$^{c}P+P^{2}$	^{c}T	$^{b}S+S^{2}$	$^{b}B+B^{2}$
Poa spp.	$^{c}C+C^{2}$	^{a}N		^{c}P	$^{c}T+T^{2}+T^{3}$		$^{a}B+B^{2}+B^{3}$
Polygala paucifolia	$^{c}C+C^{2}$				$^{b}T+T^{2}$	^{a}S	$^{b}B+B^{2}+B^{3}$
Prunus pumila	$^{b}C+C^{2}$		^{b}O	^{c}P	$^{c}T+T^{2}$	$^{c}S+S^{2}$	$^{c}B+B^{2}$
Pteridium aquilinum	^{c}C	$^{a}N+N^{2}$	$^{c}O+O^{2}$	$^{c}P+P^{2}$	^{c}T	$^{a}S+S^{2}+S^{3}$	
Rubus allegheniensis	^{b}C	^{a}N			$^{a}T+T^{2}$	$^{a}S+S^{2}+S^{3}$	
Schizachne purpurascens	^{c}C		$^{a}O+O^{2}+O^{3}$	$^{b}P+P^{2}+P^{3}$	^{a}T		$^{c}B+B^{2}+B^{3}$
Trientalis borealis	^{c}C		^{a}O	^{b}P	$^{a}T+T^{2}$	$^{c}S+S^{2}$	$^{a}B+B^{2}$
Vaccinium angustifolium	$^{b}C+C^{2}$	^{a}N		$^{a}P+P^{2}$	^{c}T		$^{c}B+B^{2}$
Vaccinium myrtilloides	$^{a}C+C^{2}$		$^{b}O+O^{2}$	$^{a}P+P^{2}$			
Vaccinium pallidum	$^{c}C+C^{2}$	^{c}N					
Viola adunca	^{c}C	$^{a}N+N^{2}+N^{3}$		^{c}P	^{b}T	$^{a}S+S^{2}+S^{3}$	$^{c}B+B^{2}+B^{3}$
Waldsteinia fragarioides	^{c}C	^{a}N	$^{b}O+O^{2}$	$^{c}P+P^{2}$	^{c}T	^{b}S	$^{b}B+B^{2}$

Model chi-square = $^{a}P<0.10$, $^{b}P<0.01$, $^{c}P<0.001$

Table 5. Optimal positions for significant species as determined from logistic regression models.

Species	*Canopy*	*Nutrient Index*	*Organic Matter*	*pH*	*Slope Position*	*Severity Index*	*Bracken Densities*
Acer rubrum	100	62		4.8	1		28
Agropyron trachycaulum	0			6.3	5		21
Amelanchier spp.	100	35					
Anemone quinquefolia	100		2.1		3	-1	0
Apocynum androsaemifolium	34			4.2	0	-1	28
Aster ciliolatous	0	62	2.4	6.3	5	-1	
Aster macrophyllus	100	62	5.5	4.7	1		28
Bromus kalmii	0		5.5	6.3	5		0
Calystegia spithamaea	0				0	-1	28
Campanula rotundifolia	0		1.1	6.3	4	-1	0
Carex pensylvanica	69			6.3			
Comandra umbellata	33			6.3		-1	18
Comptonia peregrina	12	12			0	1	28
Corylus cornuta	100		5.5	4.6	1	-0.4	5
Danthonia spicata	0		1.1	6.3	5	1	0
Diervilla lonicera	100				1		28
Gaultheria procumbens	83		3	4.7	0	-0.37	7
Hieracium aurantiacum	0		5.5	6.3	5	-1	11
Lysimachia quadrifolia	100				3	1	
Maianthemum canadense	100	41	5.5	4.7	0	-1	28
Melampyrum lineare	56			4.7			
Oryzopsis asperifolia	100	62	3.5	4.7	0	-0.16	28
Poa spp.	0	62		6.3	5		21
Polygala paucifolia	54				4	-1	9
Prunus pumila	36		5.5	6.3	3	1	0
Pteridium aquilinum	100	35	3	4.5	0	0.04	
Rubus allegheniensis	100	62			2	1	
Schizachne purpurascens	0		5.5	5.2	5		19
Trientalis borealis	100		1.1	4.2	3	-0.59	28
Vaccinium angustifolium	52	12		4.6	0		28
Vaccinium myrtilloides	53		3.4	4.8			
Vaccinium pallidum	28	12					
Viola adunca	0	12		6.3	5	-1	0
Waldsteinia fragarioides	100	62	3.3	4.7	0	-1	28

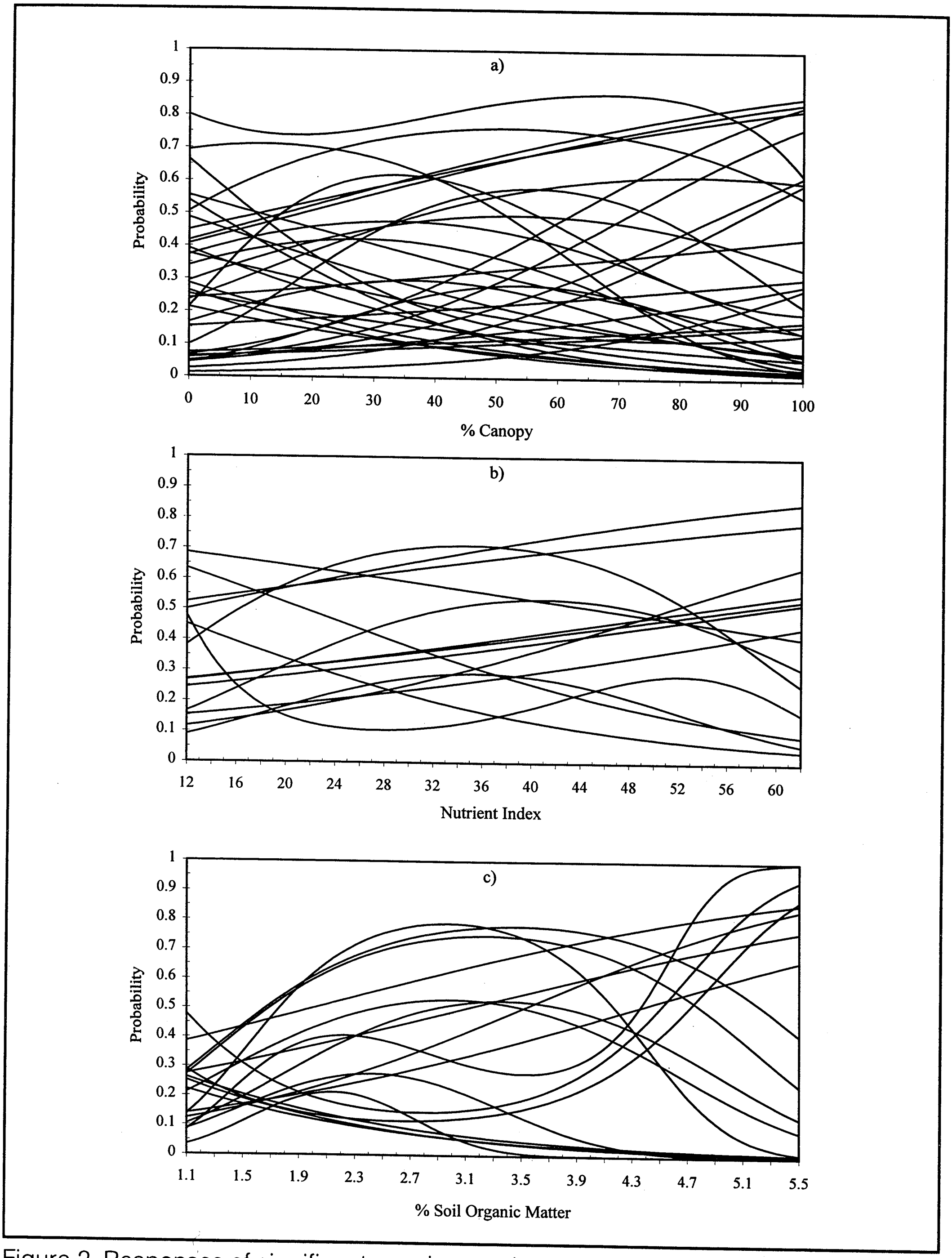
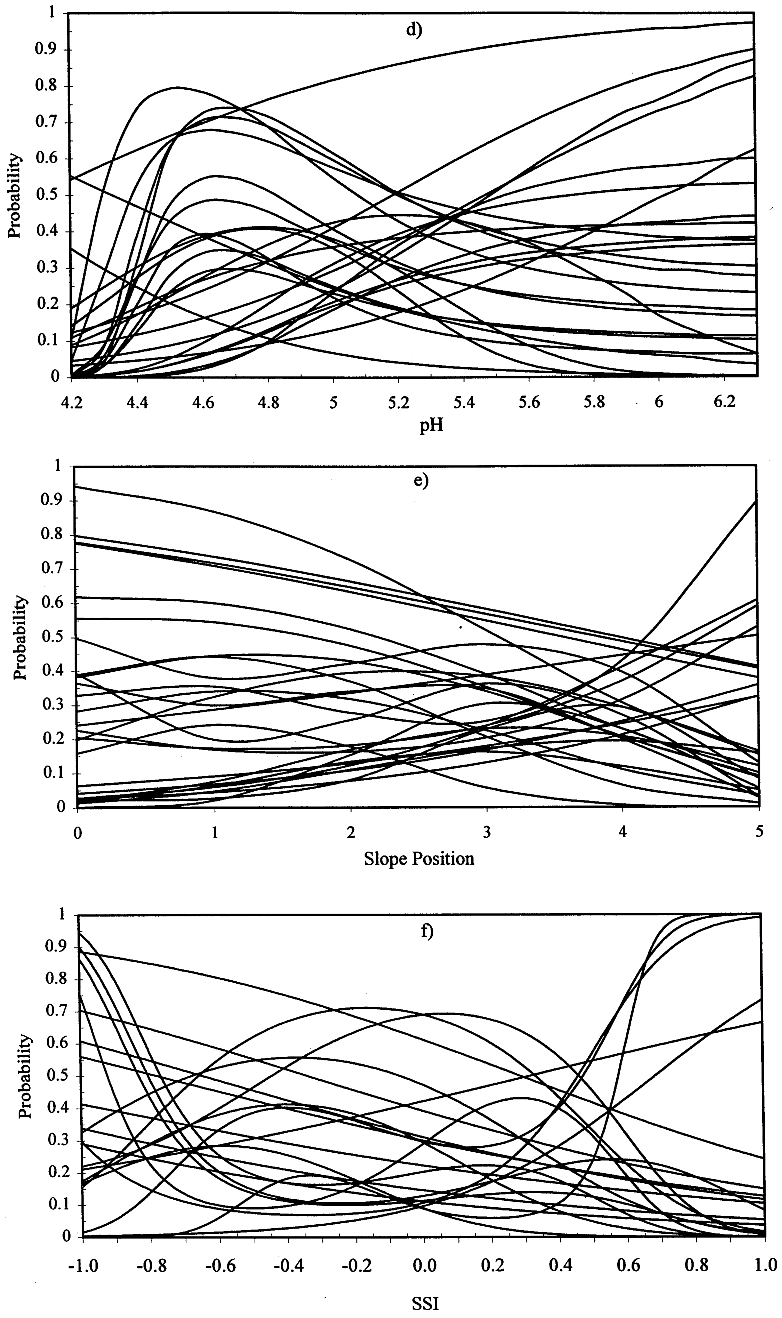


Figure 2. Responses of significant species, as determined by logistic regression, showing shape, optimal position, and distribution patterns of species across the gradients of canopy (a), nutrient index (b), soil organic matter (c), pH (d), slope position (e), site severity index (f), and bracken frond densities (g).



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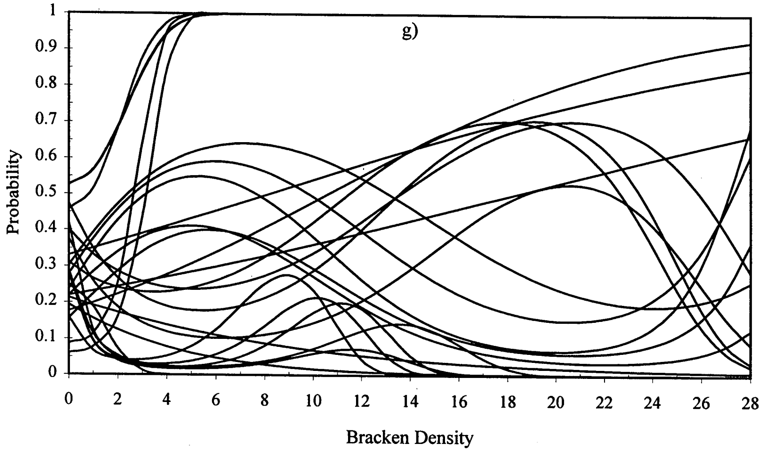

Figure 2, continued.

successional species for nutrient accumulation in these nutrient poor sandy soils. The significant *Vaccinium* species also maximized their position in these sites, which corresponds to the general patterns of Ericaceae species world wide.

Soil Organic Matter

Half of the species modeled were significantly affected by this gradient (Table 4). Species response models were primarily quadratic and linear, with only one being cubic (Figure 2c). Species optima tended to occur in both the mid and high ranges of the gradient, with only a few occurring in the low portion (Table 5). The species most likely to occur in low soil organic matter sites were the species *Campanula rotundifolia, Danthonia spicata,* and *Trientalis borealis,* while species such as *Corylus cornuta, Hieracium aurantiacum, Maianthemum canadense, Prunus pumila,* and *Schizachne purpurascens* tended to optimize probabilities in high soil organic matter. There does not appear to be any patterns between the two guilds.

pH

Most species were significant along this gradient (Table 4). For this variable, however, both logarithmic scaling and arithmetic equivalents were used. The species response types, then, turned out to be balanced between linear and quadratic functions (Table 4, Figure 2d). The majority of species had optimal positions in the high pH range with only a few species in both the mid and low ranges, such as *Apocynum androsaemifolium, Trientalis borealis,* and *Vaccinium myrtilloides* (Table 5). The species occurring with optimums in the high pH range were those associated with fairly open canopies (μ = 10.5% SE ± 7.4, n = 10) representing savanna communities, while species associated with low and mid pH ranges occurred in higher canopies (μ = 82.9% SE ± 7.4, n = 12) associated with forest communities.

Slope Position

This variable contained a high majority of significant models, indicating the importance of topography (Table 4). The response functions were again primarily quadratic and linear, with some complex cubic responses (Table 4, Figure 2e). Interestingly, most of the species had optimal positions in either the frost pocket/valley bottom or upland plains (Table 5). The upland plains' guild includes species such as *Apocynum androsaemifolium, Calystegia spithamaea, Comptonia peregrina, Gaultheria procumbens, Maianthemum canadense, Oryzopsis asperifolia, Pteridium aquilinum, Vaccinium angustifolium,* and *Waldsteinia fragarioides.* The frost pocket guild included such species as *Agropyron trachycaulum, Aster ciliatous, Bromus kalmii, Danthonia spicata, Hieracium aurantiacum, Poa* spp., *Schizachne purpurascens,* and *Viola adunca.*

The apparent difference between these two guilds is that the first guild (upland) is characterized by species typically found in northern dry forest and boreal communities (77.8%), while the second guild of species (frost pockets) are representative of a bracken-grassland communities (100%). This would point to the possibility that the topography variable of slope position may be critical in determining which community will occupy a site. Bracken-grasslands are found primarily in the kettles and valleys of pitted outwash, while forests tend to occupy the more upland positions.

Site Severity Index (SSI)

Site Severity Index was significant in explaining distribution patterns for many of the species (Table 4). A fairly balanced distribution of linear, quadratic, and cubic model functions were used (Table 4, Figure 2f). Optimal response patterns revealed that most species occurred on the mesic end of the gradient (SSI = -1), while a few species used the xeric (SSI = 1) and mid portions (Table 5). The xeric guild included the species *Comptonia peregrina, Danthonia spicata, Lysimachia quadrifolia, Prunus pumila,* and *Rubus allegheniensis,* which are common species to pine barrens and bracken-grasslands. The mesic guild contains species common to boreal forests, northern dry mesic forests, northern dry forests, and bracken-grasslands.

Bracken Fern

The change in bracken fern frond densities proved to play an important role in determining species distributions, with most species being significant (Table 4). Species responses were primarily cubic, with a fair number of both quadratic and linear functions (Table 4, Figure 2g). The cubic response may point to the complex interaction bracken fern may present to other species, with a set of interactions including allelopathy, nutrient competition, and light interception. Another possibility that may promote the unusually complex responses of species are that bracken clones are not at an equilibrium with the landscape. The clones are constantly invading outward with underground rhizomes at least 1 m in advance of emergent fronds (Watt 1940).

Regardless of bracken fern dynamics, a few species seem to respond positively to increasing bracken densities, which is interesting since bracken fern is thought to be an effective competitor and inhibitor (allelopathy). Most of the species showing positive responses to bracken densities (Table 5, Figure 2g), were also species that tended to have optima in high canopy conditions (μ = 72.5% SE ± 12.1, n = 11), while those that were negatively associated with increasing bracken densities tended to have optima in low canopy conditions (μ = 22.7% SE ± 16.6, n = 6). Thus, many typical forest species (northern dry forest) are located in the open bracken-grasslands. This distribution may partially be a function of bracken fern densities, with interception of light acting as a type of canopy. This, then, may infer advantages for species that can photosynthesize under low light conditions and hence may able to out compete species normally associated with the grasslands.

Discussion

Results indicate that canopy, topoedaphic variables, and bracken fern are all significant factors accountable for distribution patterns of plant species at Spread Eagle Barrens. Canopy appeared to be the most influential predictor for many species. Since canopy is also the easiest of the gradients to manipulate, a potential exists for management of desired species under certain conditions. Based on other environmental conditions, responses of species should be able to be predicted from logistic regression equations.

Topographic variables (slope position and site severity index) are often ignored. We found them to be key factors in determining both plant and community distributions. For instance, slope position influenced both community species patterns and individual species distributions. In particular, bracken fern, a keystone species, was most significantly related to slope position, presumably due to its frost sensitivity. Of the edaphic variables examined, both soil pH and % organic matter were influential for a number of species. However, the nutrient index created for the study was not related to the distribution of a majority of species.

Bracken fern had a cubic response in distribution models for many species. These responses suggest a complex relationship between bracken fern and other species, with the interactions of allelopathy, nutrient competition, and light interception being important. It was initially assumed that both allelopathy and competition would result in negative responses for many species, but our results indicate that the reverse was true. This may be explained by the fact that most positively associated species were those that would be classified as "forest" species, perhaps pointing to the importance of light interception by bracken fern.

According to Austin and Gaywood (1994), the ecological responses of species will be increasingly skewed toward the far ends of a gradient, representing the increasing role of physiological tolerance, while the center of the gradient will be dominated by responses of species occurring due to the increasing role of competition. The more superior competitors should then be found in the center of a gradient, resulting in high dominance and low diversity (Austin and Smith 1989). If this were the case, bracken fern, a noted competitor with high dominance, should be found in the center of direct gradients. This seems to be occurring for the variables of nutrient index, organic matter, pH, and site severity index at Spread Eagle Barrens. Removing or controlling bracken fern might produce an associated shift in species composition due to the releasing of competitive interactions. Bracken fern influence on species responses, including factors that influence bracken fern, are important considerations in the management of Midwestern Savannas. In fact, by selectively harvesting the woody species based on site characteristics that promote domination by bracken fern or within a frost pocket, maintenance may occur through competitive inhibition or the microclimate, instead of intensive management.

Appendix A. Species selected for logistic regression modeling based on frequency of occurrence (> 10%) within 1 m^2 herbaceous quadrats at Spread Eagle Barrens. Curtis fidelity represents the number of native communities, out of 34 identified, in which the species was found. The community maximum describes which plant community a species achieved maximum presence (Curtis 1959).

Genus	*Species*	*Family*	*Common Name*	*Curtis Fidelity*	*Community Maximum*
Acer	*rubrum*	Aceraceae	red maple	12	NDM
Agropyron	*trachycaulum*	Gramineae	wheatgrass	9	BG
Amelanchier	spp.	Rosaceae	serviceberry		
Anemone	*quinquefolia*	Ranunculaceae	wood anemone	18	NDM
Apocynum	*androsaemifolium*	Apocynaceae	spreading dogbane	18	ND
Aster	*ciliolatus*	Asteraceae	Lindley's aster	9	BG
Aster	*macrophyllus*	Asteraceae	large leaved aster	14	BF
Bromus	*kalmii*	Gramineae	Kalm's brome	10	BG
Calystegia	*spithamaea*	Convolvulaceae	low bindweed	11	ND
Campanula	*rotundifolia*	Campanulaceae	bluebell; harebell	14	CG
Carex	*pensylvanica*	Cyperaceae	Pensylvania Sedge	16	SDM
Comandra	*umbellata*	Santalaceae	bastard toadflax	21	OB
Comptonia	*peregrina*	Myricaceae	sweetfern	8	BG
Corylus	*cornuta*	Betulaceae	beaked hazlenut	9	BF
Danthonia	*spicata*	Gramineae	poverty oatgrass	5	BG
Diervilla	*lonicera*	Carpifoliaceae	bush-honeysuckle	17	BF
Gaultheria	*procumbens*	Ericaceae	wintergreen	13	ND
Hieracium	*aurantiacum*	Asteraceae	orange hawkweed	5	BG
Lysimachia	*quadrifolia*	Primulaceae	whorled loosestrife	8	PB
Maianthemum	*canadense*	Liliaceae	Canada mayflower	18	BF
Melampyrum	*lineare*	Scrophulariaceae	cow-wheat	4	ND
Oryzopsis	*asperifolia*	Gramineae	rice-grass	9	BF
Poa	spp.	Gramineae	bluegrass	10	BG
Polygala	*paucifolia*	Polygalaceae	gay-wings	6	ND
Prunus	*pumila*	Rosaceae	sand cherry		
Pteridium	*aquilinum*	Polypodiaceae	bracken fern	22	BG
Rubus	*allegheniensis*	Rosaceae	common blackberry	14	SD
Schizachne	*purpurascens*	Gramineae	false melic	8	BG
Trientalis	*borealis*	Primulaceae	star-flower	15	BF
Vaccinium	*angustifolium*	Ericaceae	low sweet blueberry	16	ND
Vaccinium	*myrtilloides*	Ericaceae	velvetleaf blueberry	11	NW
Vaccinium	*pallidum*	Ericaceae	hillside blueberry		
Viola	*adunca*	Violaceae	sand violet	8	BG
Waldsteinia	*fragarioides*	Rosaceae	barren-strawberry	8	ND

Acknowledgments

This research was supported by the Department of Defense Legacy Resource Management Program and the Sand County Foundation. We would like to thank the UW-Stevens Point Oak Savanna Legacy crew, in particular Angela Collada, for both field and logistical support. In addition, guidance by Mark Boyce, James Cook, and Evelyn Merrill was much appreciated in the analytical phases of this project.

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Neal D. Niemuth and Mark S. Boyce

Disturbance in Wisconsin Pine Barrens: Implications for Management

Abstract *We compared cover, structure, and diversity of woody vegetation in three types of early successional habitat patches in the pine barrens of northwestern Wisconsin. Patch disturbance types included repeated prescribed burning, crown fire, and clearcutting. All three disturbances set back succession, but with distinct differences in vegetation structure and composition. Vegetation in patches created by crown fire had greatest tree density, diversity of structure and composition, and cover by jack pine and large woody debris. Differences in woody vegetation among disturbance types may influence the success of savanna restoration and landscape management projects at providing habitat for savanna wildlife species in the pine barrens.*

Timber harvest is frequently alluded to as a surrogate disturbance for fire in forested ecosystems because both reduce vegetative structure and/or create habitat harboring similar animal communities (e.g., Urban et al. 1987, Hansen et al. 1991, Hunter 1992, Sharitz et al. 1992, Vora 1993). Yet the relative effects of timber harvest on plant and animal communities are rarely quantified (but see Hansen et al. 1991, Fitzgerald and Tanner 1992, Greenberg et al. 1995).

In Wisconsin pine barrens, large-block timber harvest has been proposed as a landscape-level management tool that would create large habitat patches for area-sensitive grassland and shrubland bird species (Niemuth 1995, Parker 1995, Strand and Epperly 1995). Many grassland and shrubland bird species readily accept early successional habitat created by clearcutting in pine barrens (Niemuth 1995), although the relative effects of fire and clearcutting on pine barrens vegetation structure and composition are largely unknown.

Fire is the primary natural disturbance in the region (Curtis 1959), although pine barrens are also subject to catastrophic windthrow (Canham and Loucks 1984), ice storms (Vora 1993), and infestations of jack pine budworm (*Choristoneura pinus*; Volney and McCullough 1994). Before fire control began in the 1920s, recurrent fires swept the pine barrens, creating extensive openings largely devoid of trees (Norwood 1852, Murphy 1931, Curtis 1959, Vogl 1970). Because of fire control and tree planting, most of the region is currently forested, and timber production is the primary land use. Timber harvest is the dominant vegetation-removing disturbance in the pine barrens, as most wildfires are quickly extinguished and are limited in extent. However, early successional habitat is maintained in the region at four savanna reserves larger than 1,000 ha, along with several smaller reserves and fuelbreaks. Reserves are managed primarily to provide habitat for sharp-tailed grouse *(Tympanuchus phasianellus)*. Early successional vegetation is maintained at these reserves through frequent prescribed burning, which, over time, creates a vegetation community that may differ considerably from pre-settlement conditions (Mossman et al. 1991, Parker 1995).

We compared characteristics of woody vegetation in 40 patches created by crown fire, clearcutting, and repeated prescribed burning in northwestern Wisconsin pine barrens. We focused on structure of woody vegetation because woody vegetation is an important nesting and foraging substrate for wildlife (Niemuth 1995). In addition, structure of woody vegetation will be determined largely by management practices and disturbance type rather than by plant species' range and response to site characteristics. Our goal was to show how woody vegetation structure differed among disturbance types, as well as provide direction for future experimental analysis of vegetation response to disturbance in the pine barrens.

Materials and Methods

Study Area

Sampling took place during July of 1993 and 1994 in Burnett, Douglas, and Bayfield counties in northwestern Wisconsin (Figure 1). Pine barrens in the region are delimited by xeric, outwash sand soils; predominant tree species included jack pine *(Pinus banksiana)*, red pine *(P. resinosa)*, quaking aspen *(Populus tremuloides)*, big-toothed aspen *(P. grandidentata)* and red, Hill's, and burr oak *(Quercus rubra, Q. ellipsoidalis, and Q. macrocarpa)*. Oak, hazel (*Corylus* spp.), and cherry (*Prunus* spp.) shrubs were common in the openings we sampled. Typical ground cover included blueberry (*Vaccinium* spp.), sweet fern *(Myrica asplenifolia)*, bluestem (*Andropogon* spp.), and sedge (*Carex* spp.). The surrounding landscape primarily was forested, with timber production and recreation being the primary land uses.

Study Sites

Selection criteria included (1) location on outwash sand soils; (2) mean vegetation height visually estimated to be < 1.2 m; (3) creation or maintenance of opening by fire or clearcutting, rather than other management practices, frost, or edaphic conditions; (4) > 1 year since site was clearcut or burned; and (5) well-defined patch with forest > 5 m tall surrounding 90% of site. All known crown fire sites (n = 4) and savanna reserves (n = 11) within the region

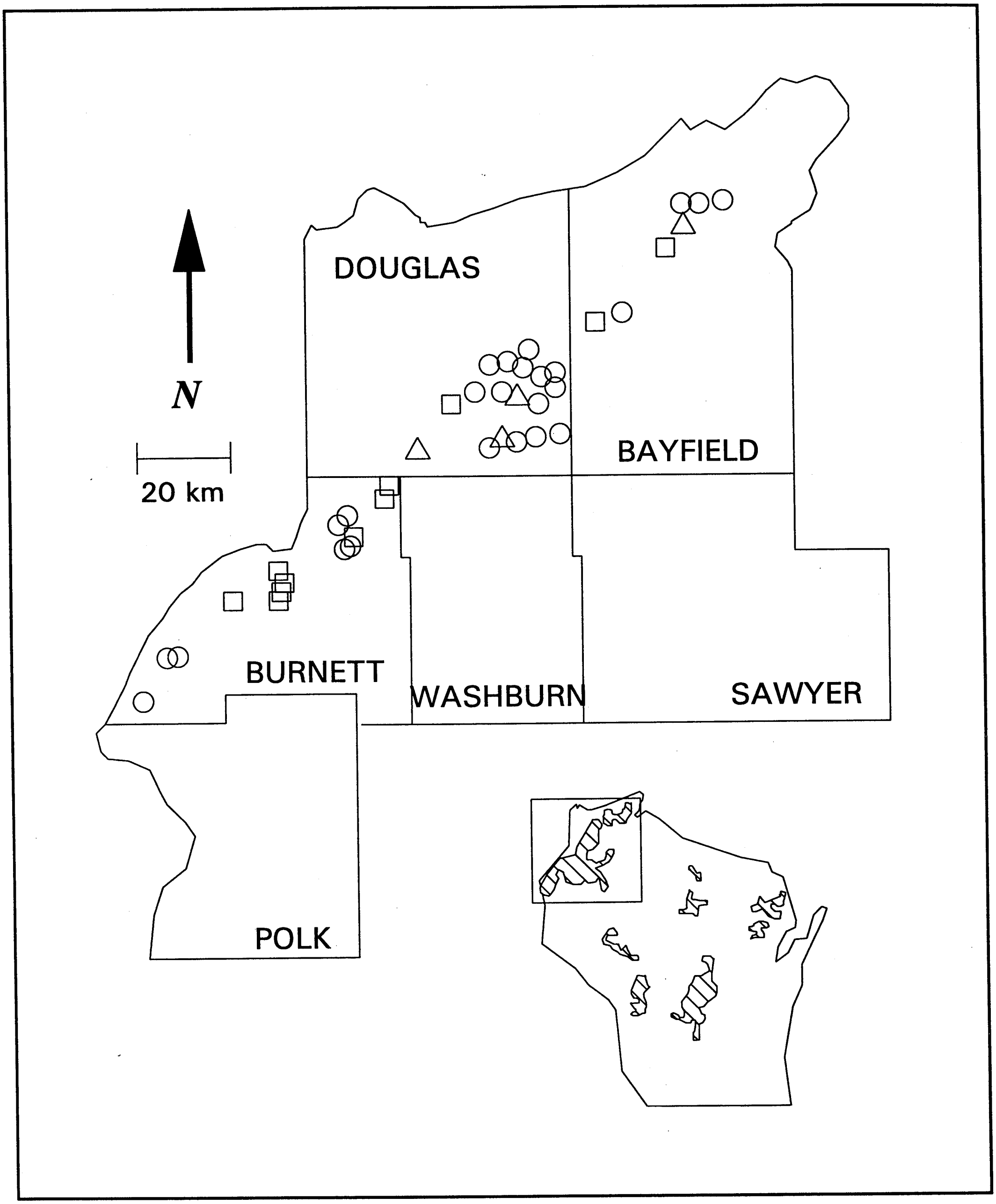

Figure 1. Location of sample sites. Squares represent savanna reserves; triangles represent openings created by wildfire; circles represent clearcuts. (Inset) Distribution of historic Wisconsin pine barrens, after Curtis (1959). Study took place within region bounded by square.

that fit these criteria were sampled. Known clearcut sites within the study region meeting selection criteria were stratified by size, and 25 were randomly selected (Figure 1). All sample sites were > 1 km apart.

Sampling Methods

Woody vegetation was sampled using the line intercept method (McDonald 1980). Intercept lines were 250 m long, although shortened intercept lines were used in seven patches that were too small to contain a 250-m sample line. Sampling of sites was proportional to patch size (n = 2 * log [estimated patch area in ha]), with the number of lines per patch ranging from one to eight. In patches containing multiple lines, sample lines were randomly placed off a systematically divided baseline with a random starting point. Height and intercept length were recorded for eight variables: percent cover by oak, pine, cherry, hazel, willow (*Salix* spp.), aspen, large woody debris, and dead standing trees of any species. Only woody vegetation > 0.5 m in height, length, or width was recorded. In addition, all live and dead trees > 12 cm diameter at breast height and within 10 m of the transect line were counted. Diversity of woody vegetation was calculated for each site using the Shannon-Wiener diversity index:

$$H' = -\sum_{i=1}^{k} p_i \ln p_i$$

where k is eight and p_i is the proportion of line intercept coverage found in each of the eight woody vegetation covertype categories. Horizontal patchiness was calculated as the number of times woody vegetation cover types were encountered along a 250-m transect.

Statistical Analysis

We used direct discriminant analysis (SPSS Inc. 1990) to maximally differentiate line intercept data for the three patch types. We treat the discriminant analysis as descriptive, rather than a test of null hypotheses concerning differences among treatments because of inequality of the discriminant function variance-covariance matrices, lack of experimental control, and unknown management history (e.g., agricultural use, fire interval, pre-settlement vegetation, logging history). Descriptive statistics are presented to aid in understanding differences in woody vegetation among management types.

Results

The discriminant function created a two-dimensional ordination showing relative scores for the three patch types. The first discriminant function (Figure 2) accounted for 56.9% of the total variation in the data set and showed that greatest tree density, woody debris cover, and jack pine cover occurred at crown fire sites (means and standard deviations in Table 1). Savanna reserves scored lowest for these variables, and clearcuts were intermediate. The second discriminant function accounted for 34.2% of the total variation in the data set and showed that greatest height variation and Shannon-Wiener diversity were found in crown fire patches. Clearcuts scored lowest for these variables; savanna reserves were intermediate (Figure 2). Horizontal patchiness was greatest at savanna reserves and lowest in clearcuts. Greatest correlation between variables included in the discriminant analysis was 0.42. Category classification success in the discriminant analysis ranged from 75% to 92%, with an overall correct classification rate of 87.5% (Table 2).

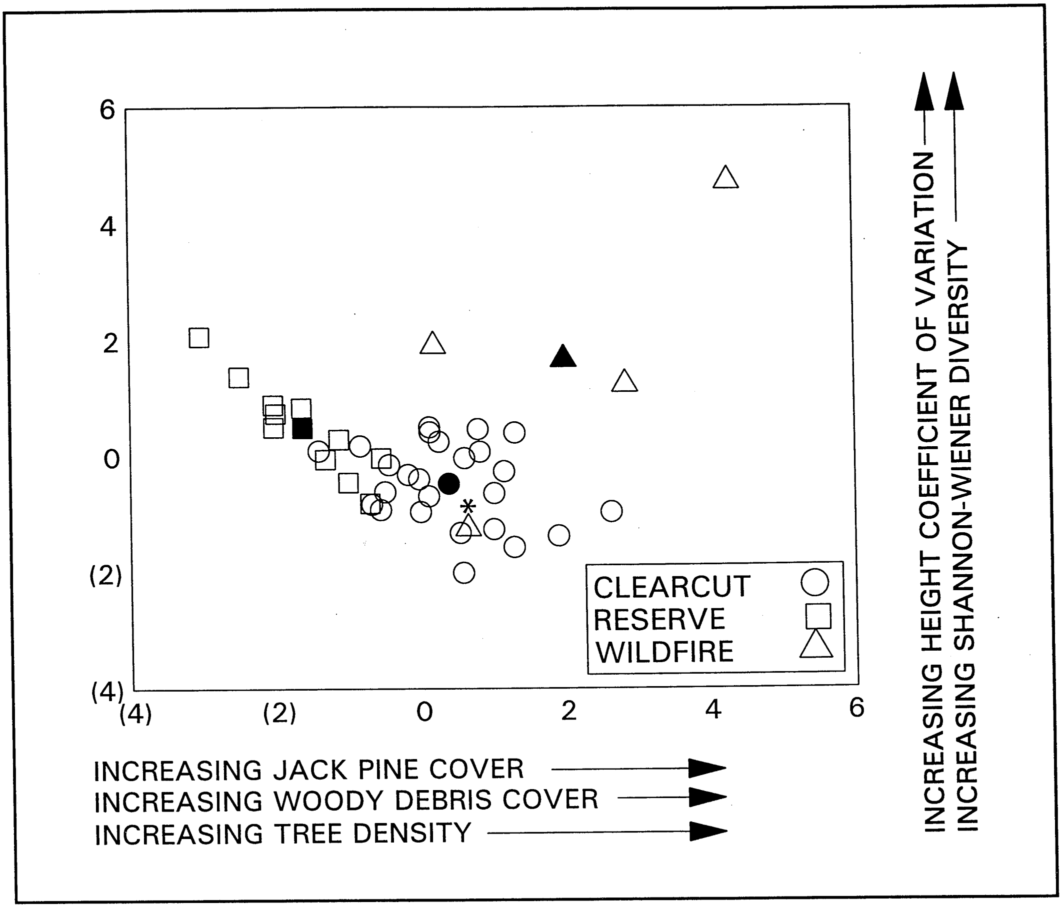

Figure 2. Woody vegetation discriminant function scores for 15 clearcut patches, 11 savanna reserves, and 4 wildfire-created savanna patches in northwestern Wisconsin pine barrens. Solid symbols represent centroids for each group. Triangle with * represents the Loon Lake wildfire, which burned twice in 11 years.

Discussion

Relative Effects of Disturbance Type on Vegetation Structure and Pine Barrens Wildlife

The most obvious difference among the three patch types was greater density of trees at crown fire sites than managed or clearcut sites. Trees, whether dead or alive, are an important habitat component in the pine barrens. For example, tree density is a significant predictor of Eastern bluebird *(Sialia sialis)* and tree swallow *(Tachycineta bicolor)* presence in Wisconsin pine barrens savanna; conversely, other savanna species such as the horned lark *(Eremophila alpestris)* and vesper sparrow *(Pooecetes gramineus)* prefer areas of lower vegetation (Niemuth 1995).

Differences in tree quality for nesting and foraging may also exist among the three disturbance types. The few trees that remain at savanna reserves are generally oaks and red pine that are sufficiently large to survive

Table 1. Mean (± standard error) of vegetation and structure variables at three patch types in Wisconsin pine barrens.

Variable	*Disturbance Type* *Wildfire*	 *Clearcut*	 *Reserve*
Trees/0.5 ha	20.36 ± 3.9	3.11 ± 1.6	0.88 ± 2.36
Large woody debris (%)	7.69 ± 1.7	7.98 ± 1.6	0.65 ± 0.21
Shannon-Wiener diversity	1.32 ± 0.16	1.24 ± 0.06	1.31 ± 0.09
Height coefficient of variation	0.82 ± 0.11	0.66 ± 0.04	0.76 ± 0.07
Jack pine cover (%)	7.94 ± 4.2	1.97 ± 0.6	0.11 ± 0.07
Patchiness (intercepts/transect)	117 ± 41	90 ± 17	197 ± 25

Table 2. Classification results for predicted group membership of three patch types based on discriminant analysis. Percent correct for each group in parentheses; 35 (87.5%) of 40 cases were correctly classified.

Actual Group	*Number of Cases*	*Predicted Group Membership* *Clearcut*	 *Savanna Reserve*	 *Wildfire*
Clearcut	25	23 (92)	2 (8)	0 (0)
Savanna reserve	11	2 (18.2)	9 (81.8)	0 (0)
Wildfire	4	1 (25)	0 0	3 (75)

repeated prescribed burns (pers. obs.). But crown fire patches were dominated by injured and dead trees, which typically have different physical attributes than live trees. Sloughing bark on dead trees provides cover for invertebrates and foraging sites for bark-gleaning birds, and rotting wood hosts invertebrates and simplifies excavation by primary cavity nesters (Evans and Conner 1979, Cline et al. 1980, Mannan et al. 1980).

Woody debris is also an important component of pine barrens vegetative structure. Woody debris provides escape cover, foraging habitat, and perch sites for many bird species (Mossman et al. 1991). Nests of Brewer's blackbirds *(Euphagus cyanocephalus)* and brown thrashers *(Toxostoma rufum)* are frequently associated with woody debris in pine barrens, and black bears *(Ursus americanus)* regularly turn over and tear apart large woody debris in search of food (pers. obs.). Woody debris is also an important substrate for fungi and provides cover for invertebrates and small vertebrates (Zappalorti and Burger 1985, Gillis 1990, Hansen et al. 1991, Haim and Izhaki 1994). In addition to providing cover for wildlife, woody biomass is an important nutrient reservoir in pine ecosystems (Boerner 1982). The relative scarcity of woody debris at managed sites is apparently caused by repeated prescribed burns with relatively little time for regeneration of woody vegetation between burns.

Density of jack pine varied greatly among the three patch types. Jack pine density was greatest at crown fire sites, where serotinous cones opened in response to fire. Some jack pine cones in the region open in response to high ground temperatures (D. Epperly, pers. comm.), allowing jack pine regeneration in many clearcut patches. Repeated burns eliminate age cohorts of jack pine before regeneration can occur (Anonymous 1931, Vogl 1970), explaining extremely low jack pine densities at managed savanna reserves. Curtis (1959) described the jack pine as the most usual tree on the pine barrens, yet management practices intended to perpetuate savanna have virtually eliminated jack pine from savanna reserves.

Fire frequency strongly influences structure and composition of vegetation at a site. For example, the Five-Mile Fire burned approximately 5,400 ha of jack pine-dominated forest in northwestern Wisconsin in 1977 (Gregg 1987). Jack pine quickly regenerated following the fire, and most of the area was soon covered with dense growth of jack pine saplings. Without further disturbance, jack pine at the site would have grown to maturity. But in June 1988, the Loon Lake Fire burned a portion of the Five-Mile Fire. Jack pines were eliminated from that patch, and the Loon Lake Fire became a brush prairie, with characteristics similar to clearcuts in the area (Figure 2).

Fire frequency also affects densities of blueberries, which provide food for wildlife and humans. Blueberry cover was greatest at crownfire sites and lowest at managed savanna reserves (Niemuth 1995). Burning stimulates blueberry growth (Murphy 1931, Vogl 1970), but Buell and Cantlon (1953) found that blueberry cover decreased at their New Jersey study site when burns became more frequent than every three years.

Clearcuts had reduced Shannon-Wiener diversity and height range of woody vegetation, which may negatively impact many savanna wildlife species. For example, species richness and density of savanna birds along transects are positively correlated with Shannon-Wiener diversity of woody vegetation in early successional habitat in the pine barrens (Niemuth 1995).

Management Implications

Altering management practices can address some of the differences in which clearcuts and savanna reserves differed from crown fire patches. For example, tree density can easily be increased in clearcuts by leaving dead and live trees during timber harvest. Diversity of woody vegetation in clearcut patches could be increased by discontinuing management practices that reduce diversity such as release of young pines by removal of deciduous shrubs. Lengthening the return interval for prescribed fires at savanna reserves will allow added growth of woody vegetation and, over time, potential for more woody debris. With a longer fire return interval, trees can (1) grow larger and develop thicker bark, better enabling them to survive fire (see Vogl 1970) or (2) survive long enough to produce seed, permitting seedlings to regenerate even if parent trees are lost to fire.

Landscape-level management could add a dimension of spatial and temporal variability that is largely absent from present disturbance in the pine barrens. Presently, most clearcuts are small relative to proposed management (Parker 1995, Strand and Epperly 1995), leading to habitat fragmentation. Also, savanna reserves in Wisconsin pine barrens are spatially static, and vegetation is burned approximately every five years.

Temporal variation in disturbance was noted by Vogl (1964), who observed that "brush prairie savanna undoubtedly reverted back and forth from brush to forest and forest to brush again, depending on the absence or presence of fire." Depending on the time of observation, a site might accurately have been described as brush prairie, pine savanna, or forest. Indeed, such variation would have influenced the pre-fire vegetation at crown fire sites we sampled, influencing post-fire characteristics to which we compared vegetation at prescribed burn and clearcut sites.

Of course, fire is not the only factor shaping the pine barrens. Vogl (1970:200) noted that "all factors including soil type, soil fertility, topography, climate, drought, and fire are inseparably linked. . . . Fire is one of the essential ingredients . . . but the critical factor . . . is not so much fire, but the presence of sandy plains; sites with low fertility that lend themselves to droughts and fires of the proper intensities and frequencies to produce a vegetational structure and composition called barrens." The myriad forces that shape pine barrens vegetation are too complex and variable for managers to duplicate, illustrating a key problem experienced at many nature reserves: trying to preserve that which changes (White and Bratton 1980).

The influence of disturbance on other processes and taxa in the pine barrens must also be considered. Our analysis demonstrated that disturbance type can influence the structure and composition of woody vegetation persisting after disturbance occurs. But disturbance size and intensity can also alter the trajectory of succession, influencing composition and growth form of vegetation established following disturbance (Canham and Marks 1985).

Duplicating pre-settlement conditions will be difficult, if not impossible, when the "natural" disturbance regime is unknown, but through active adaptive management and simulation modelling, habitat quality on managed landscapes can be improved (see Walters and Holling 1990, Boyce 1993, Hansen et al. 1993). An understanding of the range of vegetation types and disturbances in a dynamic ecosystem can guide management (Sprugel 1991). Management of the pine barrens, whether through timber harvest or prescribed burns at dedicated reserves, must reflect the dynamic nature of the ecosystem.

Acknowledgments

Support was provided by the American Forest and Paper Association, Wisconsin Department of Natural Resources, and a George E. Menkens, Jr. Memorial Scholarship from the University of Wyoming Department of Zoology and Physiology. L. H. Niemuth and L. Rantala assisted with sampling. We thank W. L. Baker, K. Gerow, J. R. Lovvorn, J. O. Evrard, D. H. Knight, V. Radeloff, and one anonymous reviewer for helpful comments on earlier drafts of this paper.

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Rebecca L. Power and Alan Haney

Adaptive Management: A Solution to Restoration Uncertainties

Ecosystem management has encountered two diametrically opposed areas of resistance, each with some merit in their arguments. On one hand, many prominent ecologists have argued that ecosystems are more complex than we understand (Egler 1977), and some believe that we lack sufficient knowledge to make good restoration decisions (Haney and Boyce 1997), at least when uncertainty is high. On the other hand, many natural resource professionals consider ecosystem management an affront to their ability to make proper management decisions (Rudzitis 1996). The latter believe they have been managing ecosystems well for decades and cite evidence of commodity increases, such as timber volume, or game numbers to justify past decisions. Those who argue that their management decisions have been within the limits of sustainability will usually acknowledge a lack of data pertaining to ecosystem processes or structure, including biological diversity. They may also point out that ecologists often disagree on the importance of various measures of sustainability, such as diversity. Baskin (1994), for example, concluded that the risks associated with biodiversity loss were largely unknown. More recently, Tilman (1997) reported both direct and indirect evidence that ecosystems become less functional as diversity is lost. We (Haney and Power 1996) previously suggested that adaptive management is an excellent model for guiding ecosystem decisions. Here, we offer an adaptive management model to guide ecosystem restoration. Adaptive management not only helps us address uncertainty, it offers an opportunity to validate and improve good management practices, including decisions not to intervene in natural processes.

This paper was developed from research supported by the Department of Defense Legacy Resource Management Program funded through the Sand County Foundation.

Restoration generally requires a more complex set of decisions than other types of management. For example, one is immediately confronted with the decision of whether to intervene, how, and to what extent, either by modifying natural processes or altering human impacts. Because they typically involve greater shifts in ecosystem processes or structures, these decisions tend to be more value-laden and controversial than those associated with ongoing ecosystem management. Consequently, a high level of social input is often needed to support the successful implementation of restoration plans. Aldo Leopold demonstrated remarkable foresight when he wrote in an unpublished essay in 1935 that "the inevitable fusion of these two lines thought [social science and natural science] will, perhaps, constitute the outstanding advance of the present century" (Bradley 1997). The adaptive management model proposed by Walters and Holling (1990) melds social issues with good scientific methods. We further develop it here for guiding ecosystem restoration decisions. We believe the adaptive management model, as we have applied it, addresses the concerns of those who might otherwise use a priori arguments to oppose ecosystem restoration, and other forms of ecosystem management.

Inventory and Information Exchange

Figure 1 is modified from our previous adaptive management model (Haney and Power 1996). High quality information and effective communications comprise the foundation for all management decisions (Figure 1). During the process of gathering and communicating information, goals and objectives for ecosystem management begin to emerge. Information is needed not only to set goals, but also to guide the acquisition of additional information. Managers must be creative in searching for sources of information; technical literature, historical documents, maps and survey notes, interviews, and focus groups are examples. It is especially important to solicit and involve stakeholders (those groups or individuals with a vested interest in management decisions) throughout the process.

The success of restoration, like other genres of ecosystem management, is dependent on the attitudes and agendas of people (Gunderson et al. 1995). Stakeholders are a storehouse of useful information for resource managers. This does not mean that resource managers should undervalue their own professional expertise. Exchanging information with stakeholders is an integral part of the process; however, using information wisely is probably the greatest art in ecosystem management.

Goals and Objectives/ Desired Future Condition

Goals and objectives are based on available information, including opinions and attitudes of stakeholders and assumptions or hypotheses to be tested. The Ecological Society of America Committee on Ecosystem Management identified clear operational goals and sound ecological models and understanding as the highest priorities in developing a comprehensive ecosystem management system (Christensen et al. 1996). For the purposes of this paper, goals are the overarching principles and guiding vision for proactive management (Figure 1). They are the desired future toward which management is directed. Objectives are the concrete actions that need to be taken to achieve goals. Goals determine the direction we will move, or where we will move, to achieve a desired condition. Objectives determine how

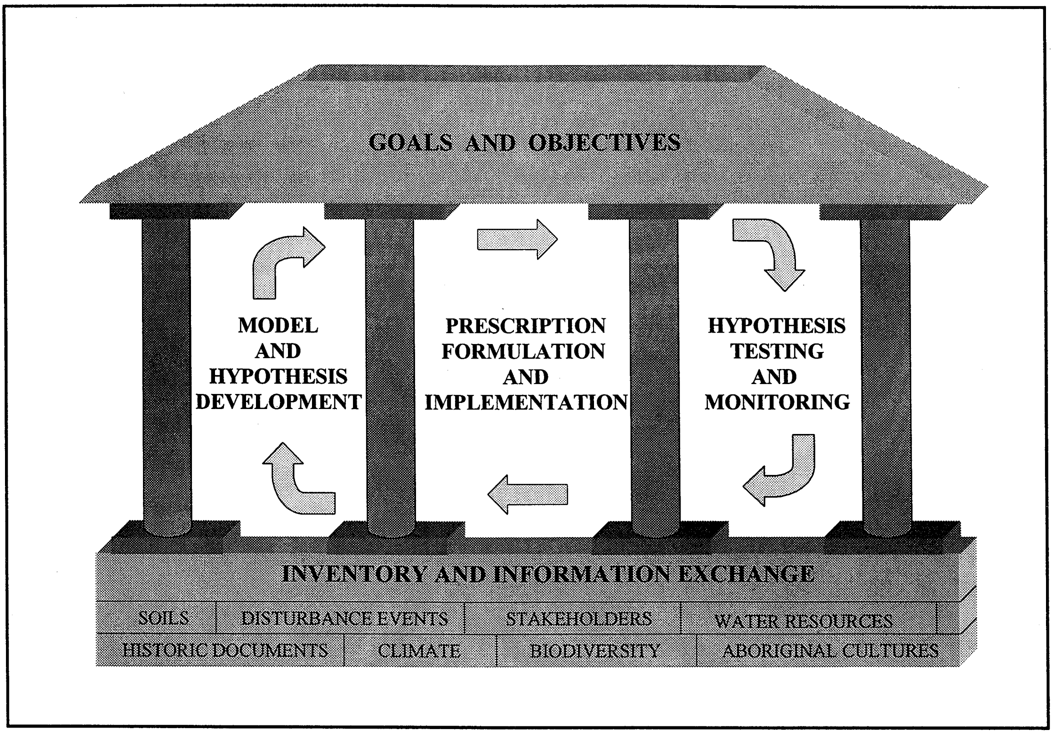

Figure 1. A conceptual model of adaptive management. Information is the foundation supporting the overarching goals and desired future conditions. The process, which stems from information and goals, involves model and hypothesis development, prescription formulation and implementation, monitoring, and hypothesis testing, in a continuous process.

we will move (U.S. Department of the Interior Fish and Wildlife Service, Division of Refuges 1996).

One should not worry excessively that insufficient information is available for setting goals and objectives. In fact, it is often the case that more information leads to greater uncertainty. For example, in overgrown savannas, canopy reduction results in an increase in total diversity and herbaceous diversity (Vogl 1964, Nuzzo 1986, Haney and Apfelbaum 1990, Stritch 1990), but there is much less information about the relative effects of different approaches to canopy reduction. Is timber harvest or mowing as effective as fire when the goal is to restore the herbaceous layer? What differences occur with annual fires of low intensity compared to less frequent intense fires? How does grazing compare to fire or mowing? How does fire affect various invertebrate populations? These and dozens of other questions arise continually as managers consider infinite alternative management approaches.

When information about stakeholder opinions is added, uncertainty increases even more. For example, managers have believed for years that fire is the best tool for maintaining savanna ecosystems. However, some stakeholders oppose fire (Swengel 1996). This dichotomy of opinions can be restated as one or more hypotheses, and the experiments to test the hypotheses can be incorporated into management plans (see Model and Hypothesis Development). Difficulties arise, not from acting on assumptions, but from lack of information about the validity of assumptions. Administrators, scientists, and other stakeholder groups may have different assumptions about the way that components of an ecosystem will respond to a treatment. In a roundtable discussion on biological diversity convened by the Chequamegon and Nicolet National Forests, Crow et al. (1994) found that an effective way to reach consensus, or at least diffuse potentially volatile disagreements, was to reduce points of contention to testable hypotheses. If stakeholders are involved in stating the hypotheses and designing the experiments to test them, they are more likely to become partners in the management of the ecosystem, rather than antagonists.

Because ecosystems provide many services for many constituencies (Daily 1997), inevitable conflicts of interest will arise. Gunderson et al. (1995) pointed out that consensus building is an essential part of adaptive management. Costanza and Folke (1997) laid out a 12-step process for consensus building leading to development of a scoping model that is helpful in showing how social values are related to ecological objectives. These steps are the primary tools for relating information to stakeholders. Stakeholders, in turn, often can contribute information useful in understanding an ecosystem or setting goals. For example, some may recall historic events of importance or conditions that once existed in the ecosystem. In soliciting this input, managers typically gain cooperation necessary for ecosystem management. The most obvious stakeholders are those who visit and use the ecosystem, but others include adjoining property owners, other neighbors, environmental and conservation groups, local schools, and staff who work on the property or for the managing organization.

People are sometimes fearful that misguided goals may lead to irreparable damage to the ecosystem. This is usually an exaggerated concern. Consider, for example, that most of the national forest land in eastern United States was once cleared and pastured or cultivated, then abandoned in lieu of taxes. Some of these acres are now wilderness, and most support productive forests (MacCleery 1993). Patric (1995) reported another remarkable illustration of ecosystem resilience. Two watersheds in West Virginia were matched for a study in which one was clearcut and kept barren for five years with regular application of herbicides. Now, 30 years later, essentially no difference in diversity or soil fertility can be found between the clearcut and herbicide-treated ecosystem and the control. Conversely, there are examples where goals and objectives not supported by sufficient information and monitoring have led to management decisions that compromised ecosystem sustainability. For example, doing nothing to counter successional degradation of savannas may result in long-term ecosystem damage, perhaps much more than inappropriate intervention. Apfelbaum and Haney (1991) reported that degraded mesic savannas in northern Illinois were losing topsoil in excess of 50 tons per acre per year. When restored, these savannas lost less than 5 tons of soil per year and supported plant and animal diversity that was approximately 10 times greater than unrestored savannas. This example also demonstrates the importance of coupling baseline data to continuing monitoring (Goldsmith 1991).

The inevitable uncertainties that cloud our view of the future necessitate testing hypotheses. Hypotheses and models will guide selection of the management alternatives that best accomplish desired outcomes.

Model and Hypothesis Development

Assumptions can be formally stated as hypotheses, then organized as models to indicate how the manager believes the system will respond. Model and hypothesis development is supported by information; they are part of the structure that supports goals and objectives (Figure 1). This is where sound science is coupled to restoration. Good management requires that we take time to state assumptions, develop underlying hypotheses, and design prescriptions to test those hypotheses. Every time a management decision is implemented, it is an experiment. A heuristic approach to management leads to a more objective basis for evaluating responses of the ecosystem. Often this is simply a matter of replicating treatments (prescriptions) and leaving controls, thereby providing a stronger statistical basis for evaluating responses and separating the influence of confounding factors, such as site histories and yearly variation in weather patterns (Goldsmith 1991). Through this process, science is employed to increase knowledge about the way the ecosystem responds. Furthermore, managers who participate in the scientific process will usually find willing scientists to partner with them; scientists who engage in dialogue with managers become more aware of management concerns and limitations.

In the adaptive management model, assumptions, which follow from uncertainties, are restated as hypotheses and models; these, in turn, drive prescriptions, and all drive monitoring. Therefore, the following issues need to be addressed during hypothesis formation.

System Components

The three primary elements that make up ecosystems being restored or managed are composition, structure, and function (Crow et al. 1994). Composition refers to the units that are present in a system. They can take the form of genes, species, cover types, cultures, communities, and ecosystems. Structural considerations address the size, shape, and patterns of distribution of compositional elements across space and time. Fire patches, return intervals, and how fire creates successional patterns at landscape scales are structural questions that might be addressed when developing savanna restoration models and hypotheses, for example. The functional elements of a system are process oriented. In the broadest view of ecosystems, we need to consider both the human and non-human components. Thus, predator-prey relationships, the dynamics of stakeholder interactions at public meetings, the way that disturbances such as insect outbreaks and disease influence fire return intervals and intensity, and carbon and nitrogen cycling are all functional aspects of ecosystems. Our management success is often more dependent on the social components than the non-human elements and should not be neglected. The ecosystem components are the framework around which models and hypotheses are developed.

Scale

Hypotheses can be formulated that address several scales of time and space. The concept of scale can be thought of as a nested hierarchy (Allen and Star 1982), with managers choosing to address different issues at different points, depending on their goals and objectives. The compositional, structural, and functional components of natural systems can be examined at the genetic, species, community, ecosystem, and landscape levels. The scale that managers choose significantly affects the information that results. For example, Knopf and Samson (1996) found that maximizing site (alpha) diversity may reduce regional (gamma) diversity in birds in western riparian areas. When diversity was low, river corridors supported species that were regionally less common. When diversity was higher, corridors supported a greater number of generalist species, sometimes to the detriment of rarer species. Likewise, local populations of bird species vary with vegetation structure (MacArthur and MacArthur 1961, Anderson and Ohmart 1977) and floristic composition (Holmes and Robinson 1981, Rotenberry 1985, Wiens 1989). This variation can be significantly affected by single disturbance events such as fire or flooding (Knopf and Sedgwick 1987). If hypotheses address only site diversity, population changes occurring at longer temporal scales can be obscured (Knopf and Sedgwick 1987). Therefore, both spatial and temporal scale must be considered when asking questions about ecosystems. Hypotheses can test for movement toward desired future conditions (goals) that encompass a range of conditions, rather that those that occur at one set point in time (Morgan et al. 1994).

Keystones or Indicators

The concept of keystones or indicators up until recently has been confined to organisms (Mills et al. 1993). Keystone species have wide-ranging effects on ecosystem composition, structure, and function, often greater that their numbers would suggest (Noss and Cooperrider 1994). There has been debate about the usefulness of the keystone species concept because of the potential to lose sight of the complexity of ecological interactions (Mills et al. 1993). However, deMaynadier and Hunter (1997) have expanded the keystone concept to include keystone ecosystems such as large rivers that serve as a fire breaks in savanna landscapes, and Holling (1992) discusses biotic and abiotic processes that have disproportionately large effects on ecosystem function. For example, in northern hardwood forests in the eastern United States, spruce budworm populations cycle every 30–40 years (Morris 1963). This cycle is driven by an interaction among the budworm, insectivorous songbirds, and trees (Holling 1988). The changes that occur in the forest as a result of this interaction cannot be understood by looking at spruce budworm population dynamics alone; understanding the dynamics of the northern hardwood forest ecosystem is contingent upon understanding the keystone process.

Prescription Formulation and Implementation

The best prescription will result from the most desirable outcome with the greatest probability of occurrence (Walters and Holling 1990). After hypotheses have been developed, management prescriptions should be written in a way that facilitates hypothesis testing. In the adaptive management process, a framework of goals and information supports both hypothesis development and prescription formulation. To ensure reliable knowledge, an experimental approach should be taken in developing and implementing prescriptions, using controls and replication as much as possible. If necessary, consult with scientists or statisticians within your own organization or develop a working relationship with academic institutions that can offer the appropriate technical assistance. Involvement of scientists supports the objectivity of management decisions and reassures stakeholders who question the goals or methods being implemented.

Initially, data are gathered to establish baseline conditions or provide background that is useful for setting goals. Baselines are often important to assess shifts in populations and processes and will be the foundation of the monitoring program. Therefore, presume that inventories will be repeated and develop protocols to facilitate re-surveying.

Partnerships may be useful, and opportunities to cultivate them should not be overlooked. Good working relationships often emerge from involvement of stakeholders. Faculty or students from local schools, environmental groups, or citizens from surrounding neighborhoods can assist in gathering and compiling information. For example, students and faculty from the University of Wisconsin-Stevens Point are involved in a regional savanna restoration project involving six different restoration sites in Wisconsin and Illinois, working with both public and private agencies. The students collected information for long-term restoration monitoring and conducted separate research projects related to the goals and objectives of their respective sites. Partnerships like this refine understanding of savanna restoration techniques, facilitate communication, enhance interest in the ecosystem, and add educational value to the project.

If the rest of the adaptive management process has been done well, the implementation of prescriptions is the most straightforward task in restoration. Involving stakeholders in restoration activities such as prescribed fire, brush and noxious weed removal, and seed harvesting help promote understanding and teamwork as well as getting the job done.

Even when stakeholders have agreed on ecosystem goals, they may differ in how best to achieve them. For example, we (Haney and Power 1996) hypothesized that the use of the oak wilt fungus *(Ceratocystis fagacearum)* might be used to reduce tree cover during oak savanna restoration (Collada and Haney, in press), but many stakeholders would strongly object to using it. Gypsy moths are effective in reducing woody vegetation, but neighbors and resource managers alike would likely object if these insects were introduced into a degraded savanna. Ideally, the majority of stakeholder groups should understand the ecosystem, share their opinions, and be involved in deciding future conditions and management actions. If necessary, employ conflict resolution to resolve differences before proceeding. Creative solutions are often possible. For example, timber sales followed by fire can be used to reduce woody biomass in overgrown savannas, thereby recovering economic value in the process and providing benefits to stakeholders who may otherwise object to restoration (Haney and Power 1996).

Although many stakeholders will have opinions about prescriptions, it is ultimately the responsibility of the manager to decide how to proceed. This is the art of ecosystem management. An implementation index is a way to assess the applicability of a prescription to a particular management situation. Table 1 is an example of an implementation index for treatment options for barrens restoration at Necedah National Wildlife Refuge. The political feasibility, technical feasibility, and efficacy ratings are based on conversations with stakeholders and past management experience. It is a model representing our best understanding

Table 1. Implementation index. Alternative treatments are evaluated according to political feasibility, technical feasibility, and efficacy. Values may be weighted to correspond to individual management situations.

Treatment Options	*Political Feasibility (PF*	*+*	*Technical Feasibility TF)*	*x*	*Efficacy (E)*	*=*	*Implementation Index I*
Timber removal	4		4		4		32
Prescribed fire	3		4		3		21
Herbivory	2		2		1		4
Insect introduction	1		4		1		5
Disease introduction	1		4		2		10
Herbicide	2		4		2		12
No treatment	5		5		1		10

of the way these treatment options interact with the current political climate, the Refuge's technical and logistical capabilities, and the composition, structure, and function of the ecosystem. The implementation index, I, is calculated as

$$I = (PF + TF) \times E$$

where PF = political feasibility, TF = technical feasibility, and E = efficacy. In the Necedah model, timber removal and prescribed fire had the highest indices and therefore were the preferred options. In addition, we know through previous management experience that these two treatments work better in combination than separately. I can also be calculated for combinations of treatments, when appropriate, as

$$I = [(PF_1 + PF_2) + (TF_1 + TF_2)] \times (E_1 + E_2)$$

For more discussion on the use of this index, see Haney and Power (1996).

Monitoring

Monitoring methods follow directly from the models and hypotheses being tested. Once restoration has begun, monitoring responses of the ecosystem to management activities facilitates the improvement of management techniques, increases understanding of the ecosystem and how it functions, and facilitates sharing objective results with stakeholders.

The adaptive management model is particularly useful in sorting through the myriad issues surrounding monitoring. Monitoring can address different scales of time and space, from the effects of heat on seeds in the soil at a particular point during a fire, to the survival of a cover type over an entire landscape. Monitoring programs have more rarely addressed the human dimensions of resource management. Stakeholder opinions and effects on the landscape both need to be included to achieve a sustainable desired future condition. (For more information about choosing variables to monitor, see Model and Hypothesis Development).

Noss and Cooperrider (1994) listed three types of monitoring necessary for adaptive management. Implementation monitoring keeps track of whether managers accomplished what they said they would. Unfortunately, some agencies do not get beyond implementation monitoring, which is rarely pertinent to hypothesis testing. Effectiveness monitoring, on the other hand, answers the question "Did the prescription meet its goal?" Validation monitoring goes farther and answers the question ”How well did the prescription meet its goal?” It is this level of monitoring that is most useful for testing hypotheses. For example, songbird populations on a restored savanna were hypothesized to increase 10% because of an increase in structural diversity. Although effectiveness monitoring revealed that songbird populations did increase by 10%, validation monitoring indicated that the reason was actually an increase in the cover of warm-season grasses.

Issues of efficiency are also important when designing a monitoring program. Linking monitoring to hypothesis testing is the best way to make the use of limited resources. This ensures that the questions that need to be addressed to meet goals and objectives are first priority. Choosing keystone or indicator variables to monitor and integrating the elements of a biological monitoring program into nested units also increases efficiency. For example, we developed a biological monitoring strategy for Necedah National Wildlife Refuge (Figure 2). It integrates the monitoring components that we hypothesized were important for monitoring long-term change over time, as well as provides information about savanna habitat and associated species of concern. Monitoring plots will be randomly located in savanna habitats across the Refuge. Plant, invertebrate, avian, soils, and fire effects monitoring plots are all located around a single plot origin point. This strategy saves time and energy in

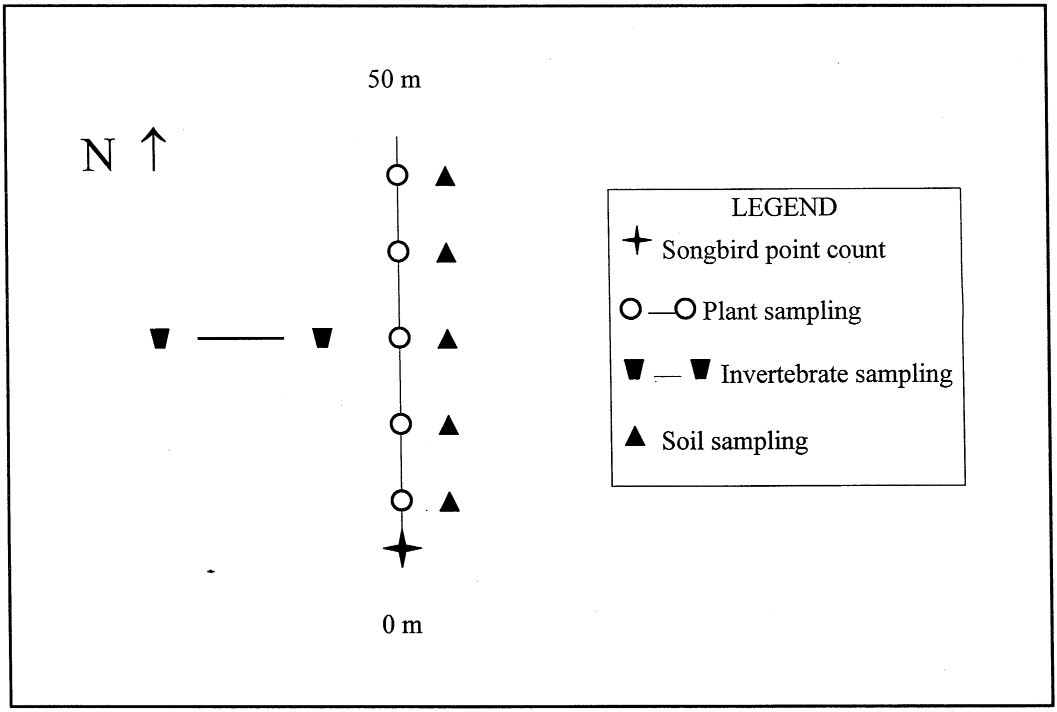

Figure 2. A biological monitoring plot at NNWR. Monitoring needs to provide the information necessary to test hypotheses, as well as evaluate responses of ecosystems to management activities.

documenting and traveling to plot locations, especially if field technicians vary from season to season. It also provides a clear, concise framework for explaining the program to others, especially to administrators for whom efficient use of time and money is a primary consideration. However, not all monitoring variables can be linked in this way, especially those dealing with human dimensions or rare species.

The final step is analyzing the data and sharing it with stakeholders. This begins the next cycle. At the very least, this increases the knowledge and understanding of stakeholders. In some instances information from monitoring may cause us to reconsider our goals, develop new models and hypotheses, modify prescriptions, and involve additional stakeholders. Thus, the adaptive management cycle is a continuous, integrated process that generates information and guides management decisions.

Summary

Ecosystems are far more complex than we can understand. Moreover, extraneous variables such as climate, exotic species, disease, and public opinions are changing constantly and cannot be predicted well. Adaptive management is a model to guide ecosystem managers in dealing with uncertainty; it recognizes that ecosystems are resilient, and that we can adjust our management as we learn more about the ecosystem or as goals change. Adaptive management is an ongoing process that couples social values to ecological knowledge using consensus building and good science.

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Analyzing Forest Landscape Restoration Potential: Pre-settlement and Current Distribution of Oak in the Northwest Wisconsin Pine Barrens

Abstract *Ecosystem restoration and management requires knowledge of the species composition, ecological processes, and structure of natural landscapes. Current forest landscapes of Wisconsin are the result of over a century of human use. Certain ecological processes, such as fire, cannot be studied in the current human-dominated landscape. Our study objective was to reconstruct the historical, large-scale pre-European landscape of the Pine Barrens in northwestern Wisconsin and to compare the extent and abundance of the oak component to its current importance. Our questions were (1) does the current distribution of oak resemble pre-settlement conditions and (2) did oak savannas exist at pre-settlement times, which would indicate a high frequency but low intensity fire disturbance regime. We used a species-level satellite image classification to map the current distribution of oak. The pre-settlement conditions were reconstructed using the U.S. General Land Office (GLO) surveyor notes dating from 1847–59 in a geographical information system (GIS).*

Our results indicate that oak increased in the Pine Barrens landscape over the last 150 years. The increase is particularly strong where nineteenth-century surveyors mentioned oak understory. Fire suppression may have contributed to the oak increase by permitting these understory oaks to reach canopy height. Oak savannas were not widespread in the pre-settlement landscape, but likely did exist in the south-central part of the Pine Barrens, where larger, dispersed bur oaks were noted by the surveyors. Our study demonstrates the value of the GLO data for the broad scale reconstruction of pre-settlement vegetation and disturbance characteristics. These historical data can provide managers with additional information about ecosystems and can assist in restoration management.

Ecosystem restoration and management requires knowledge about the species composition, structure, and processes of the system under consideration. This poses a challenge, because very basic information can be difficult to obtain for current landscapes in Wisconsin due to changes imposed by over a century of land use by European settlers.

Our study focuses on the Pine Barrens region in northwestern Wisconsin (Figure 1). The Wisconsin Department of Natural Resources (DNR) chose this ecoregion as the first in Wisconsin to be assessed as a regional ecosystem. In 1993, the DNR workshop "The Future of Pine Barrens in Northwest Wisconsin" (Borgerding et al. 1995) summarized current understanding of this ecosystem and identified some information gaps regarding the structure and composition of the pre-settlement forest landscapes. For example, the amount of open habitat and forest density present prior to 1840 was a point of discussion. This question is important for ecosystem management of the Pine Barrens; an answer requires study of historic data sources because of ecosystem changes during the last 150 years of European settlement.

The Pine Barrens ecosystem is located on a glacial outwash plain with extremely coarse and nutrient-poor sandy soils. The excessive drainage makes the region prone to drought and frequent forest fires (Curtis 1959). In pre-settlement times, these factors favored tree species such as pine and oak that are adapted to frequent fire. Jack pine *(Pinus banksiana)* has serotinous cones that are

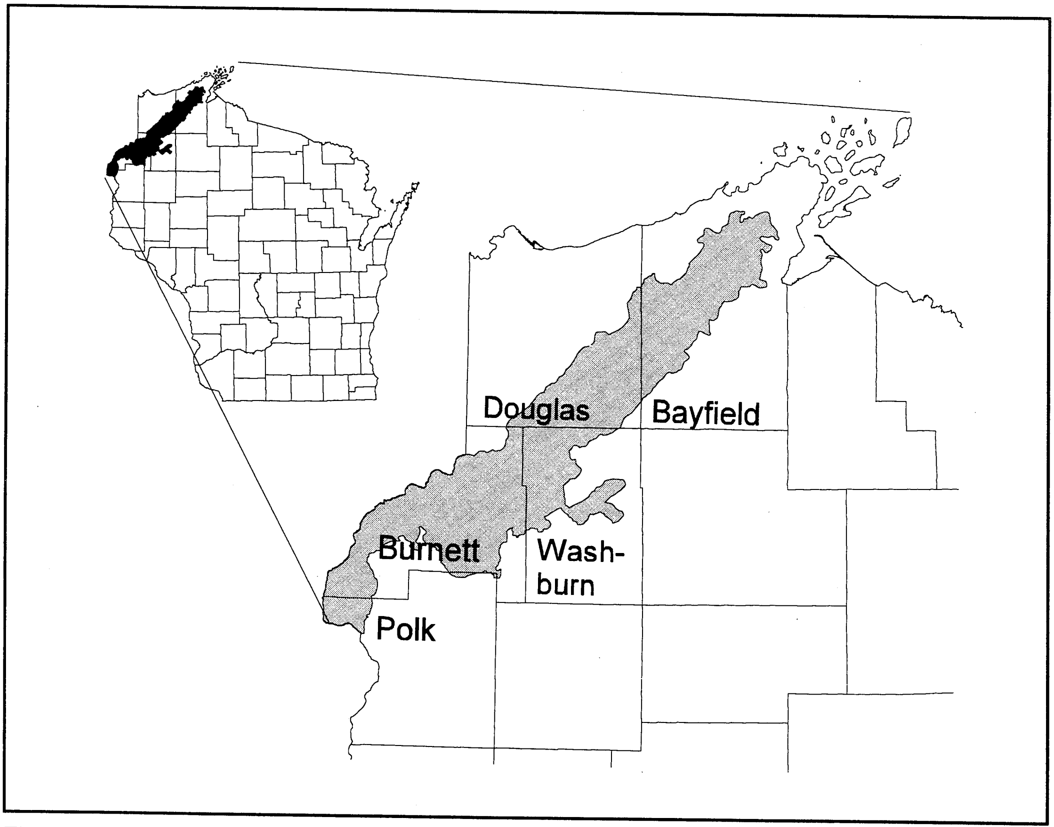

Figure 1. The counties of the Pine Barrens region in northwest Wisconsin.

sealed with resin. High intensity fire melts the resin and opens the cones, releasing the seeds. Regeneration usually follows on the exposed mineral soil. Mature red pine *(P. resinosa),* bur oak *(Quercus macrocarpa),* and to a degree white pine *(P. strobus),* are protected by thick bark from damage by less intense surface fires. Northern pin oak *(Q. ellipsoidalis)* and bur oak are able to resprout if their stems are killed by fire (Curtis 1959).

Very few descriptions exist of the Pine Barrens vegetation before European settlement during the second half of the nineteenth century. Geological surveyors wrote that "in the 'barrens'. . . the trees are either scrub pine *(P. banksiana),* or black-jack oaks *(Q. ellipsoidalis),* averaging in diameter about three or four inches and in height not over fifteen feet. In some places . . . the trees are at considerable distances from each other" (Sweet 1880). Some portion of the Pine Barrens "are covered with scrub pine to the exclusion of all else save underbrush. . . . Other areas are covered with burr, black, and even white oak bushes, with occasional trees of these species" (Strong 1877). Finley, in his analysis of the General Land Office (GLO) surveyor notes, classified the region as "jack pine, scrub (Hill's) oak forests and barrens" (Finley 1951).

All these sources describe forests of low density that contained pine and oak to varying degrees. However, these sources do not provide details about spatial variability of forest composition and structure across the Barrens landscape. Did soil differences affect the pattern of forest structure? Did meso-climatic differences (e.g., the lake effect in the North) result in different forest types? Were the southern parts of the Barrens, being closer to the prairie border, more open?

These questions are highly relevant for ecosystem management, but answering them is difficult. Changes during the last 150 years due to logging, farming, and forestry make it difficult to assess what the pre-settlement ecosystem looked like and how it functioned in relation to past disturbance regimes.

Logging, starting around 1850, focused first on white pine and later red pine (Murphy 1931). Loggers were followed by settlers because the sandy soils were easy to plow (Vogl 1964). Intense forest fires increased due to the slash from the logging operations and also opened the forests. Around 1910, jack pine logging began after technology became available to use jack pine wood for pulping. At this time, the combination of logging and farming probably created more open habitat than ever before. In the 1930s, the economic depression and the depletion of the inherently nutrient-poor and droughty soils caused many farmers to abandon their land. Much tax-delinquent land became the starting point for creating county forests, timber industry holdings, and the Chequamegon National Forest (Vogl 1964). Civilian Conservation Corps workers planted large tracts with jack pine, and the Wisconsin Conservation Department began fire suppression programs. These developments created the present-day forest, which may be much denser than before European settlement.

Our research questions are: what was the relative importance of oak throughout the Pine Barrens, and did oak savannas and woodlands exist in the Pine Barrens before the advent of European settlers? How did the oak component in the landscape change since European settlement?

Savannas are best defined structurally; they have less canopy coverage than forest. Any distinct boundary between savannas and forests is somewhat arbitrary; we follow Curtis (1959), who suggested less than 50% canopy coverage as a threshold to define savanna.

Currently, oak is common in the region, especially in the northern and southern parts. Restoration efforts in the Pine Barrens have focused on open Barrens habitat (Vogl 1964, Vora 1993). Our study investigates whether the existence of oak savannas in pre-settlement times suggests we should discuss their restoration also.

We analyzed the Pine Barrens pre-settlement vegetation using the U.S. General Land Office survey notes in a geographical information system (GIS). We compared these data with the current forest cover as mapped from Landsat satellite imagery. Because the GLO data were not recorded for scientific purposes, they contain some bias. For instance, some surveyors favored certain species over others as witness trees. In some areas, different surveyors mapped the township boundaries (exterior lines) and the township area (interior lines). Nevertheless, the GLO data set is one of the best data sets available for reconstructing pre-settlement vegetation (Galatowitsch 1990, Manies 1997) and for studying pre-settlement vegetation in relationship to soils (Whitney 1982, Delcourt and Delcourt 1996), fire (Lorimer 1977, Kline and Cottam 1979, Grimm 1984), and windthrow (Canham 1984). A number of studies used GLO data to examine landscape changes (Stearns 1949, Mladenoff and Howell 1980, Iverson and Risser 1987, Iverson 1988, White and Mladenoff 1994, Whitney 1994). Studies that analyzed the GLO data on an individual witness tree level usually examined areas no larger than a few townships (Thomson and Fassett 1945, Delcourt and Delcourt 1996). For some Midwestern states, generalized maps of the pre-settlement vegetation have been generated (Finley 1951). However, these maps required a classification of the witness tree data into general cover classes, thus losing much detail.

Methods

GLO Data analysis

Wisconsin was initially surveyed around the middle of the nineteenth century. The land was divided into townships (6 x 6 miles), sections (1 x 1 mile), and quarter-sections (0.5 x 0.5 mile) so that it could be sold to homesteaders and logging companies. To establish the location of each township, section, and quarter-section, survey posts were placed at each corner (all referred to as corners in the following). The surveyors marked 2–4 witness trees in the vicinity of each corner. In their journals, the surveyors recorded the species, diameter, and distance from the corner for each tree. Sometimes, they also described understory vegetation.

Our study is one of the first to analyze GLO witness tree data in a GIS for a large ecoregion. The advantage of the GIS-based approach is that a high level of detail can be maintained for extensive areas. The data set is part of a larger database of the entire state of Wisconsin currently under development at the Department of Forest Ecology and Management at the University of Wisconsin-Madison in cooperation with the Wisconsin DNR (Manies 1997). For our analysis, we used only the witness trees at township, section, and quarter corners and disregarded trees along section lines and at so-called meander corners, where survey lines intersected water bodies. The data set contains point information for 5,086 corners with a total of 11,153 trees in the Pine Barrens. For each corner, we calculated the mean distance traveled from the corner to record the witness trees. We did not interpolate between the corners to derive forest type polygons, but rather analyzed the complete data set.

Satellite image analysis

To compare the GLO data with the current vegetation cover, we utilized a species-level satellite image classification previously derived for northwest Wisconsin (Wolter et al. 1995). A number of studies have used satellite imagery to map forest cover (Hopkins et al. 1988, Moore and Bauer 1990, Hall et al. 1991, Bolstad and Lillesand 1992, Woodcock et al. 1994). Image processing software uses reflectance differences between tree species to classify raw satellite data into land cover maps (Lillesand and Kiefer 1994). The distinction of deciduous from coniferous forest usually can be achieved with an accuracy greater than 85%. However, differentiating among deciduous species is difficult and less accurate when only a single satellite image is used. For instance, the reflectance of sugar maple *(Acer saccharum),* trembling aspen *(Populus tremuloides),* and red oak *(Q. rubra)* are not different during the peak of the growing season. Single-species classification accuracy can be improved by analyzing a suite of images throughout the time of senescence and leaf flushing (Wolter et al. 1995). Peak fall colors for red oak are about two weeks later than for sugar maple. In spring, trembling aspen leafs out about one week earlier than other hardwoods. Satellite imagery captured at these different points can identify the distribution of various species. Using a total of five satellite images, Wolter et al. (1995) were able to classify nineteen types of forest cover and eight other land cover types with an overall accuracy of 83.2%.

In the satellite image classification, red oak occurs predominantly in the northern half and pin oak in the southern half of the Pine Barrens (Plate 2b; see p. 201). For red oak, the producer's accuracy of the classification was 86.7% and for pin oak 81.6%. Producer's accuracy indicates what percentage of the pixels on the ground was correctly identified in the classification. The user's accuracy was 84.8% for red oak and 100% for pin oak. User's accuracy indicates what percentage of the pixels in the classification is actually that species on the ground. For example, all pin oak on the map is pin oak on the ground, but 18.4% (100%–81.6%) of all pin oak on the ground was mapped as other classes in the image classification. The satellite image classification does not identify bur oak because there were not enough pure stands of this species to use as references for the classification algorithm (Wolter et al. 1995).

Data integration

Examining landscape changes by comparing GLO data to a satellite image classification is not straightforward. The two data sets have very different data capture methods and spatial resolutions. The GLO surveyors mapped points at 0.5 mile distances. They sampled between one and four trees, commonly two, in the vicinity of the corner. The species chosen were not necessarily the dominant canopy species. In contrast to the GLO data, the satellite image classification contains a continuous grid with a 28.5 x 28.5 m pixel size. Each pixel is classified according to its dominant canopy species, thus containing only one tree species.

Processing was required before the two data sets could be compared. Each GLO corner location falls within a single pixel of the satellite image classification. However, the surveyors chose witness trees from a larger radius than 14.25 m, which is half of a pixel (28.5 m). Therefore, we recorded presence or absence of oak in the satellite classification in circles, or buffers, around each corner. This operation was performed three times with different buffers (5, 9, and 21 pixel) to evaluate the effect of different buffer sizes on our analysis (Figure 2). We re-classified the GLO data to represent the presence or absence of oak at each corner, thereby making the two data sets compatible. In the integration of GLO data and the current classification, each corner was classified as either (1) oak present only in the GLO data, (2) oak present only in the satellite image classification, (3) oak present in both data sets, or (4) oak not occurring.

For a general comparison of data sets, we calculated the relative occurrence of oak in comparison to other tree species in the GLO data set and the satellite image classification of single pixels. In the GLO data we summarized how often the surveyors found each tree species and calculated percentages for each species. The calculation of relative occurrence of tree species in the satellite image classification was based only on forest classes because classes such as water or settlements were not recorded in the GLO data, but classified in the satellite image. The comparison of relative occurrences is independent of buffer sizes.

Results

GLO data

The distribution of pre-settlement forest vegetation derived from the GLO data suggests that the Pine Barrens was not a homogenous region (Plate 1a; see p. 200). The northern part in the Bayfield Peninsula was dominated by red pine, intermixed with white pine, red oak, and jack pine.

The central part of the Barrens in Douglas County was covered predominantly by jack pine. Red pine occurred largely along the edges of the outwash plain or in the vicinity of natural firebreaks such as lakes. The central part also contained a 5-km long patch where no trees were recorded by the surveyors. Their field notes mention that charred sticks were used as corner posts in this patch, indicating a recent fire.

The southern part of the Barrens, in western Burnett and in Washburn Counties, was characterized by a north-south gradient, with jack pine dominating in the north and red pine, oak, and white pine dominating the south. Pin oak and bur oak often occurred

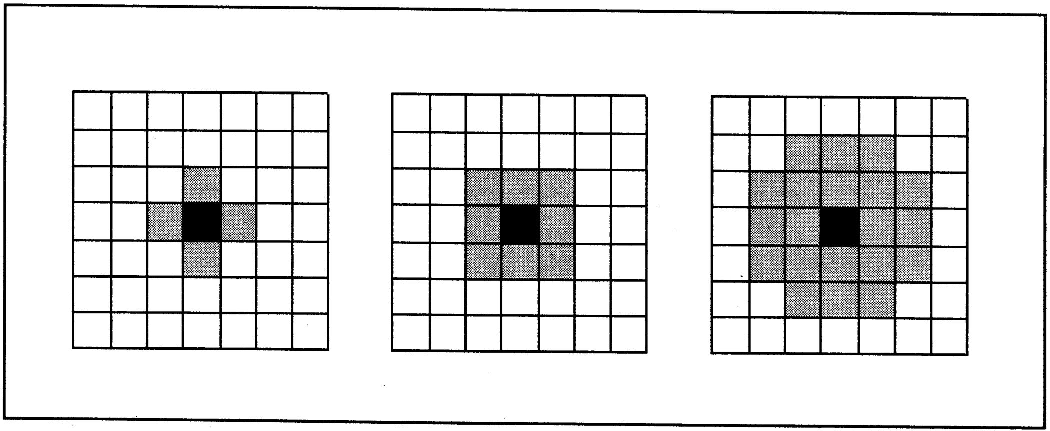

Figure 2. Different buffer sizes used to estimate oak presence around corners in the satellite image classification.

close to lakes, which are particularly abundant in this area (Plate 1b).

The extreme southwestern part of the Barrens, in southwest Burnett and northwest Polk Counties, showed a similar north-south gradient, though the surveyor of the townships in Polk County (H. Maddin) did not distinguish among pine species. Bur oak was the most common oak, occurring along the valley of the St. Croix River and the edge of the outwash plain. Corners where no trees could be found were located in marshy areas.

Oak diameters in the GLO data were not randomly distributed across the Barrens (Plate 1c). In the north and central Barrens, most of the oaks were small (10–30 cm diameter), with some trees as large as 50 cm. The largest oaks, up to 85 cm in diameter, were recorded in the southern and southwestern parts, usually in close vicinity to lakes and streams.

A characteristic of savannas is their low tree density. Large distances between a corner and its witness trees in the GLO data indicate low relative tree density (Plate 2a). The largest distance class (251–2000 m) represents corners where surveyors found very few trees due to recent fires or marshes. The distribution of these points follows no clear pattern except in one patch in the central Barrens mentioned above. The corners in the smaller distance classes (<25–250 m) demonstrate a strong northeast-southwest gradient of the forest densities. Forest density was highest in the northeast and much lower in the southwest of the Pine Barrens.

Comparison of GLO and satellite data

The abundance of oak region-wide increased between pre-settlement times and today. The apparent amount of increase is partly dependent on the buffer size used for detecting oak in the satellite image classification. Larger buffers will always result in a greater increase (Greig-Smith 1983). However, even with the most conservative five-pixel buffer, the oak increased from 1850 to 1987 by 198% (9 pixel: 253%; 21 pixel: 371%).

Table 1. Number of corners where oak was present or absent in 1850 and 1987 depending on the buffer size used for detecting oak by satellite classification.

	Buffer size (# of Pixel)		
	21	*9*	*5*
Oak only in 1850	226	304	343
Oak only in 1987	1,539	1,050	819
Oak in 1850 and 1987	259	181	143
Never oak	3,057	3,548	3,779

The absolute number of corners where oaks occurred only in 1987 increased by 720 (48%) when the buffer size is increased from 5 to 21 pixels (Table 1) and conversely, the number of corners without oak decreased by 722 (19%). For corners with oaks in the GLO data, 53% also had oak in the satellite image classification when calculating a buffer of 21 pixel, but only 29% when a buffer of 5 pixels was used.

Many changes in oak occurrence are rather local (Plate 2c). We present only the increase estimated with the largest buffer size; maps from the two smaller buffer sizes reveal the same areas of oak increase. Especially in the south, there are many cases where a given corner contained oak only in the GLO data and the neighboring corner had oak only in the satellite image data. These changes are most likely due to local patch dynamics.

In the north, there are fewer corners where oak occurred only at pre-settlement times, and many of the corners contained oak in both data sets. There is also a strong increase in oak throughout Bayfield County. The central part of the Barrens experienced the smallest increase of oak (Figure 3). The areas where

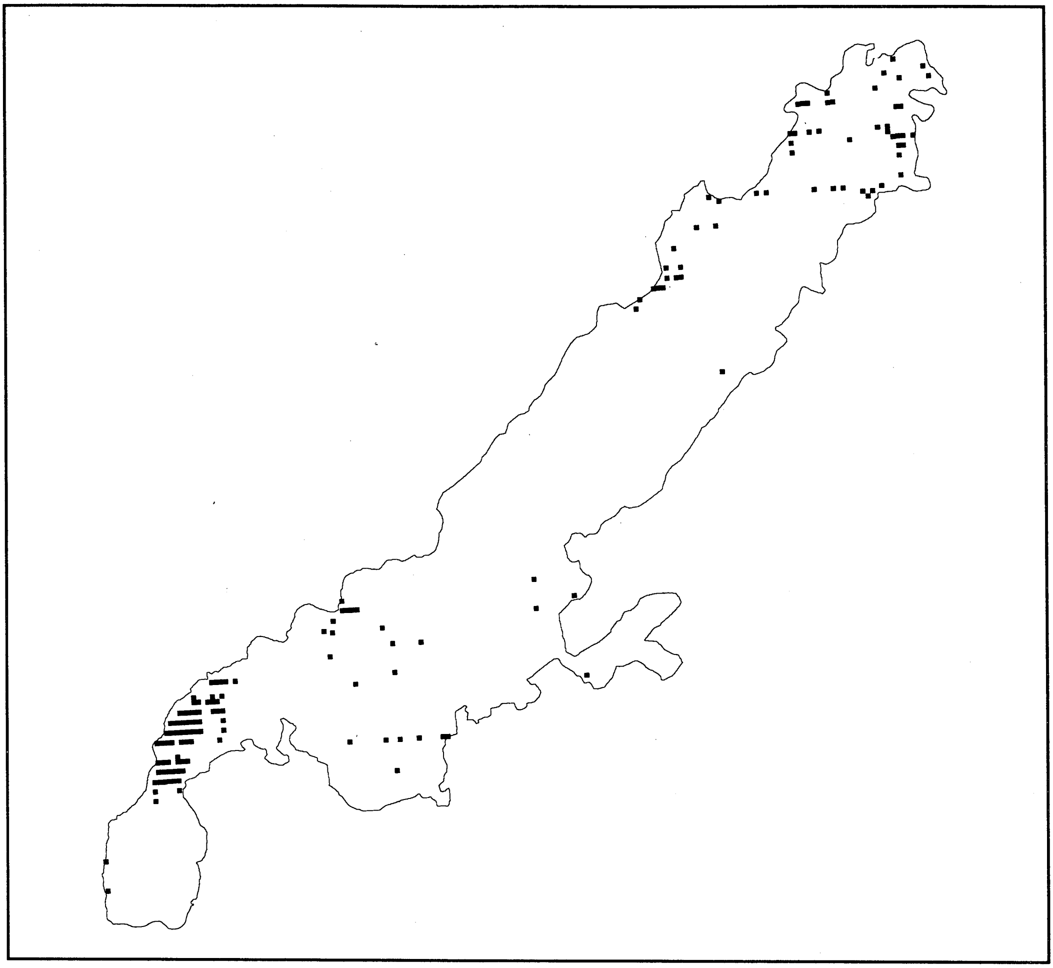

Figure 3. Corners with oak understory in the GLO data.

oak was mentioned in the understory from GLO surveys are the same areas where a strong increase of oak occurred by 1987.

The relative occurrence of oak versus other cover types as represented in GLO data and the satellite image classification of the Pine Barrens region as a whole agreed with the results obtained with the buffer analysis (Figure 4). Out of the total area covered by forest, oak and pine combined occupied about 62%. However, oak alone increased from 8 to 23%, and pine decreased correspondingly.

Discussion

Ecosystems are dynamic entities, and studying them at only one point in time (e.g., the GLO survey date) provides an incomplete picture. Disturbance events, like large crown fires, alter the environment drastically over short time periods. A study that analyzes only data taken before the fire is likely to underestimate the influence of fire, while a study based on data captured after the fire might carry the opposite bias.

Furthermore, ecosystems adapt to long-term

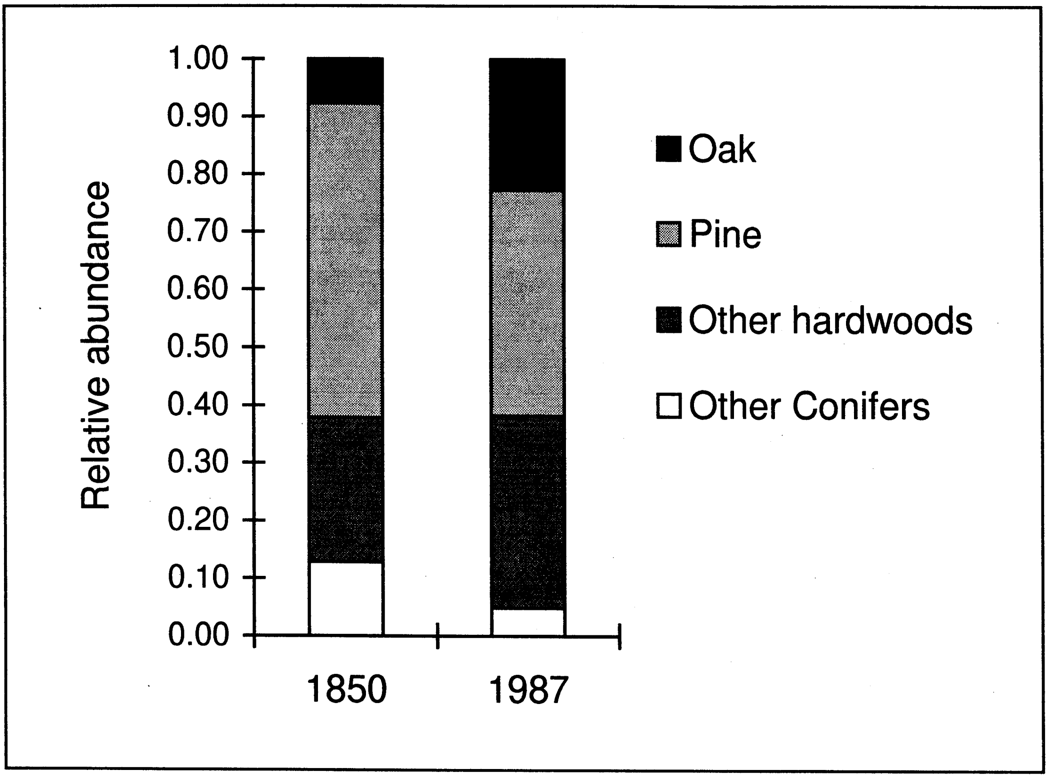

Figure 4. Relative amounts of tree species groups in the forests of the Pine Barrens ecoregion as calculated from GLO data and satellite image classification.

environmental changes. Climate has changed throughout the Holocene, and with it, vegetation cover has changed (Davis 1986, 1993, Webb et al. 1993). Predicting how the vegetation would have changed since 1850 in the absence of European settlement is problematic.

The pre-European settlement vegetation was not entirely natural or free of human alterations. Native Americans deliberately burned parts of the landscape to increase berry production and hunting opportunities (Murphy 1931), but the magnitude of ecosytem changes by Native Americans is difficult to assess, particularly in northern forest regions (Lewis and Ferguson 1988, Clark and Royall 1996).

The GLO data are not equivalent to the potential natural vegetation. When analyzing the pre-settlement vegetation, these limitations have to be kept in mind. We do not consider the vegetation cover suggested by the GLO data as a necessary goal for resource managers, nor do we advocate restoration of the landscape to a specific point in time. However, the pre-settlement vegetation cover was certainly less altered by humans than the current forest cover. Analyzing the pre-settlement vegetation provides a unique opportunity to study ecosystem composition, structure, processes and variability in relatively more natural conditions. Pre-settlement vegetation data are highly relevant where ecosystem management is being attempted, because they provide evidence of vegetation patterns at another point in time and under different disturbance regimes.

The importance of surveyor bias contained in the GLO data has been discussed in various publications (Bourdo 1956, Delcourt and Delcourt 1974, Grimm 1984, Iverson and Risser 1987). Opinions range from "the information recorded by the surveyors provides an unbiased sample of vegetation cover as it existed in presettlement days" (Vogl 1964, p. 161) to much more conservative analyses of surveyor bias and attempts to quantify it (Bourdo 1956, Delcourt and Delcourt 1974, Manies 1997). The species recorded at a given location may have been a singular occurrence. Also, absence of a tree species does not necessarily indicate that the species was absent from the landscape. The ability of surveyors to identify tree species correctly is variable. In Polk County, in the southern Barrens, the surveyor (H. Maddin) recorded only 'pine' without further distinction. The occurrence of black oak *(Quercus velutina)* in the Pine Barrens is very unlikely, because its northern range does not reach this region. However, several surveyors recorded black oak (Plate 1b), probably referring to the black oak group that contains northern pin oak, northern red oak, and black oak (Curtis 1959). The raw information of the surveyor notes needs to be interpreted carefully before ecological conclusions can be drawn.

The scale of the GLO data limits its minimum mapping resolution (Delcourt and Delcourt 1996). This makes analysis of small areas, such as single townships, questionable. However, the resolution of the GLO data appeared to be adequate to interpret regional trends at the scale of the Pine Barrens landscape (450,000 ha). Regional trends can be concealed when data are classified and aggregated before the analysis. The use of a GIS allowed us to handle the large amount of detailed information, without classifying it initially. This was essential for our approach to compare species occurrence at each section corner.

Despite potential problems, the GLO data contain a vegetation sample of tremendous value. The data were collected during a relative short time period. The survey of the Pine Barrens was completed in twelve years (1847–1858), and 68% of the data were collected in two years (1855–1856). During these few years the Pine Barrens landscape presumably did not experience major changes. The brief survey period of the Barrens ensures that spatial vegetational differences reflect environmental gradients and not temporal changes.

The data collection was standardized, and single surveyors covered large areas. For instance, three surveyors (H.C. Fellows, E. Sears, and A.C. Stuntz) surveyed 74% of all corners in the Pine Barrens. The small number of surveyors minimizes the impact of personal bias.

The sampling scale of the GLO survey is uniform, which makes regional comparisons possible. There are no other detailed presettlement vegetation data available for large regions. The value of the GLO data for vegetation analysis, despite all constraints, becomes apparent when examining the species composition of the Pine Barrens (Plate 1a). The occurrence of red pine and oak throughout the Barrens is associated with soil, topographic, and hydrologic features that influenced fire patterns. Slight differences in soil quality, topography, and hydrology are reflected in the GLO data. Detailed soil maps for the Pine Barrens are not available, but the mapping of Landtype Associations by the Wisconsin DNR provides a coarse picture of soil productivity (Figure 5). On the poorest soils, jack pine forms pure stands. Slightly more productive soils carried mixtures of red and white pine. The best soils in the Pine

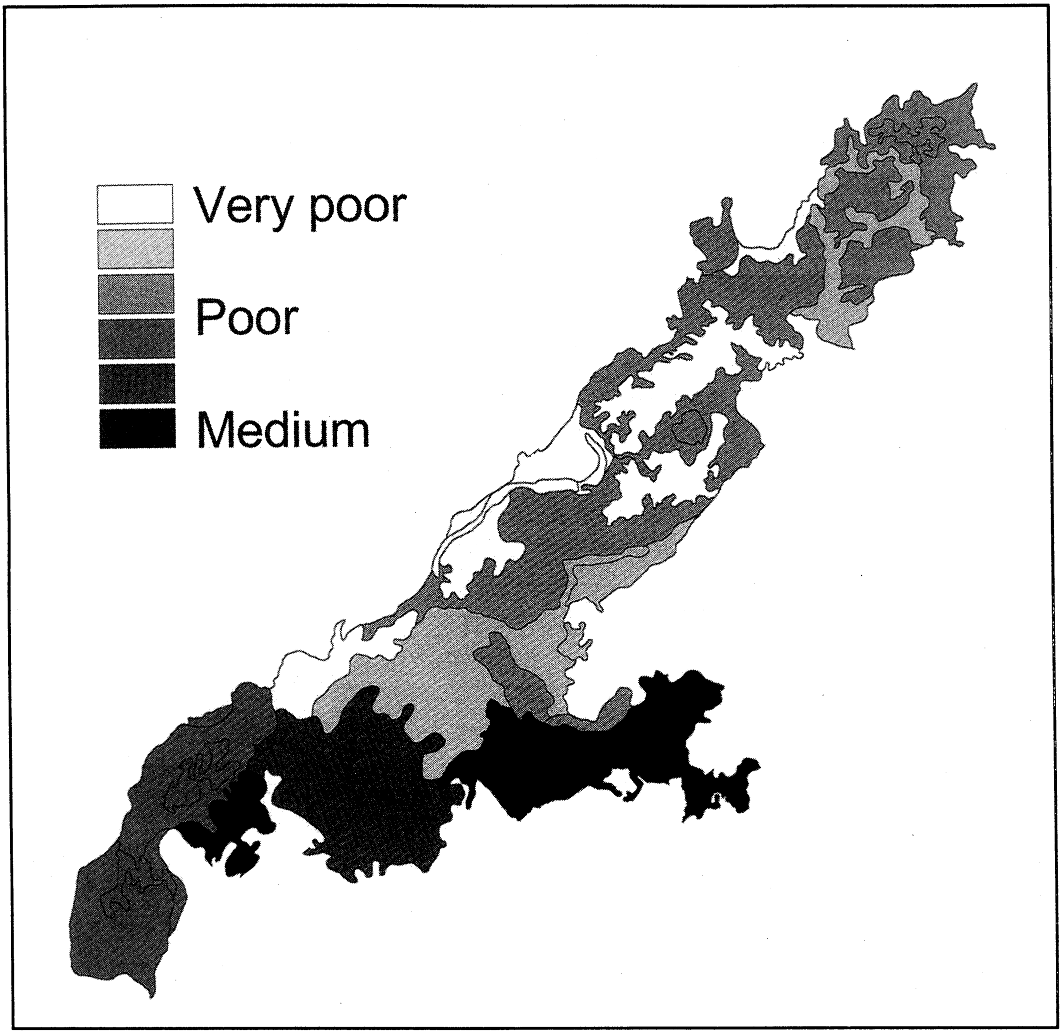

Figure 5. Soils of the Pine Barrens ranked according to their soil productivity (Wisconsin Department of Natural Resources).

Barrens supported oaks. The forests in the northwestern Pine Barrens are dominated by red pine, despite the poor soils. The higher precipitation, lower summer temperature, and lower evapotransporation due to the lake effect might have limited fire in this area. Furthermore, the rolling topography of the Bayfield Peninsula provided microhabitats where trees other than jack pine found favorable growing conditions.

Stand densities reveal a strong gradient, generally being lower in areas closer to the forest-prairie border region (Plate 2a). The recorded values in the southern Pine Barrens, which are often between 25 and 250 m, indicate landscapes of open forest and solitary trees. For comparison, in mesic hardwoods the average distance between corners and witness trees is about 11.6 m (K. Manies, unpublished data).

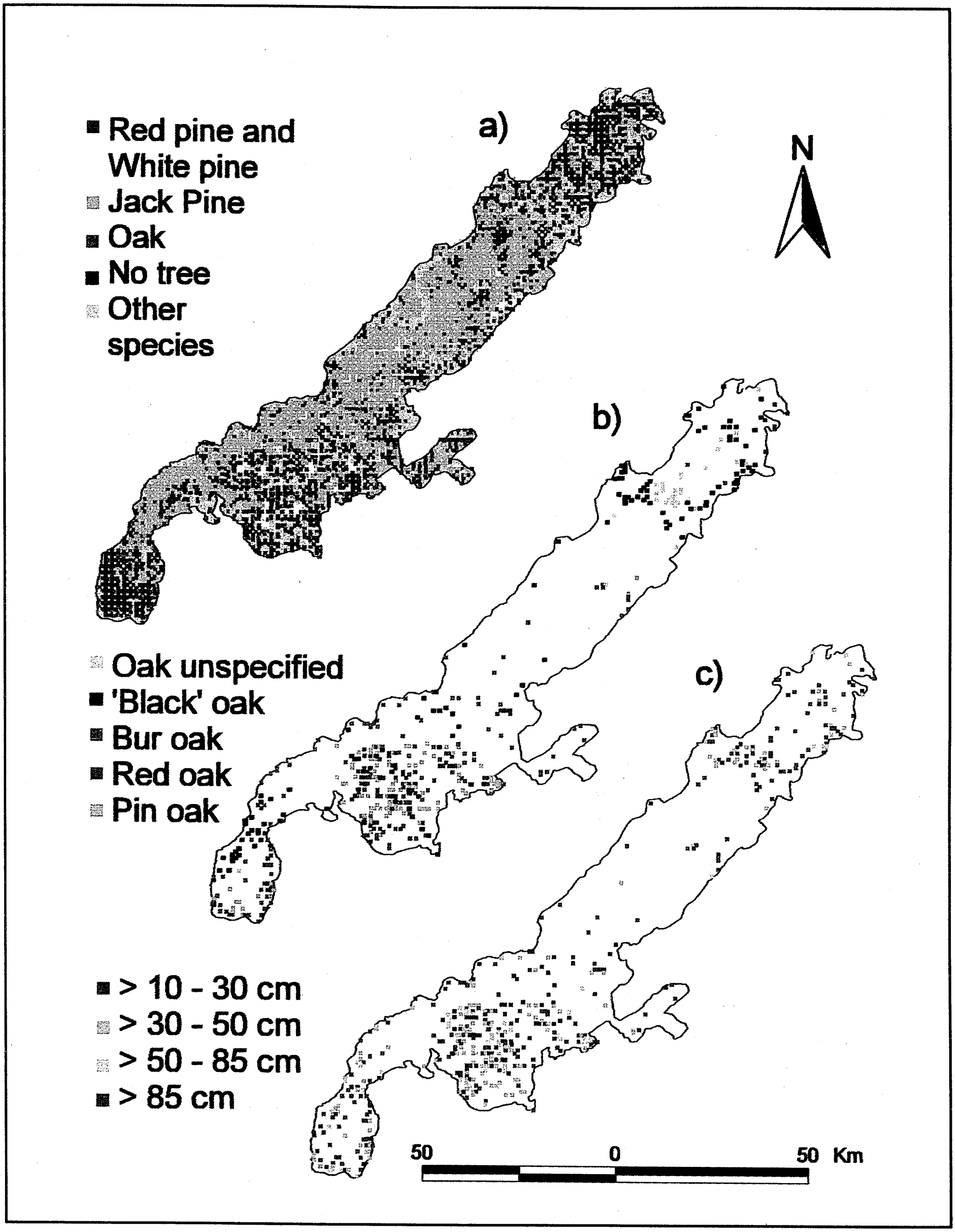

Plate 1. (a) Dominant tree species in the GLO data, (b) oak species distribution in the GLO data; (c) average diameter of oak in the GLO data.

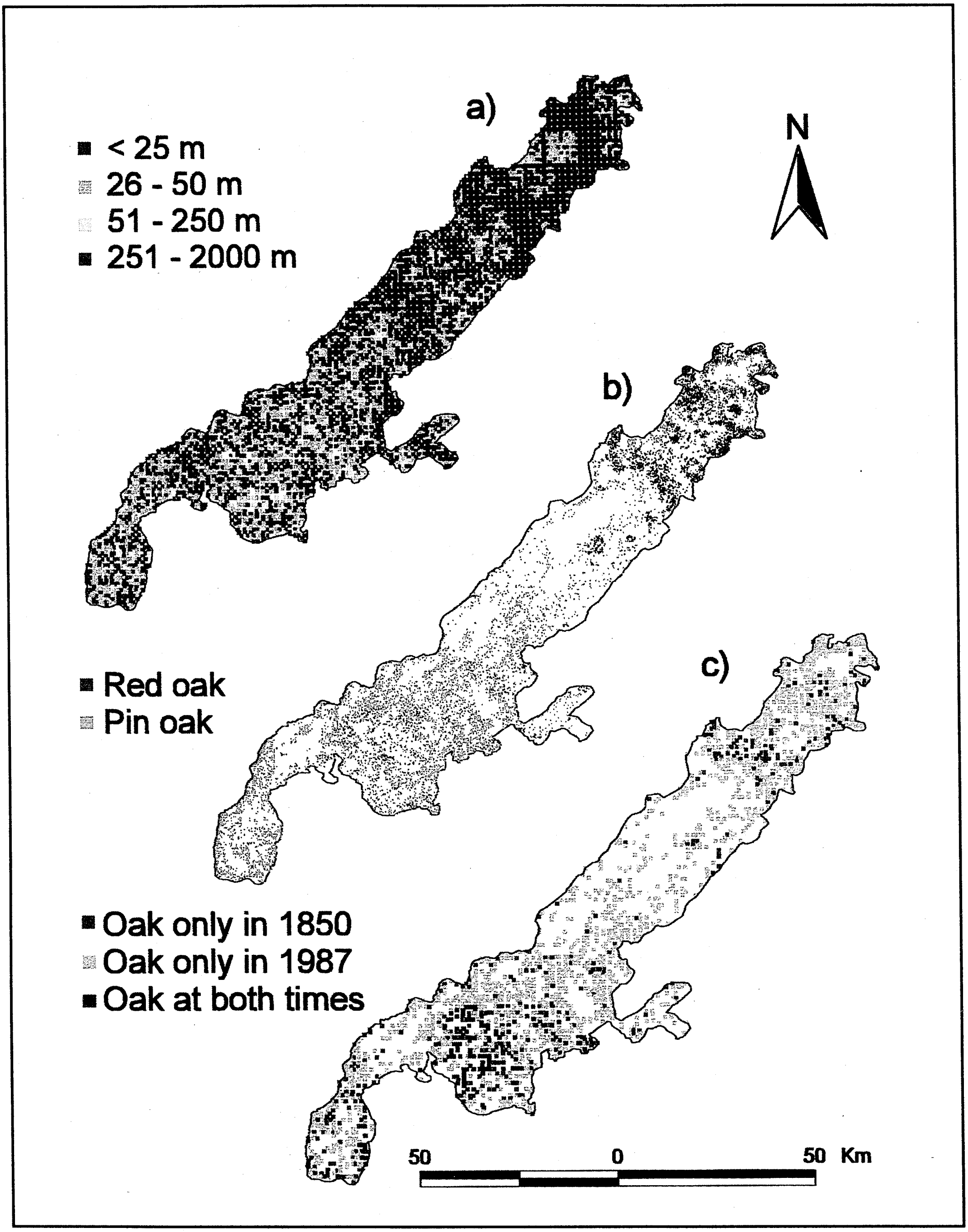

Plate 2. (a) Average distance between witness trees and corners; (b) oak occurrence in the species level satellite image classification; (c) changes in the oak distribution from pre-settlement to today when examining the satellite image classification with a 21 pixel buffer (compare Figure 2).

Conclusions

Our GLO data analysis suggests that oak savannas were not widespread, but possibly existed as localized patches in the southern and southwestern Pine Barrens. In these regions, soil quality, stand densities, the presence of bur oak, and the relatively large tree diameters in the GLO data match the characteristics of oak savannas.

The increase of oak from pre-settlement times to today was detectable with different methods, and increases were particularly strong in areas where the GLO data contained oak as an understory species. This increase of oak is probably related to pine logging and fire suppression, which allowed oak sprouts to grow until they became part of the canopy.

What are the implications of our results for ecosystem management of the Pine Barrens? First, the Pine Barrens were not uniform in terms of oak occurrence. The surveyors mentioned red oak only in the northeastern Barrens. Pin oak was mostly recorded in the south-central Barrens and bur oak in the southwestern part of the Barrens. The poorest soils in the central Barrens probably did not contain much oak in pre-settlement times. This general distribution of oak species still occurs in the current landscape, but oak has increased overall.

The strong northeast-southwest density gradient at pre-settlement times (Plate 2a), when forests were more open in the southwest and denser in the northeast, diminished as forest came under management and fires were suppressed. Landscapes in the central part of the Pine Barrens were probably shaped by high intensity crown fires with return intervals of less than 50 years (Givnish 1995). Jack pine dominated this area as the fires and droughts prevented other species from dominating. If restoration of the pre-settlement conditions is attempted in this area, management should focus on large patches of open habitat that can resemble openings of fire origin. These open patches might shift in the landscape, and their features could be partially achieved by clear-cutting (Niemuth 1995). Upon the creation of a new, large open patch, a previous patch could be regenerated with jack pine. This management could mimic typical jack pine regeneration after fire for some habitat purposes. However, all processes typical of the fire-controlled landscape would not be duplicated with only logging. Areas of low tree density and substantial open areas (mean tree-corner distance of 0.25 – 2 km) also occurred within the jack pine-dominated central Barrens, on the poorest soils.

The northern Barrens in Bayfield County contained more diverse forests with a species mix of jack pine, red pine, white pine, and red oak. These mixed forests were relatively dense. The ecosystem in this area would probably benefit from forest management that maintains all species in the landscape. Large-scale disturbances were much less common in this area, but smaller, intense disturbance patches can be assumed due to the complete lack of trees at some corners.

In the southern and the southwestern Barrens, extensive crown fires were probably rare due to a higher density of lakes that functioned as fire breaks. In this region, red pine, white pine, and oak were interspersed with jack pine, but fires with lower intensity, although perhaps higher frequency, allowed oaks to reach diameters of 50 cm and more. The average distance between witness trees and the surveyed corner was often more than 50 m. This is the region where we assume local oak savannas occurred. Given that fire is a stochastic process, locations of oak savanna were not stationary. One area with repeated low intensity fires might have become a savanna. Another area, after no fires for several decades, might have experienced a crown fire exposing mineral soil and creating conditions favorable to dense jack pine regeneration.

Ecosystem management and landscape restoration needs to take such natural variation into account, aiming for a constantly changing and heterogeneous mosaic at broad scales. Ideally, conservation efforts and restoration attempts should not focus on single sites but rather on the landscape as a whole, permitting all stages of natural vegetation types to exist. Such efforts need to be coordinated among landowners to be feasible at large scales, which can be difficult. However, it offers a chance to manage forests and to generate revenues while preserving ecosystem characteristics and varied habitat values. For example, during the harvest of a jack pine stand with an oak component, a resource manager may leave sparse cover of oaks and use prescribed burning in subsequent years to prevent jack pine regeneration. This stand could be maintained as an oak savanna for a few decades before the oak is removed and jack pine is seeded again. Such a savanna would not be identical to a pre-settlement savanna; its origin does not resemble a natural process. However, such management alternative may provide habitat as well as revenues in areas where large-scale prescribed burns are difficult.

We do not understand the Pine Barrens ecosystem enough to explain fully the influence of species composition and structure on long-term sustainability. However, our analysis helps us to know the general structure and species composition of the Pine Barrens at pre-settlement times even without a full understanding of the ecosystem's complexity. These conditions were the result of an evolution of the Pine Barrens over thousands of years. When we think about the future of the Pine Barrens, the past can contribute useful guidelines.

Acknowledgments

We appreciate comments on the manuscript from G. Bartelt, T. Gower, R. Guries, J. Kotar, J. Kovach, R. Scheller, S. Weber, D. Zastrow, and one anonymous reviewer. This research is funded by the Wisconsin Department of Natural Resources, in part by funds from the Federal Aid in Wildlife Restoration Act, Pitman-Robertson Projects #W-160-P and W-160-R; and by the College of Agricultural and Life Sciences, University of Wisconsin-Madison, McIntire-Stennis Project #3885.

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Plate 1. A reconstructed depiction of a landscape scene in the oak savanna-woodland ecotone prior to development by European settlers (courtesy of The Nature Conservancy).

Stanley A. Temple

Surviving Where Ecosystems Meet: Ecotonal Animal Communities of Midwestern Oak Savannas and Woodlands

Abstract *The animal communities associated with Midwestern oak savannas and woodlands have a typical ecotonal character. They are relatively rich in species, but they are composed mostly of species that have the centers of their geographic ranges in either the deciduous forest biome to the east or the prairie biome to the west. Few species have ranges centered on the transition zone (or ecotone) between these major biomes. Within the ecotone, species show individualistic patterns of habitat selection, with most species associated with a particular habitat type within the ecotone's complex mosaic of patches, ranging from prairies, through savannas and woodlands, to forests. The characteristics of the landscape surrounding a remnant patch of oak savanna or woodland (its context) influence the composition of the animal community in the patch, in some cases even more strongly than the characteristics of the patch itself. At a large biogeographical scale, most species in the ecotone are near the edges of their ranges, and it is likely that their fitness is lower than it is nearer the centers of their ranges. At a smaller landscape scale, the patchy mosaic of habitats in the ecotone produces ecological phenomena, such as edge effects, that can reduce fitness of some species. Populations of species near the edges of their ranges or in relatively small habitat patches are often sink populations that require subsidies of dispersing immigrants from source populations either nearer the center of the range or in larger patches of forest or prairie habitat to remain viable. The remnant patches of oak savanna and woodland in the Midwest are now small, degraded, isolated and out of context. Scale and context (both regional and local) are, therefore, important predictors of the composition and viability of animal communities in these remnant patches. Current efforts to manage and restore remnant oak savannas and woodlands must address these needs of the animal community if they are to truly reproduce the characteristic diversity of species associated with the ecotone.*

The debate over whether Midwestern oak savannas and woodlands are a biome (a discrete regional ecosystem) or an ecotone (a transitional zone between the deciduous forest biome to the east and prairie biome to the west) has so far focused almost exclusively on characteristics of the associated plant communities (e.g., Curtis 1959 versus Packard 1988), but the outcome also has important implications for animal communities and biodiversity conservation efforts. The following quote from the "Midwestern Oak Savanna and Woodland Recovery Plan" highlights the debate: "[This] controversy may be the single most important scientific issue that must be resolved if we are to recognize and preserve oak savannas—or, as a practical matter, reconstruct them. . . ." (Fralish et al. 1994). The distinction between a biome and an ecotone is more than ecological semantics. It influences strategies for preservation and restoration, and it may affect animals more than plants. In the case of Midwestern oak savannas and woodlands, I will show that the animal communities associated with these ecological systems have typical ecotonal characteristics and, therefore, present special challenges for conservationists.

Ecologists have recently focused renewed attention on phenomena associated with the transition zones between adjacent ecological systems (di Castri et al. 1988). Whether they are continental-scale transitions between biomes or landscape-scale transitions between different vegetation patches in a mosaic, these ecotonal situations are usually associated with dynamic gradients in the physical environment (Gosz 1993). Across these environmental gradients there are parallel gradients in the structure and composition of the biotic community (Risser 1993). These biotic changes are in part related to the fact that many organisms reach distributional limits in or near transition zones (Hansen and di Castri 1992). In biome ecotones many species typical of the communities in the adjacent biomes reach the peripheries of their geographic ranges, and in patch ecotones many species reach edges of their home ranges where habitats change (Gosz 1993).

In contrast, within a biome or within a vegetation patch, environmental and species-compositional gradients are not as steep, and the composition of the biotic community tends to be relatively homogeneous. To some extent, it is the homogenous character of within-biome and within-patch communities that defines these ecological systems. In contrast, it is the relatively rapid changes in community composition that occur across ecotones that define them (Risser 1993).

Ecotones are often inhabited by an unusually rich-but-delicate diversity of species (Hansen and di Castri 1992). Transition zones between ecological systems often possess some biotic and environmental characteristics of both adjacent systems, as well as a few characteristics that are unique to the ecotone. The overlap of these normally segregated elements contributes to the biological richness of ecotones. In the case of biome ecotones, some species whose geographic ranges are centered on adjacent biomes, as well as a few species endemic or nearly endemic to the zone of transition, are found together in the ecotone (Gosz 1993). In the case of patch ecotones, species from adjacent habitat patches, as well as "edge species" that preferentially occupy the interface, have home ranges that overlap in the transition zone (Gosz 1993).

The maintenance of this unusual assemblage of species within an ecotone often depends on the proximity of adjacent biomes or patches that support demographically healthy populations. Without these "source populations" near the core of their range or habitat, peripheral "sink populations" near the edges of their range or habitat may be unable to maintain themselves intrinsically (Fahrig and Merriam 1985, Temple and Cary 1988, Hansen and Urban 1992). For those species populations at the edges of their ranges or habitat, persistence may depend on subsidies of dispersing individuals that immigrate from source areas (McCullough 1996, Wiens 1996,). Without these subsidies, marginal sink populations have difficulties persisting in an ecotone. This reduction in fitness near the edge of the range or habitat is one of the fundamental premises of biogeography (Brown and Gibson 1983, Cox and Moore 1993).

These patterns associated with ecotones have important implications for conservation and restoration of ecotonal communities (Holland et al. 1991; Risser, in press). Because many species will be at the limits of their distribution in a biome ecotone, they may be marginal in terms of demographic viability. Already coping with less than ideal conditions in marginal environments, they are especially vulnerable to the types of environmental swings (Figure 1) that often characterize ecotones (Gosz and Sharpe 1989).

Within the Midwestern oak savanna-woodland ecotone, a good example of such a variable environmental feature is precipitation (an important ecological factor in the

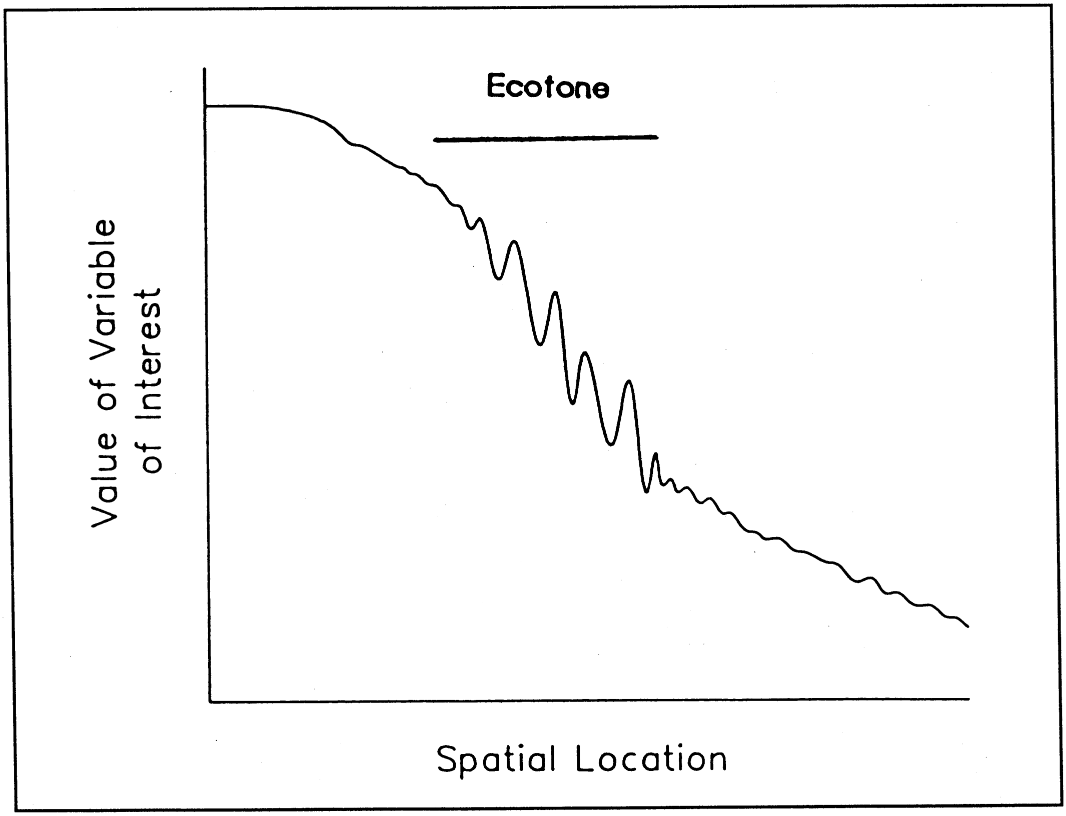

Figure 1. General trends in environmental conditions within biomes and across the ecotone that separates them.

oak savanna-woodland region), which is more variable year to year in the ecotone than it is in either the prairies to the west or the forests to the east. This pattern is confirmed by a continent-wide analysis of coefficients of variation in annual precipitation during June, July, and August, 1979–1996. Within the Midwestern oak savanna-woodland ecotone (as mapped in Figure 2), coefficients of variation for 2.5-degree blocks were in the range of 0.3–0.5, whereas they were in the range of 0.1–0.3 over both the eastern deciduous forest and the tallgrass prairie regions (J. Foley, personal communication).

Preserving sink populations as members of the ecotonal community can be very challenging. Persistence of marginal populations in a biome ecotone may depend crucially on immigration from source populations nearer the centers of species' ranges in adjacent biomes. If those source populations are not

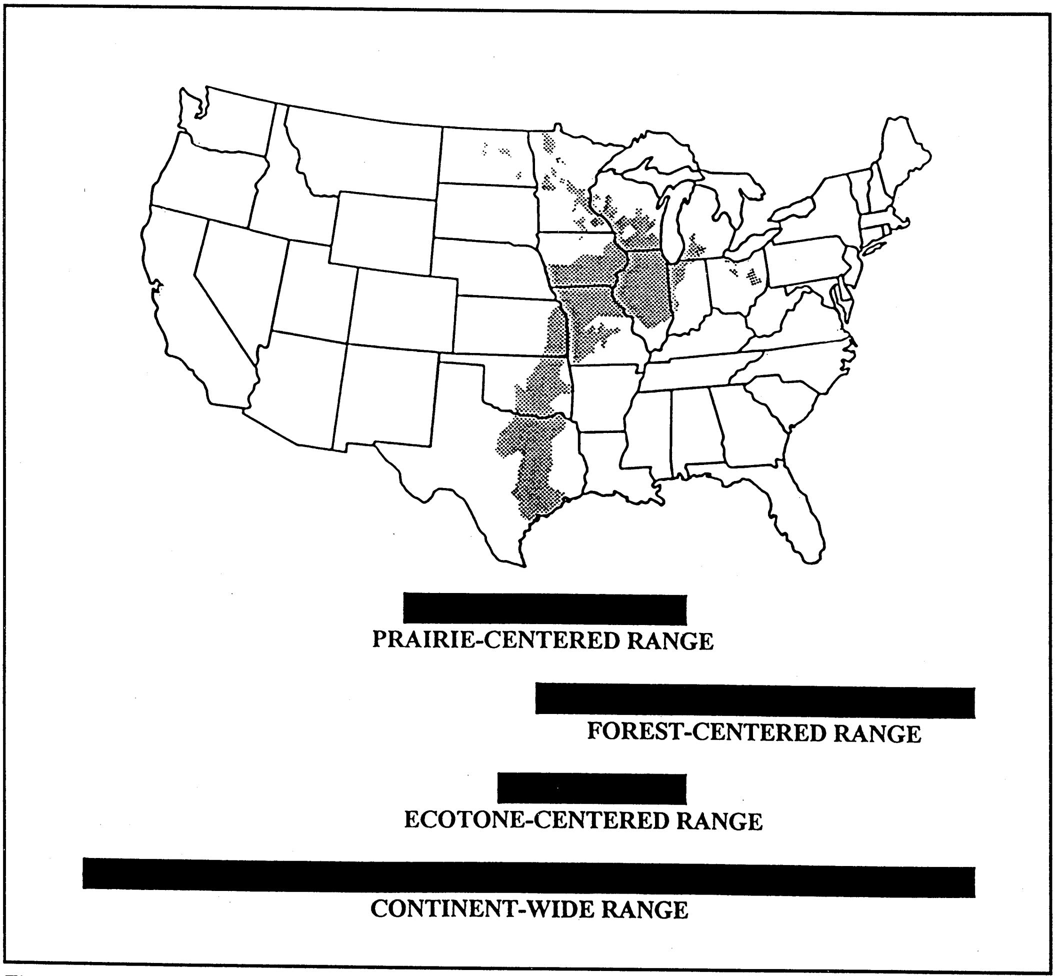

Figure 2. Overlapping geographic ranges of four groups of species found in the Midwestern oak savanna-woodland ecotone (which is indicated by the stippled area of the map).

thriving, centrifugal dispersal movements may be inadequate to maintain peripheral populations in the ecotone. As a result, the presence and persistence of a species in a biome ecotone may depend as much, or more, on conditions in adjacent biomes than on conditions in the ecotone itself (Wiens et al. 1985). As an example, the Dickcissel *(Spiza americana)* has its geographic range centered on the tallgrass prairie biome, but its range extends into the Midwestern oak savanna-woodland ecotone. Basili et al. (1998) have shown that populations near the center of the range have better reproduction and population stability than the peripheral populations in the upper Midwest.

Parallel patterns exist at the landscape-scale in ecotonal patches (Holland et al. 1991). The richness of species and the composition of the community in a patch ecotone depends importantly on the characteristics of the species pools in adjacent habitat patches (Temple et al. 1979). The size of a habitat patch can be a powerful predictor of the types and number of habitat specialists found in it (Harris 1984, Shafer 1990). An ecotone between two small patches should, therefore, have fewer species than an ecotone between larger patches. Furthermore, in a landscape in which one patch type dominates, the composition of the community in patch ecotones can be expected to be heavily biased towards the species from the dominant patch type.

The viability of populations of habitat specialists within a habitat patch may depend on the size of the patch and its proximity to other patches of the same habitat. A landscape composed of a mosaic of small, isolated habitat patches and their associated patch ecotones should support few source populations of habitat specialists. In such a landscape, many habitat specialists may be represented by sink populations incapable of producing a surplus of individuals that leave prime habitat in the core of patches and settle into marginal habitat in ecotones between patches.

Midwestern Savannas and Woodlands as Biome Ecotones

If the Midwestern oak savannas and woodlands represent a biome, there should be characteristic animal species with geographic ranges centered on the region. Alternatively, if they represent a biome ecotone between forests and prairies, there should be few species with ranges centered on the region and many with ranges centered on adjacent biomes. I examined the biogeographic affinities of 186 vertebrates (all species of amphibians, reptiles, birds, and mammals) and 224 invertebrates (a subset of well-studied Lepidoptera and Orthoptera) that are found in the region that has been described as oak savanna and woodland (Nuzzo 1986). The lists were prepared by the Midwest Regional Office of The Nature Conservancy based on the distributional data in the Natural Heritage Inventories for the 10 states (MN, WI, MI, IL, IA, IN, MO, NB, OK, TX) that contain examples of the ecotone. Inspection of a variety of range maps for these well-studied animal species (e.g., Opler et al. 1995, Sauer et al. 1996) allowed me to assign them to four groups: those with broad transcontinental ranges and those with the geometric centers of their ranges located in either the prairie biome, the deciduous forest biome, or the oak savanna-woodland region (Figure 2). The results are shown in Table 1, which reveals a clear pattern. Only 0.4% of these animals have geographic ranges centered on the oak savanna-woodland region. The largest component (50% of the sample animal species in the oak savanna-woodland

Table 1. Biogeographic affinities of 410 animal species found within the oak savanna-woodland region of the Midwest. The four distributional categories are illustrated in Figure 1.

Taxa	*Number of Species Examined*	*Percentage of Species Having Affinity With:*			
		Continental	*Forest*	*Prairie*	*Ecotone*
Vertebrates	186	34	48	15	3
Invertebrates	224	8	52	36	4

region) has biogeographic affinities with the deciduous forest biome. These 410 species are obviously just a sample of the fauna of the region, but distributional data are not readily available for other groups of lesser-known animals. The pattern, though based on a biased sample, is so compelling that it is difficult to believe it is merely an artifact of the taxa examined.

Many of the species found in the oak savanna-woodland region reach the limits of their geographic ranges there or nearby. Even allowing for the possibility that some species endemic to the oak savanna-woodland region may have been extirpated before modern biogeographers documented their ranges, the distributions patterns are consistent with the conclusion that animals of the oak savanna-woodland region form a typical ecotonal community.

Within a biome, the spatial diversity of vegetation patches is relatively low, but within a biome ecotone the diversity of patches is higher (Figure 3). Although we have few depictions of the landscape of the original oak savanna-woodland region, the eye-witness accounts and reconstructions based on them (Leach and Ross 1995) paint a picture of a landscape composed of a patchy mosaic of prairie, savanna, woodland and forest (e.g., Packard and Mutel 1997; see Plate 1). This landscape pattern is consistent with the oak savanna-woodland region being a biome ecotone rather than a biome.

Animal Communities of Midwestern Ecotonal Patches

At the landscape scale, the oak savanna-woodland ecotone is composed of a mosaic of patches of vegetation (typically tens to thousands of hectares in size), ranging from open prairie grasslands through closed-canopy forests (Figure 4). If one assumes that patches with less than 10% woody cover are true prairie and patches with more than 65% woody cover are true deciduous forest, the remaining areas with 10–65% woody cover can be considered ecotonal patches (see Leach and Ross 1995 for a discussion of these criteria). These three landscape elements form complex mosaics across the oak savanna-woodland region of the Midwest.

Animal species in the region show individualistic patterns of habitat selection within this mosaic (Herkert 1994, Swengel 1994, Panzer et al. 1995). The animal communities within patches of either prairie or forest tend to be composed of typical habitat specialists, but the composition of the communities in ecotonal oak savannas and woodlands tends to be a much more variable mix of species, reflecting both the vegetation structure of the patch ecotone and the surrounding landscape.

This variability can be seen in the composition of the bird communities in 4 patches of prairie, 14 patches of oak savanna-woodland, and 8 patches of

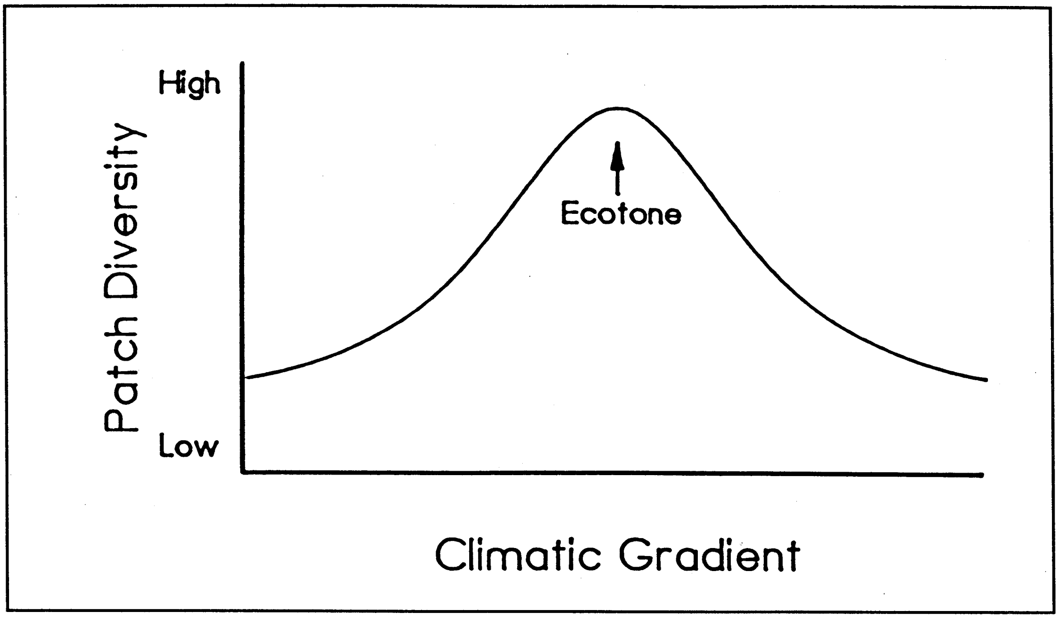

Figure 3. Spatial diversity of habitat patches within biomes and the ecotone that separates them.

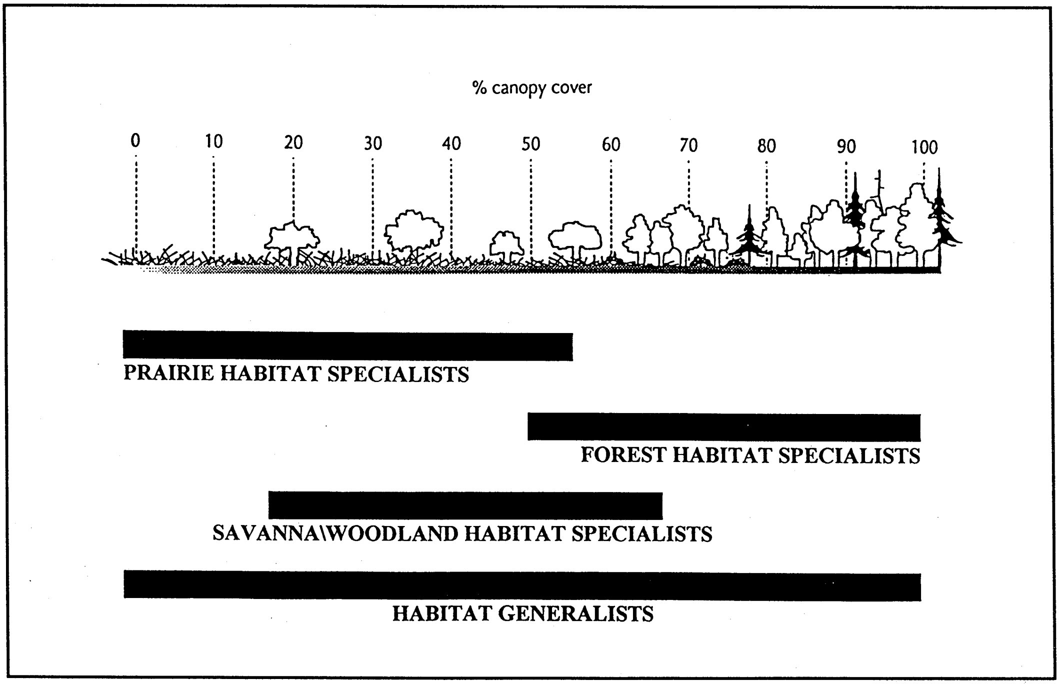

Figure 4. The range of habitat patches found in the Midwestern oak savanna-woodland ecotone and how four categories of species are distributed among patches differing in canopy cover.

deciduous forest in southern Wisconsin. Bird species lists for these 26 sites (ranging from 19 to 54 ha in size) were assembled during multiple visits during the breeding season. Reflecting the relatively small size of the sites, the number of bird species detected on the oak savanna-woodland sites ranged from 19 to 46, out of a potential total species pool of about 70 species recorded in the ecotone. The percent woody cover at the site and the surrounding landscape (within 1 km of the site) was assessed on air photos. Each species of bird was assigned an "affinity value," ranging potentially from 0 for species with strong prairie affinity to 100 for species with a strong forest affinity. These affinity values were based on the percentage of the species' geographic range that lies within the deciduous forest biome, determined from range maps prepared by Sauer et al. (1996). An overall "bird community index" was calculated as the mean affinity value for all of the bird species recorded at a site.

As expected, the prairie sites had lower bird community indices (<55) than the forest sites (>70). Among oak savanna and woodland sites with intermediate indices, there was a significant correlation between the % woody cover at a site and the bird community index (Figure 5), indicating that as an ecotonal patch became more woody it was inhabited by birds with a stronger affinity to forest. The coefficient of determination for this relationship was 0.202.

In a second analysis of these bird data, I examined the relationship between each site's bird community index and the percent woody cover on the landscape surrounding

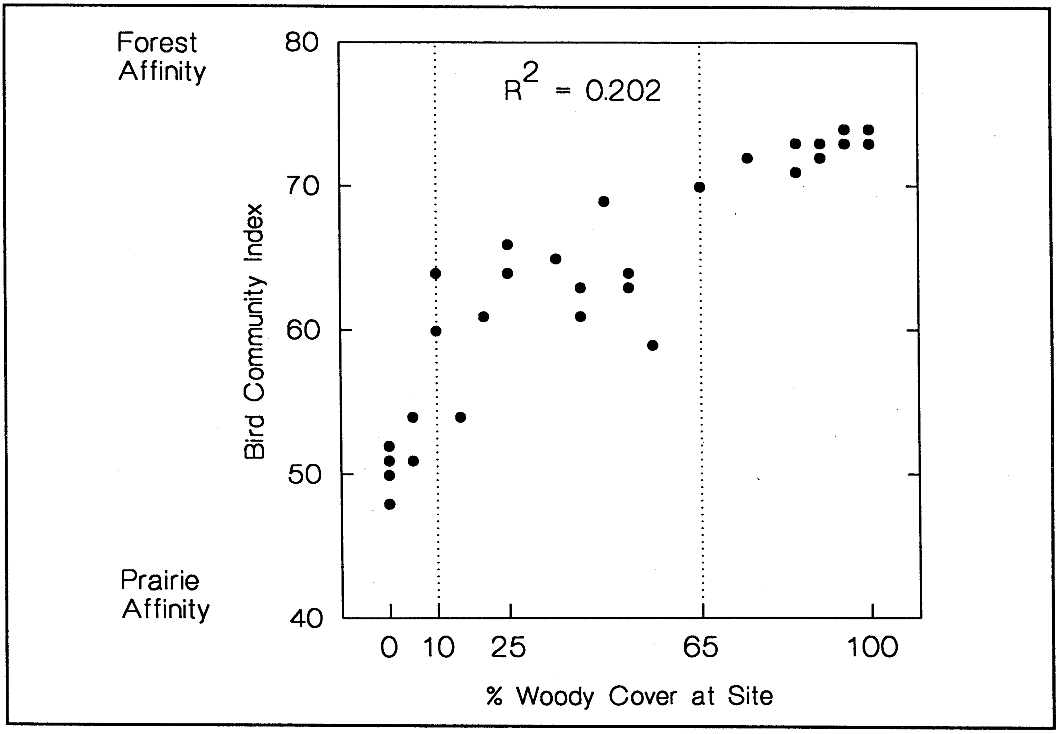

Figure 5. Biogeographic affinities of the bird communities in 26 patches of habitat in Wisconsin that varied in percent woody cover at each site.

the site. Among oak savanna and woodland sites, there was a significant correlation between the percent woody cover on the surrounding landscape and the site's bird community index (Figure 6). But, in this case, the coefficient of determination was 0.804.

These results highlight how important the context of an ecotonal patch can be in determining the composition of the animal community. At least for birds, it appears that the composition of the community in an ecotonal patch is influenced more by characteristics of the surrounding landscape than by characteristics of the ecotonal patch itself. Entomologists who have collected widely around the Midwest also report a similar pattern in the composition of the lepidopteran communities associated with oak savannas and woodlands (L.A. Ferge, personal communication). Hence, two identical patches of oak savanna-woodland could have very different animal communities, depending on whether the surrounding landscape is dominated by closed (forest) or open (prairie) conditions. This relationship reinforces the view that the animal community associated with patches of oak savanna and woodland can be highly variable depending on landscape context.

Population Dynamics in Biome Ecotones and Patch Ecotones

If, as I have predicted, ecotones are often inhabited by sink populations of species from adjacent ecosystems, there should be evidence of reduced fitness among individuals living in transition zones (i.e., sub-

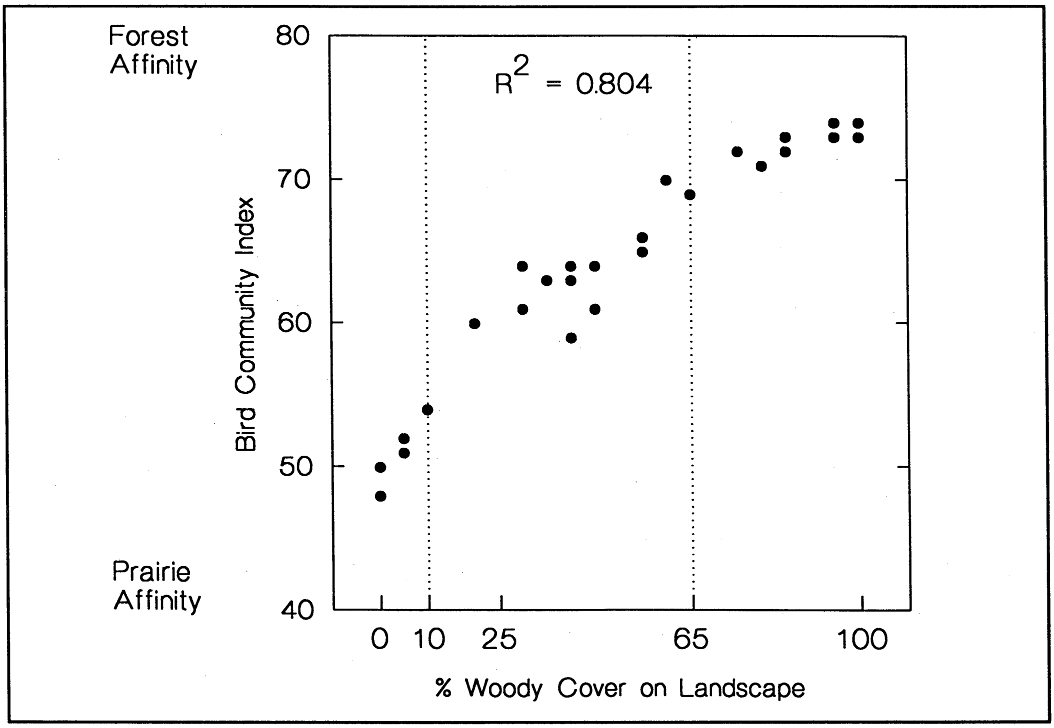

Figure 6. Biogeographic affinities of the bird communities in 26 patches of habitat in Wisconsin that varied in the percent woody cover on the landscape within 1 km of each site.

standard rates of reproduction and survival in ecotones as compared to biomes or patches). Using data that my students and I have collected for several species of birds that breed in the oak savanna-woodland region of Wisconsin, I find just such evidence at both the biome scale and the landscape scale.

For a few birds that have the centers of their geographic ranges in either the deciduous forest or prairie biomes, but have the margins of their ranges in the Midwestern oak savanna-woodland ecotone, there is useful information on geographic variation in reproductive performance. Basili et al. (1998) studied the breeding biology of Dickcissels throughout their geographic range (Figure 7), which is centered on the tallgrass prairie but extends into the oak savanna-woodland ecotone of the Midwest. They documented longer nesting seasons, larger clutches, higher nest success, and higher productivity in the core of the Dickcissel's range than at the periphery. Nolan (1978) studied the breeding biology of the Prairie Warbler, which, despite its name, has its range centered on the deciduous forest biome (Figure 8). Comparing his data on nesting success near the core of the range with data from the North American Nest Record Card Program for the periphery, it appears that nesting success is below average for this species at the Midwestern edges of its range: 1.6 young per pair in Illinois, Missouri, and Arkansas (n = 46) versus 2.2 young per pair in

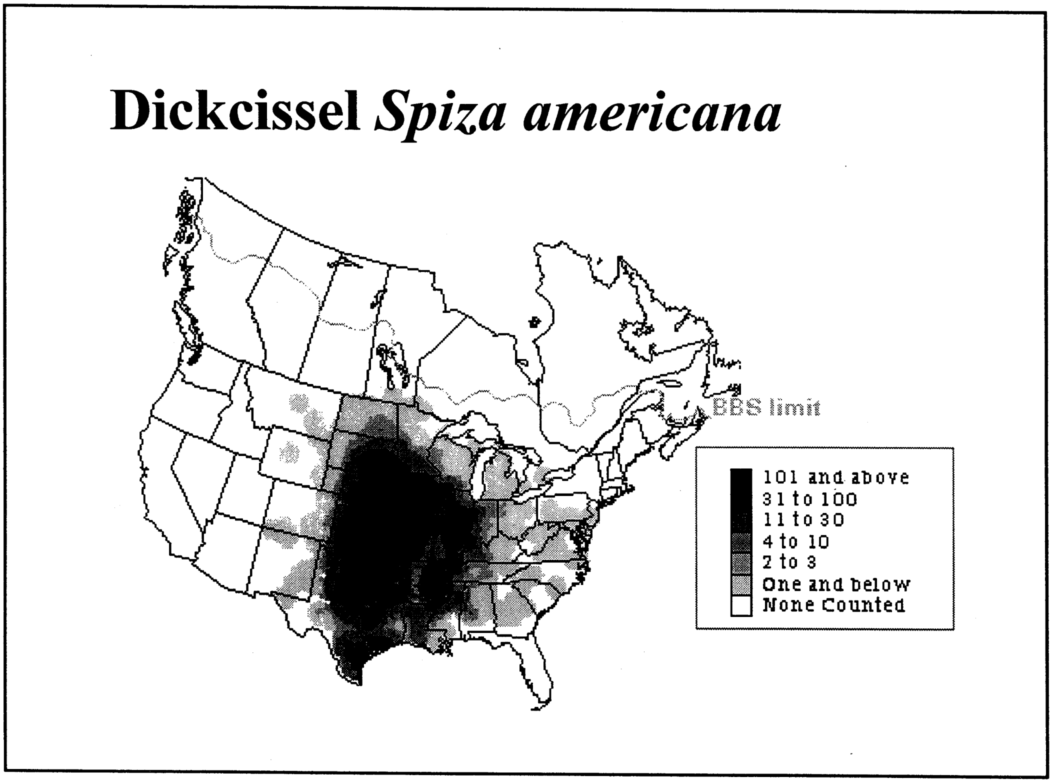

Figure 7. Geographic range of the Dickcissel during its breeding season in North America (from Sauer et al. 1996).

southeastern Indiana (n = 129). It is difficult to know whether or not the patterns shown by these two species are typical of other birds because few studies have examined geographic variations in reproductive performance throughout the ranges of appropriately distributed species.

There should also be evidence that species characteristically associated with ecotones (endemics to biome ecotones or edge species in patch ecotones) have high levels of fitness in transition zones. For the few birds that have portions of their geographic ranges centered on the Midwestern oak savanna-woodland ecotone (e.g., Bell's Vireo), there are too few data on reproductive performance across their range. Hence, I can not demonstrate that their fitness is higher in the ecotone.

Within the Midwestern oak savanna-woodland ecotone there are useful data on how important vital rates vary among patches and their associated ecotones, especially how nesting success of birds varies between closed (forest) and open (grassland) habitats and across the transition zones between them. Over the years, my students and I have accumulated relevant data on the nest success—calculated using the Mayfield (1961) method—of 22 species of songbirds that nested in Midwestern habitats that ranged from patches of closed forest to patches of open grassland. I categorized these birds as either forest birds (Acadian Fly-

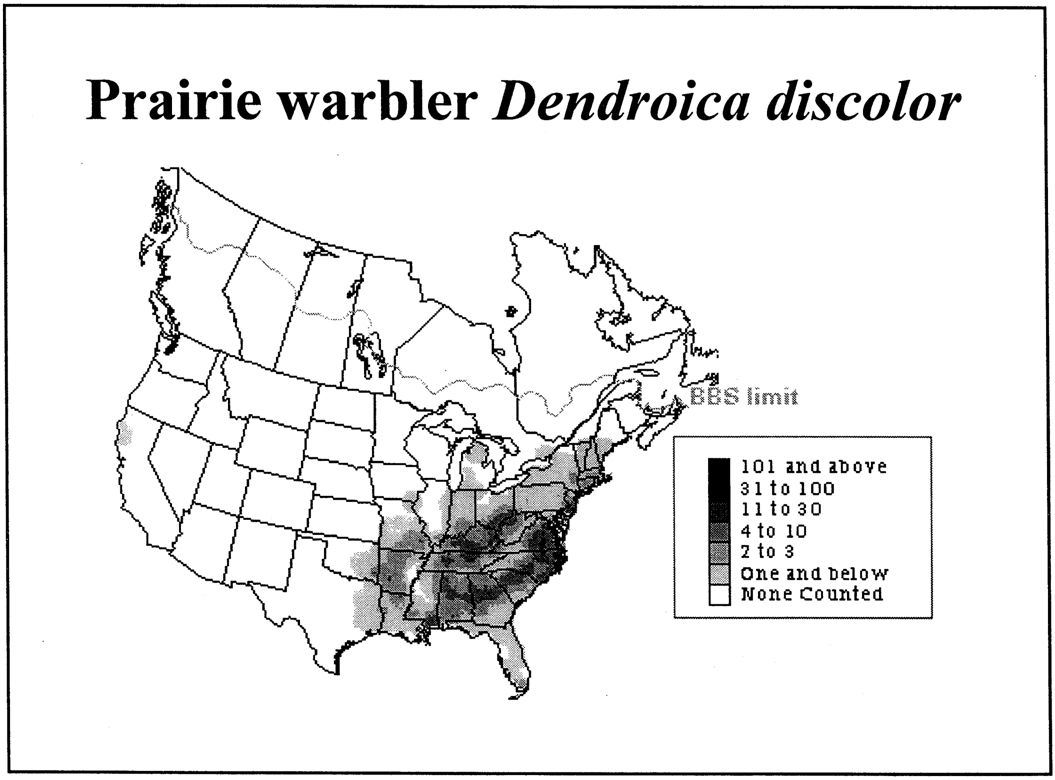

Figure 8. Geographic range of the Prairie Warbler during its breeding season in North America (from Sauer et al. 1996).

catcher, Eastern Wood-pewee, Wood Thrush, Red-eyed Vireo, Ovenbird, Scarlet Tanager, Rose-breasted Grosbeak), grassland birds (Dickcissel, Savannah Sparrow, Grasshopper Sparrow, Bobolink, Eastern Meadowlark, Western Meadowlark), or edge birds (American Robin, Brown Thrasher, Gray Catbird, Yellow Warbler, Northern Cardinal, Indigo Bunting, Rufous-sided Towhee, Field Sparrow, Song Sparrow, American Goldfinch), depending on the habitat where they normally nest.

Forest birds had higher nest success when the area within 50 m of the nest had over 65% woody cover (54%, n = 112) than in areas with a lower percent woody cover (21%, n = 46). Grassland birds had higher nest success when the area within 50 m of the nest had less than 10% woody cover (48%, n = 195) than in areas with more woody cover (16%, n = 104). Edge birds almost always nested where there was 10–65% woody cover within 50 m of the nest, so comparisons between forest, oak savanna-woodland, and grassland were impossible.

Proximity to the edge of a habitat patch and patch size are strong predictors of the success of bird nests. Temple and Cary (1988) have shown that nesting success of Midwestern forest songbirds declines when nests are in small patches of forest near an edge between forest and open habitat. Johnson and Temple (1986, 1990) have shown that nesting success of Midwestern grassland birds declines when nests are in small patches of prairie near a wooded edge.

These impacts of patch size and proximity to edges on nest success and the variations in nest success across a range of habitat conditions highlight the problems that many species of birds encounter in a landscape composed of a complex mosaic of habitat patches. For many of the birds that nest in the mosaic of patches typical of the Midwestern oak savanna-woodland ecotone, fitness is reduced in small patches of their preferred habitat and where that preferred habitat is near an ecological edge.

Unfortunately, relevant population data have been collected for few of the animal species that occur in the Midwestern oak savanna-woodland ecotone. An avian bias is unavoidable because most of the relevant data are available for birds. Nonetheless, the available evidence is consistent with the proposition that in this biome ecotone—and the ecotonal patches within it—species that have geographic ranges centered on adjacent biomes and habitat preferences for large contiguous patches of either forest or prairie have reduced fitness. It is difficult to know if this situation pertained in pre-settlement times, but recent events in the ecotone and adjacent biomes have exacerbated the problems of maintaining viable populations in the Midwestern oak savanna-woodland region. As source populations in the deciduous forests and tallgrass prairies have suffered the consequences of habitat loss and fragmentation, and as the landscape within the oak savanna-woodland ecotone has been extensively altered, many species at the edges of their ranges have declined in the Midwest (Leach and Ross 1995). The result of these changes is that the animal communities of the Midwestern oak savanna-woodland ecotone have different patterns of richness and composition today than they had in the past.

Scale and Context Are Crucial for Preservation and Restoration

Midwestern oak savannas and woodlands are among the most endangered ecosystems in North America (Haney and Apfelbaum 1990, Leach and Ross 1995). Central goals of conservationists concerned about them are to preserve and restore examples of these special environments that can support the rich biotic communities typically associated with the ecotone. Much has been written about restoring and managing the ecotone's plant communities (e.g., Fralish et al. 1994, Leach and Ross 1995), but relatively little has been written about the animal communities. There is clear evidence that some of the best remaining examples of oak savannas and woodlands, many already protected as nature reserves, have severely deficient animal communities. The 14 patches surveyed in this study collectively supported less than half of the potential bird species associated with the habitat. Furthermore, the methods for restoring an intact animal community to oak savannas and woodlands—and then maintaining it—have yet to be developed.

Borrowing a line from a recent Hollywood movie, I believe conservationists have been exhibiting the "Field of Dreams Syndrome." Conservationist have naively assumed that "if you build it, they will come." That is to say, if you carefully restore the plant community, the animal community will spontaneously reoccupy the site. But today's remnant oak savannas and woodlands are unnaturally small, isolated, degraded, and out of their natural context, and it will be very difficult for the typical animal community to either reassemble itself or maintain itself over time. Few of the key components of the community (i.e., ecotone specialists, prairie specialists, or forest specialists) will thrive under current conditions.

Small, isolated patches of oak savanna and woodland will be unlikely to support viable populations of ecotone endemics, regardless of whether they have survived as relics or have been reintroduced. Without adjacent or nearby source populations of forest and prairie habitat specialists, the richness and composition of the animal community in an ecotonal patch of oak savanna or woodland will not be typical because these species will not persist. The full community can only exist when an ecotonal patch receives dispersing individuals from source populations of both forest and prairie. Some remnant oak savannas and woodlands are adjacent to patches of either forest or prairie, but few have both nearby. Furthermore, in the highly fragmented landscape of today's Midwest, most patches of forest and prairie are too small to support source populations that can enrich the communities of oak savannas and woodlands. Small patches of oak savanna and woodland, therefore, lose their typical animal community and, instead, have communities that mirror the species associated with surrounding disturbed lands.

What do the findings presented in this paper mean for efforts to preserve the biological diversity of these ecological systems? First, ecotonal patches of oak savanna and woodland managed for conservation should be as large as possible, and preserving and restoring the largest remnants should be the highest priorities. These will be the sites most likely to retain viable populations of the endemic animals of the ecotone and to have potential for their successful reintroduction. Many, perhaps most, of the sites being managed and restored today encompass only tens or hundreds of hectares and appear to be too small to support many animals that are typical of the ecotone. Second, ecotonal patches of oak savanna and woodland should be situated in a context of adjacent large patches of prairies and forests in order to maintain their full complement of animal species. Oak savannas and woodlands with only forest or prairie patches nearby can be expected to have an animal community skewed towards a species composition reflecting the adjacent habitat. Small, isolated sites surrounded by developed lands will have an animal community dominated by generalists. Third, efforts to restore oak savannas and woodlands must include more reintroductions and intensive management of wildlife; it is not enough to merely restore the plant community and leave the animal community to chance. The methodologies for managing these wildlife species remain to be perfected. Finally, conservationists should identify—and focus their efforts on—those rare sites around the Midwest where the requisite combination of scale and context either occurs or can be recreated. It is there that the best opportunities exist for recreating the rich biological diversity of this ecotone by accommodating its animals as well as its plants.

Acknowledgments

Some of the data on bird populations that I used in my analyses have been collected by my students, B. Ambuel, G. Basili, M. Brittingham, B. Fevold, D. Flaspohler, R. Johnson, M. Mossman. The Wisconsin Department of Natural Resource shared data on bird communities at several Wisconsin State Natural Areas. The Midwest Regional Office of The Nature Conservancy provide data on species distributions and allowed me to use the painting shown in Plate 1. L.A. Ferge shared information from his extensive inventories of Lepidoptera at sites around the Midwest oak savanna/woodland ecotone. Research that generated data used in my analyses has been supported by the Agricultural Experiment Station of the College of Agricultural and Life Sciences at the University of Wisconsin-Madison, the U.S. Fish and Wildlife Service, the U.S. Forest Service, The Nature Conservancy, the National Fish and Wildlife Foundation, the Wisconsin Department of Natural Resources, and the Beers-Bascom Professorship in Conservation (which is held by the author). Two anonymous reviewers made useful suggestions that improved the manuscript.

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Susan Will-Wolf and Forest Stearns

Characterization of Dry Site Oak Savanna in the Upper Midwest

Abstract *Oak savanna vegetation on dry sites in the upper Midwest can be divided into two groups based on current literature. Dry sand savanna is found on low-nutrient, well-drained sandy soils, over sand, sandstone, or other acidic parent material. Trees are usually black oak group species. "Brush prairie," "scrub oak," or stunted "oak grove" structure is more characteristic than scattered single trees. Historically, dry sand savanna occurred in relatively large patches in the landscape. In contrast, dry calcareous savanna occurs on extremely thin or excessively well-drained soils with low water availability but moderate nutrient status, over calcareous or inert parent material. Trees are usually white oak group species, found as scattered single trees or small groves. Historically, dry calcareous savanna occurred as scattered small patches. Little bluestem, Pennsylvania sedge, and leadplant are common ground layer plants of both groups. Heath family species, lupine, sand fame-flower and goat's rue are examples of characteristic ground-layer plants of dry sand savannas. Snowberry, the horse-gentians, and tick-trefoils are examples of ground-layer plants found in dry calcareous savanna. The two types of dry site savanna must be distinguished for research, restoration, and management planning.*

Savanna vegetation associated with dry, low productivity sites in the Great Lakes region (Figure 1, Chapman et al. 1997) can be divided into two general groups (Figure 2) based on a review of current literature (including much "gray literature" that is difficult to access). Dry sand savanna is found on low nutrient sandy soils with low water holding capacity or over sand or other acidic parent material. Dry calcareous savanna occurs on extremely thin or excessively well-drained soils with moderate nutrient status and medium to fine texture, overlying calcareous or insoluble parent material. Oak species of the

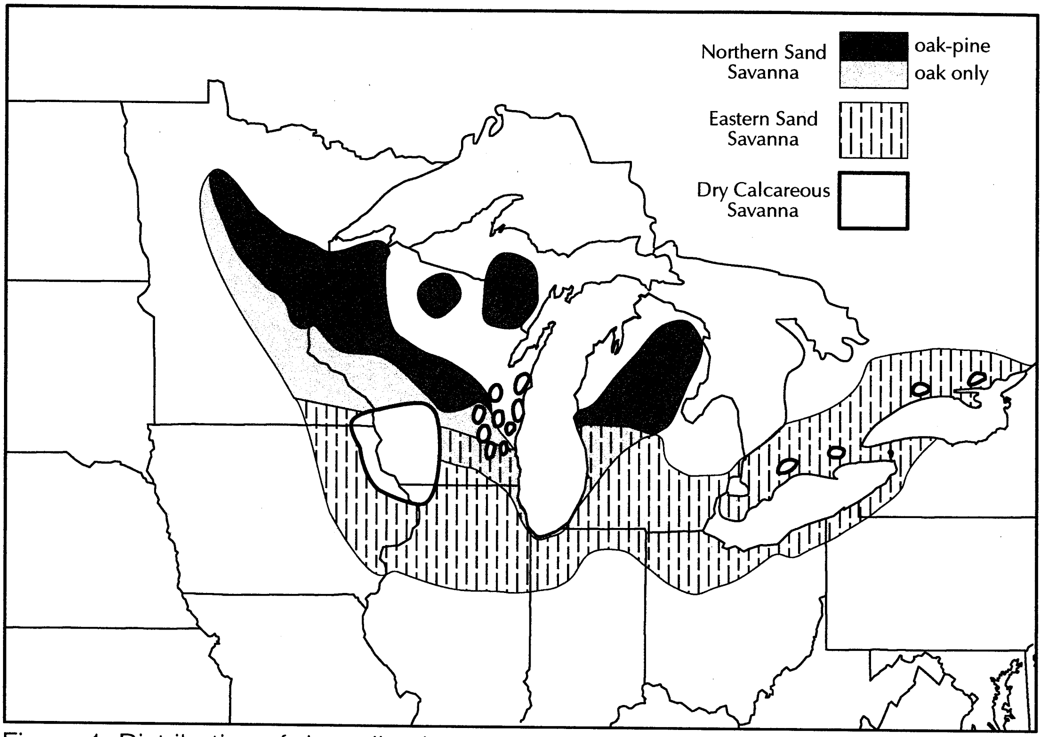

Figure 1. Distribution of dry soil oak savanna in the Great Lakes region, indicating the geographic area within which each vegetation type occurs. The location of the regional vegetation transition zone is approximated by the southern boundary of oak-pine Northern Sand Savanna. For dry calcareous savanna, sections delineated by a heavy solid line suggest the areas in which they occur. The largest and most western of these areas is the Driftless Area (see text). Map copyright Cambridge University Press, reprinted from Figure 8-1 of Will-Wolf and Stearns (in press) with the permission of Cambridge University Press.

subgenus *Erythrobalanus,* the black oak group, are characteristic of dry sand savanna, while oak species of the subgenus *Lepidobalanus,* the white oak group, dominate the tree layer of dry calcareous savanna. Thin-soil white oak-complex savanna and sandy soil black oak-complex savanna both grade into bur oak *(Quercus macrocarpa)* and/or black *(Q. velutina)* and white oak *(Q. alba)* savanna on deeper, higher nutrient, and less droughty soils (Figure 2). In southwestern Ontario dry calcareous savanna ("limestone savanna") and dry sand savanna ("sand barrens") remnants were clearly separated based on species composition (using principal coordinates ordination and cluster analysis, Catling and Catling 1993). These two savanna types have not been formally separated in the western Great Lakes region, but such an analysis would be useful.

Our distinction of dry site oak savanna types is useful for research, restoration, and management planning in several ways: (1) dry sand savanna and dry calcareous savanna differ floristically, so investigation of dis-

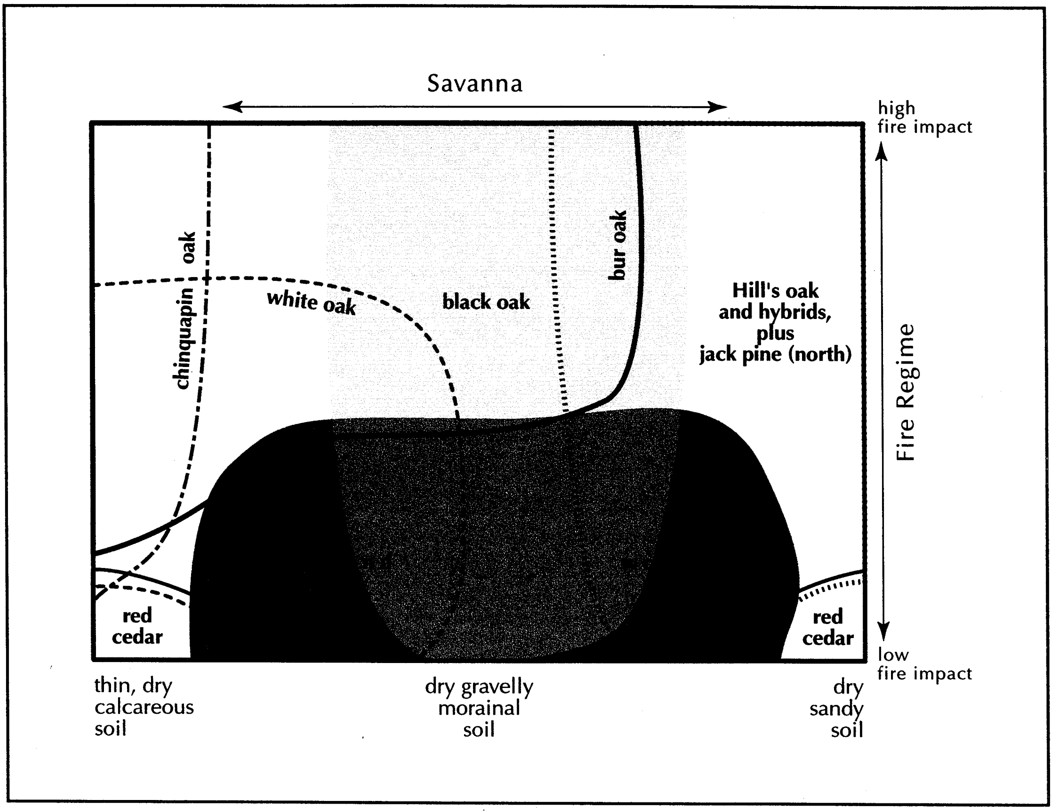

Figure 2. Distribution of tree species and savanna physiognomy along soil nutrient and fire frequency gradients for upper Midwestern dry savanna sites. Only dry site environments are represented in this diagram. However sites at the extremes of the soil nutrient gradient are also usually drier than those in the middle. Great Lakes alvar communities (see text) may fit into the dry calcareous, low fire impact region of this model.

tribution and composition should be separated, and planting lists and composition goals for management should differ; (2) management goals and expectations for structure and physiognomy should differ; (3) landscape design of preserves can differ. Since historically dry calcareous savanna sites were small and isolated, small preserves will probably be adequate to conserve rare species. Conversely, because many dry sand savannas were once extensive, species requiring large areas were part of the community. Large preserves are needed to maintain that suite of area-sensitive species. We focus in this paper on presenting species lists for different dry site oak savanna types.

Vegetation physiognomy and species composition in the Great Lakes region are related closely to interaction of fire frequency and intensity (as influenced by landscape structure and climate, Grimm 1985, Leitner et al. 1991, Will-Wolf and Montague 1994) with broad edaphic gradients (Grimm 1984, Bowles and McBride 1994). Vegetation classification, which is commonly used to define vegetation units for mapping and for management, often incorporates the assumption that site environment determines site vegetation composition and structure. Recent savanna classifications for the upper Midwest have emphasized that variation in disturbance regime, especially fire, has a strong influence on vegetation structure and composition that can be independent of site environment (Homoya 1994, Faber-Langendoen 1995, Haney and Apfelbaum 1995). Vegetation-environment relationships (see Roberts 1987) that appear to be static and deterministic in dry sand savanna complexes (e.g., Botts et al. 1994) may result from artificially uniform disturbance regimes operating over relatively short time scales in the recent past. The shifting mosaic model of vegetation dynamics (Shuey 1994, Will-Wolf and Stearns in press), which emphasizes the importance of disturbance for vegetation structure and composition, appears a more useful model for guiding conservation and restoration practices. Species lists and summaries of species relative importance should thus always be used as guidelines rather than as firm restoration targets or measuring sticks for restoration and management success.

We compiled preliminary lists from literature with species characteristic of dry sand savanna (with two subgroups) and dry calcareous savanna (Tables 1 and 2). A "characteristic" species was reported in most of the relevant studies spread across the range of a savanna type, but was absent or found irregularly in other types. Several common ground-layer species appear to be characteristic of all types of dry site oak savanna and woodland (Table 1), for example little bluestem *(Schizachyrium scoparium)*, Pennsylvania sedge *(Carex pensylvanica)*, and leadplant *(Amorpha canescens)*. Many of the species characteristic of either major group (Table 1) are relatively uncommon.

Dry Sand Savanna

Distribution

Dry sand savanna is associated with sandy (85–95% sand), acidic (pH 4.3–6.0), low nutrient (420–1,025 ppm C, 628–1,500 ppm N), droughty (AWC 14–60%) soils (Curtis 1959, White 1983, Anderson and Brown 1986, Udvig 1986, Tester 1989, Leach 1996). These soils are usually found on outwash plains, sandy lake beds, and dune systems relatively near former glacial margins. In the early 1800s, dry sand oak savanna covered large areas in the western Great Lakes region. Today there are scattered large and small remnants present (Will-Wolf and Stearns in press).

A vegetation transition zone (the "tension zone" in Wisconsin, Curtis 1959) passes through Minnesota, Wisconsin, and Michigan, trending northwest to southeast. North and east of this zone, mixed conifer-deciduous tree vegetation grows under a climate of cool summers and long winters with continuous snow cover. South and west of this zone, deciduous trees predominate, the climate has warm summers, and winters often have only sporadic snow cover. The general location of the transition zone coincides with the southern limit of oak-pine Northern Sand Savanna (Figure 1).

For dry sand savanna, scrub oak and "brush prairie" structure (open herbaceous areas interspersed with dense clumps of short-statured trees or shrubs) are more characteristic than is classic savanna structure (scattered stately trees with wide crowns). The black oak group species characteristic of sand savanna are relatively more fire sensitive than white oak group species, and they grow slowly on low nutrient sites. Frequent or intense fire can produce scrub oak structure, which was common at the time of European settlement (Rodgers and Anderson

Table 1. Vascular plants characteristic of dry site oak savanna. Species in the column on the left are common to both dry calcareous and dry sand savanna. Species in the two columns to the right are those additional species characteristic of either one or the other, but not both. The number of states where the species is listed for conservation is given in parentheses. These lists are summarized from Whitford and Whitford (1971), White (1983), Henderson and Long (1984), Glenn-Lewin and VerHoef (1988), Post (1989), Catling and Catling (1993), Homoya (1994), Kline and McClintock (1994), Faber-Langendoen and Davis (1995), Maxwell and Givnish (1995), Anderson et al. (1996), and Haney and Apfelbaum (1997). Nomenclature follows Gleason and Cronquist (1991).

Dry Soil Oak Savanna	*Dry Calcareous Savanna*	*Dry Sand Savanna*
Trees	**Trees**	**Trees**
Quercus macrocarpa	*Carya ovata*	*Quercus ellipsoidalis*
Prunus serotina	*Quercus alba*	*Quercus velutina*
	Quercus muehlenbergii	
Shrubs	**Shrubs**	**Shrubs**
Ceanothus americanus	*Cercis canadensis*	*Comptonia peregrina*
Cornus racemosa	*Lonicera hirsuta*	*Gaylussacia baccata*
Corylus americana	*Rhus aromatica*	*Salix humilis*
Rosa carolina	*Symphoricarpos spp.*	*Vaccinium angustifolium (1)*
	Viburnum rafinesquianum	
	Zanthoxylum americanum	
Herbs	**Herbs**	**Herbs**
Amphicarpaea bracteata	*Asclepias viridiflora*	*Arabis lyrata*
Amorpha canescens (1)	*Astragalus neglectus*	*Artemisia caudata*
Andropogon gerardii	*Besseya bullii* (6)	*Asclepias amplexicaulis* (1)
Aster oolentangiensis	*Carex sparganioides*	*Calamovilfa longifolia*
Carex pensylvanica	*Carex umbellata*	*Cyperus filiculmis*
Comandra umbellata	*Circaea lutetiana*	*Cyperus lupulinus*
Coreopsis palmata	*Cirsium altissimum*	*Gaultheria procumbens*
Danthonia spicata	*Desmodium glutinosum*	*Helianthemum canadense*
Euphorbia corollata	*Desmodium nudiflorum*	*Koeleria pyramidata*
Lespedeza capitata	*Oxalis violacea* (1)	*Lechea intermedia* (3)
Monarda fistulosa	*Penstemon hirsutus*	*Leptoloma cognatum*
Panicum villosissimum	*Phryma leptostachya*	*Liatris aspera*
Schizachyrium scoparium	*Pycnanthemum virginianum*	*Lupinus perennis* (1)
Smilacina racemosa	*Triosteum aurantiacum*	*Monarda punctata*
Smilacina stellata	*Triosteum perfoliatum*	*Panicum depauperatum*
Solidago nemoralis		*Panicum oligosanthes*
Sorghastrum nutans		*Pteridium aquilinum*
		Scleria triglomerata (3)
		Solidago speciosa
		Stipa spartea (1)
		Talinum rugospermum (3)
		Tephrosia virginiana (1)

Table 2. Vascular plants characteristic of either Northern Sand Savanna or Eastern Sand Savanna, but not both. A site might have one of these sets of species, in addition to those species common to all dry soil savanna, and all dry sand savanna, which are listed in Table 1. Starred species have primarily western North American distributions. Number of states where the species is listed for conservation is given in parentheses. See legend, Table 1, for sources from which these lists were summarized.

Dry Sand Savanna	
Northern Sand Savanna	*Eastern Sand Savanna*
Trees	**Trees**
Quercus ellipsoidalis — characteristic	*Quercus velutina* — characteristic
Quercus rubra — local	*Quercus marilandica* — local
Shrubs:	**Shrubs:**
Corylus cornuta	*Juniperus communis*
	Rhus copallinum
	Rhus typhina
Herbs:	**Herbs:**
**Artemisia ludoviciana* (1)	*Aster linariifolius* (2)
Baptisia bracteata	*Calystegia spithamea*
**Bouteloua hirsuta*	*Chrysopsis camporum*
Dalea candidum	*Coreopsis lanceolata*
Gnaphalium obtusifolium	*Krigia virginica* (2)
Helianthemum bicknellii (1)	*Lechea mucronata*
Helianthus x *laetiflorus*	*Lechea pulchella*
Hieracium kalmii	*Panicum colombianum* (2)
Hieracium longipilum	*Viola sagittata*
Hedyotis longifolia	
Krigia biflora	
Liatris cylindracea	
Physalis virginiana	
Scutellaria parvula (3)	
**Senecio plattensis*	
Solidago ptarmicoides	
**Sporobolus cryptandrus*	

1979), but since has become much less common with fire suppression (Curtis 1959, Bowles and McBride 1994).

Subdivision

Haney and Apfelbaum (1995) divide Great Lakes region dry sand savanna into Northern Sand Savanna and Eastern Sand Savanna. These groups differ in general geographic location within the Great Lakes region, with overlap in Wisconsin and Michigan (Figure 1). Northern Sand Savanna, in the northern and western parts of the region, characteristically has Hill's or northern pin oak *(Quercus ellipsoidalis)* and hybrids, as described later. Eastern Sand Savanna, in the southern and eastern parts of the region, has black oak as the characteristic tree species, and Hill's oak is absent or is a minor component. In contrast, Pruka and Faber-Langendoen (1995) include all dry sand savanna south of the climate transition zone and east of Michigan in a single "Black oak-lupine" savanna type. Faber-Langendoen (1995) combines black oak and Hill's oak sites for most woodland and savanna groups, which are then subdivided by physiognomy and characteristic ground-layer species. We have chosen Haney and Apfelbaum's (1995) classification for several reasons: (1) it recognizes the similarity of dry sand oak savanna north and south of the vegetation transition zone and emphasizes a floristic distinction between the northern and western vs. the southern and eastern parts of the Great Lakes region (*not* following the traditional vegetation transition zone); (2) Northern and Eastern Sand Savanna appear to be distinguished by a suite of species, not just black vs. Hill's oak; (3) it provides a model for comparing Northern Sand (oak) Savanna and jack pine barrens where they both occur in the northern part of the western Great Lakes region. Jack pine barrens likely result from a disturbance regime of infrequent (25–40 year) intense fires, with oak present as scattered small shrubs. Oak dominates under a regime of frequent, less intense fires or European management regimes including fire suppression and loss of jack pine seed source (Whitney 1987, Pregitzer and Saunders in press; Will-Wolf and Stearns in press).

The dry sand savanna groups share several common characteristic ground-layer species, such as huckleberry *(Gaylussacia baccata),* bracken fern *(Pteridium aquilinum),* and blueberry *(Vaccinium angustifolium).* They also share several uncommon characteristic species (Table 1). Some of these are state-listed for conservation: wild blue lupine *(Lupinus perennis),* sand fameflower *(Talinum rugospermum),* and goat's rue *(Tephrosia virginiana).* Most of the ground-layer species characteristic of either Northern or Eastern Sand Savanna (Table 2) are relatively uncommon.

Northern Sand Savanna Composition

Northern Sand Savanna (Figure 1) occurs in the western Lake States. The most characteristic tree, Hill's oak (Table 2), hybridizes extensively with black oak south of the vegetation transition zone (Curtis 1959) and with northern red oak *(Q. rubra)* north of that zone (Gleason and Cronquist 1991). White oak and bur oak are also found occasionally. Jack pine *(Pinus banksiana)* is frequently found in low density north of the vegetation transition zone. Characteristic ground-layer species of Northern Sand Savanna include beaked hazelnut *(Corylus cornuta),* two native hawkweeds *(Hieracium kalmii* and *H. longipilum),* orange dwarf-dandelion *(Krigia biflora),* and a goldenrod *(Solidago ptarmicoides),* in addition to four species with primarily western North American distributions and several state-listed species (Table 2). The herbaceous component of Northern Sand (oak) Savanna is moderately similar to that of jack pine barrens in the northern part of the region (Curtis 1959).

Eastern Sand Savanna Composition

Eastern Sand Savanna is found in northern and central Illinois, southern Wisconsin, and southern Michigan (Madany 1981, Pruka and Faber-Langendoen 1995, Rabe et al. 1995), northwestern Indiana (Homoya 1994), northwestern Ohio (Gordon 1966, Brewer 1989), and in southeastern Ontario (Catling and Catling 1993). Black oak is the characteristic tree, with other oak species present (Table 2). Dry sand savanna in central Illinois often has mostly blackjack oak *(Q. marilandica),* but is otherwise similar to other Eastern Sand Savanna sites (Anderson and Brown 1986). Ground-layer composition includes a short list of characteristic species including shining sumac *(Rhus copallinum),* staghorn sumac *(Rhus typhina), Aster linariifolius,* Virginia dwarf-dandelion (*Krigia virginica*), and two pinweeds (*Lechea mucronata* and *L. pulchella*), with three state-listed species (Table 2). Additional species are shared with other dry soil savanna types (Tables 1 and 2).

Dry Calcareous Savanna

Distribution

Dry calcareous savanna, like dry sand savanna, is edaphically restricted, with soils that have moderate nutrient status, are neutral (pH 7.0–7.5), have loam and silt loam texture, but are thin (8–30 cm) or excessively drained (Lange 1989, Catling and Catling 1993, Armstrong 1994). It is found throughout the region (Figure 1), in mostly small areas within complex savanna-woodland-dry prairie landscape mosaics. Examples are found on dolomite ridges in the unglaciated Driftless Area of Wisconsin, Illinois, Minnesota, and Iowa (Figure 1; Faber-Langendoen 1995, Anderson et al. 1996), on thin soils over quartzite bedrock (acid, but insoluble by groundwater) in the Baraboo Hills of southern Wisconsin (Lange 1989, Clark et al. 1993, Armstrong 1994), and on well-drained gravelly calcareous morainal ridges in the Kettle Moraine area of eastern Wisconsin (Henderson 1995). Thin soil over limestone on flat lowlands supports remnants of once more extensive dry calcareous savanna in southeastern Ontario (Szeicz and MacDonald 1991, Catling and Catling 1993).

Dry calcareous savanna is more likely than dry sand savanna to have classic savanna structure; the oak species are relatively fire tolerant, and slow buildup of herbaceous biomass reduces the likelihood of intense fires. The density and cover of woody vegetation have increased as fire frequency decreased. However, severe edaphic conditions have allowed remnants to persist (Will-Wolf and Stearns in press).

Composition

White and bur oak are the most characteristic tree species, while chinquapin or yellow oak *(Q. muehlenbergii)* occurs at either end of the range (Mississippi River valley and southeastern Ontario). Shagbark hickory *(Carya ovata)* is another characteristic species (Table 1). Of the characteristic ground-layer species (Table 2), snowberry (*Symphoricarpos* spp.) is common (Will-Wolf and Stearns in press), while most other species, like the tick-trefoils (*Desmodium* spp.) and the horse-gentians (*Triosteum* spp.), are relatively less common. Several are state-listed (Table 1). The Wisconsin sites share many herbaceous species with dry lime prairies of the same region (Anderson 1954). Ontario dry calcareous savanna (Catling and Catling 1993) has 40% of the prevalent species of Wisconsin oak openings (Curtis 1959) and also shares many species with Great Lakes alvar communities (areas of extremely thin soil over flat limestone or marble bedrock, with sparse, mostly treeless plant cover; Catling and Brownell in press).

Several state endangered, threatened, or special concern species occur on Wisconsin dry calcareous savanna sites as well as dry lime prairie, cliff communities, and cedar glades. They are round-stemmed false foxglove *(Agalinis gattingeri),* churchmouse three-awn or poverty grass *(Aristida dichotoma),* purple milkweed *(Asclepias purpurascens),* purple shooting star *(Dodecatheon radicatum),* creamy gentian *(Gentiana flavida),* violet bush clover *(Lespedeza* *violacea),* slender bush clover *(Lespedeza virginica),* brittle prickly pear *(Opuntia fragilis),* broomrape *(Orobanche uniflora),* prairie parsley *(Polytaenia nuttallii),* cliff goldenrod *(Solidago sciaphila),* and prairie fame-flower *(Talinum parviflorum)* (Clark et al. 1993, Anderson et al. 1996). One rare rush species *(Juncus secundus)* was found on an Ontario savanna (Catling and Catling 1993).

Summary

Dry sand savanna and dry calcareous savanna in the Great Lakes region differ enough in site characteristics, species composition, and structure that they must be treated separately for research, restoration and management planning. We separate dry sand savanna into two subgroups (classification of Haney and Apfelbaum 1995), emphasizing a strong east-west component to floristic differences. This may be as important for dry sand savanna as the more commonly recognized north-south differences between plant communities in the region. The dry sand savanna subgroup classification is preliminary and needs to be confirmed as useful. We welcome comments on the general lists presented here and elsewhere (Will-Wolf and Stearns in press) and additions to the studies surveyed (send to senior author), to facilitate updates of the lists.

Acknowledgments

We thank participants in the 1997 Midwest Oak Savanna and Woodland Conference for suggestions that have improved the species lists we present here. The manuscript has benefitted from comments by Roger Anderson, Ted Cochrane, and an anonymous reviewer.

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Richard Boudreau

A Sesquicentennial Look at Literary "Firsts" in Wisconsin

In the century and a half since statehood, writers from Wisconsin have reached out from purely local to regional audiences, then on to national, and in some instances, world audiences. Along the way they have garnered prestigious awards in this country, including Pulitzer Prizes and National Book Awards, as well as various citations and recognitions internationally. The state's presses, both small and commercial, and its long-standing literary organizations and support groups have fostered and continue to foster writing of all kinds, underscoring Kentucky poet Jesse Stuart's assessment of Wisconsin as the "writingest state in the union."[1] In celebration of our state's sesquicentennial, it seems particularly appropriate to step back in time and review once more and in depth the antecedents of this rich literary heritage.[2]

Wisconsin's literary beginnings predate even territorial times: the oral traditions of the Native Americans were already centuries old before European contact. But the first actually taken down were orations, recorded by translators or scribes or witnesses at treaty parleys and truces, the earliest dating back nearly three centuries,[3] and including several councils conducted by the Americans as they began taking over the area following the War of 1812.[4] One of the most moving speeches came not from a treaty conference but from a formal surrender, the so-called death-song of the Winnebago chief, Red Bird, at the Portage in 1827.[5] Besides orations there were songs: dream, war, love, hunting; chants, nearly all from religious rituals; and tales, both secular and sacred, particularly from the Ojibwa, Menominee, and Winnebago, who still maintain their dominance in the area. These were collected over the years by various ethnologists, beginning with Henry Rowe Schoolcraft, who married an Ojibwa mixed blood, his most important informant, and including work by Walter James Hoffmann with the Menominee, Paul Radin with the Winnebago, and Frances Densmore with the Ojibwa.[6]

With the inundation of the Americans into what became part of Michigan Territory came the printing press and almost immediately after, the newspaper. The first press was located in the oldest white settlement, Green Bay, and the first newspaper, *The Green Bay Intelligencer,* began its life there December 11, 1833. The first booklet published in what would be Wisconsin was an Ojibwa almanac, printed in 1834 on the Green Bay press,[7] not, as generally believed, Increase A. Lapham's study of the plants and shells on the west shore of Lake Michigan, published two years later in Milwaukee[8] on what was the third printing press in Wisconsin.[9] Lapham's *Wisconsin Gazetteer,* published in 1844, however, was the first book with "durable binding" printed in the Territory.[10] But the earliest book written by a "Wisconsinite" was Dr. William Beaumont's account, published in 1833, of his famous experiments with Alexis St. Martin, whose unhealed wound to the stomach allowed for Beaumont's remarkable research on human digestion.[11]

Such achievements in publishing in a new territory were not remarkable, perhaps, but in June 1842, *The Garland of the West,* appeared—and it was remarkable. It was the first literary magazine in the entire Northwest Territory.[12] Started by Edward Young and Julius H. Kimball in Southport (later Kenosha), it attempted to bring literature, particularly poetry (sentimentality reigned supreme) to the frontier. Its editors had good writers (one, L. P. Harvey, became Civil War governor of Wisconsin, tragically drowning on a visit to the front in 1862; another, Michael Frank, editor of the Southport newspaper, became known as "the father of the free school system" in Wisconsin) and great expectations—but little chance of success. By the third issue, that for August, Young was alone as the editor, and after some delay, he brought out the September and October issues combined as one, signalling difficulties. "Somewhat bleached and cut short of its fair proportions by the fall frosts," the *Milwaukee Courier* wryly noted.[13] Young then relinquished it to the Sholes brothers, Charles C. and C. Latham (later inventor of the typewriter), who changed the name to *Wisconsin Monthly Magazine,* promising to shift its focus to "useful reading matter instead of lovesick trash."[14] Their attempt, however laudatory, failed, but, since no copies are extant, it is not known when the magazine ceased publication.

Newspapers, however, thrived. Besides news of all and sundry, they were filled out with trivia, both informative and humorous, as well as with sketches,tales, and, particularly, verse. Newspapers were most important in fostering poetry in the new territory and state. They printed numerous single poems, called "waifs" by ambitious versifiers, most of whom were women. Famous names among Wisconsinites were Carrie Carlton (Mary Booth Chamberlain of Beloit), Ada F. Moore (Ellen E. Hall Phillips of Stevens Point), Nellie A. Mann (Helen A. Manville of La Crosse), and Nellie Wildwood (Mary Elizabeth Farnsworth Mears of Oshkosh). Each of them eventually legitimized their "waifs" by gathering them into collections published in the '60s and '70s. Despite all of their activity, however, what has been considered the first collection of Wisconsin poetry was written by a man. Adolf Schults, a self-proclaimed exile from Germany, published *Lieder Aus Wisconsin* in 1848, but his ties to Wisconsin are suspect.[15] If not Schults, either Hiram Alvin Reid of Beaver Dam or Orpheus Everts of Hudson, seem to be candidates with collections of poems published in 1856, but their residency seems suspect as well.[16]

That would seem to give Mary Elizabeth Farnsworth Mears the distinction of publishing the first book of verse in Wisconsin, a claim that has often been made.[17] Her long poem, *Voyage of Pere Marquette and Romance of Charles de Langlade or, The Indian Queen,* was printed in Fond du Lac in 1860. The long historical narrative has sometimes been referred to as Wisconsin's first "epic." But there was a much earlier claimant even to that title: *The History of Black Hawk, with which is interwoven a Description of the Black Hawk War and other Scenes in the West* by E. H. Smith, published in Milwaukee originally in 1846. Two years later Elbert (or Egbert) Herring Smith re-published the book with extensive alterations under the title *MA-KA-Tai-Me-She-Kia-Kiak; or, Black Hawk, and Scenes in the West.*[18] Other editions followed, and he evidently spent the rest of his life trying to make a living from his "epic." And since neither Smith's nor Mears's books are collections of poems and since the three male writers mentioned probably do not qualify as Wisconsinites, the honor of the first collection of poetry apparently belongs to Mary Booth Chamberlain (Carrie Carlton); her *Wayside Blossoms* appeared in 1862.

With drama the past is murky and inconclusive. The first play published in the state seems to have been *The Drummer, or New York Clerks and Country Merchants,* edited by a Mrs. Partington and published in Milwaukee in 1851.[19] But Mrs. Partington, a sort of Yankee Mrs. Malaprop, was a fictional creation of Boston printer and journalist, Benjamin Penhallow Shillaber.[20] And since the action of the play takes place in New York City with no apparent tie-in to Wisconsin and since its supposed author was a resident of Boston, it should probably be discounted. The first Wisconsin drama actually performed in Wisconsin, as far as we know, is the one written by the ubiquitous Mrs. Mears. Her play, *Black Hawk,* held the stage for a run of three weeks in Madison[21] about the time of the onset of the Civil War, but it is not known when she wrote it or whether she ever published it.

The first memoir, it has long been assumed, was the still popular and oft-published book by Juliette Magill Kinzie, *Wau-Bun, The Early Day in the Northwest, 1856.* It is primarily the account of her two and a half years at the Portage, 1830-33, with her husband, John Kinzie, Indian Agent to the Indians gathered in the vicinity of Fort Winnebago. More than that, it presents a sympathetic treatment of her nearest neighbors, the Indians, especially of the women. And the memoir delineates the last months of their sojourn there during which the Kinzies share in the restricted rations and near starvation of their neighbors. Written in a lively, engaging style, it is a moving, remarkable account.

But, as it turns out, it is not the first memoir. That achievement belongs to a Dominican priest, Rev. Samuel Mazzuchelli. Shortly after his ordination in 1830 this Italian missionary traveled extensively in the territory from Mackinac Island to Prairie du Chien, serving both Indian and White, Protestant and Catholic. Among other duties he served as chaplain to the second session of the Wisconsin Territorial Legislature which met in Burlington, Iowa, in 1836. On a trip back to his homeland after 12 years in the territory he wrote an account of his labors: *Memoirs, Historical and Edifying Among Various Indian Tribes and Among Catholics and Protestants in the United States of America.*[22] It was published in his hometown, Milan, Italy, early in 1844, about the time he returned to his missionary field in territorial Wisconsin.[23]

If we consider Mrs. Kinzie's book a memoir rather than an autobiography, then the first autobiography in Wisconsin literature was *The Life-Line of the Lone One* by Warren Chase, published in 1857.[24] Though Chase is the subject of his autobiography, he refers to himself throughout in the third person (as did Rev. Mazzuchelli in his *Memoirs*) or as the Lone One. He uses his birth year of 1813 as a starting point and arranges each chapter to cover one decade in his life. It is in the third chapter, 1833–1842, that he arrives in Southport in territorial Wisconsin, nearly destitute, with a very ill wife and a sickly first born. But his fourth chapter is of utmost interest: during that decade he joins a Fourierite socialist group, eventually becoming its leader, establishing in 1844 the communal settlement of Ceresco on land incorporated into the later village of Ripon. While he served as the leader of the "Wisconsin Phalanx," he also became a delegate to both constitutional conventions in Madison and was elected to the first state senate.[25] The Ceresco community disbanded in 1850, perhaps the only utopian community of that era to finish in the black. Chase became a spiritualist minister and moved further west, finally settling in California where he died in 1891.

The first novel in Wisconsin has for years been considered *Bachelor Ben* by Ella Giles, published in 1875, but there are a number of earlier claimants to that distinction. The first novel printed in Wisconsin was published "by a citizen of Milwaukee" in 1857. But with the story set entirely in New York State, it seems reasonable to assume it was written well before the "citizen" moved to Milwaukee. The next novel published was *Walter Ogilby* by Mrs. Kinzie of Wau-Bun fame. It appeared in 1869. That too is set in the East with no tie-ins with Wisconsin. But her second novel, *Mark Logan,* the Bourgeois, published posthumously in 1871, is set in what would become Wisconsin, along the Fox-Wisconsin river route the summer of 1827 (Mark Logan witnesses the surrender of Chief Red Bird). Because the author is certainly a writer with strong Wisconsin ties and because the story is the first involving the state as setting, it would seem to be the clearest choice for Wisconsin's first novel.[26]

Determining what could be called the first Wisconsin short story would be a monumental, if not impossible task. Copyright laws in the United States were confusing, largely ignored, and generally unenforceable; international copyright laws were not in place until much later. That meant that editors could, in effect, reprint tales and stories from any source whatever, including the best writers of the day. Nor, in fact, did the term, short story, exist; it did not come into use until the 1890s. If the first short story by a Wisconsin writer cannot be identified,[27] we can at least suggest a couple of collections that might qualify for the title of the first book of short stories. Both are by George Wilbur Peck: *Peck's Sunshine,* in 1882, which includes some of his longer humorous tales, and *Peck's Bad Boy and His Pa,* in 1883, made up of short episodes in the life of the "Bad Boy." With illustrations alternating almost equally with the text, the latter could also be considered the precursor of the comic strip.[28]

A sesquicentennial seems an ideal time for a reconsideration, and in the review just completed, we have evidence that alters a number of assumptions about our literary past. Increase A. Lapham's booklet of 1836 was not the first pamphlet published in the state, though his *Wisconsin Gazetteer* of 1844 was certainly the first book published here. And the first book written by a Wisconsinite, William Beaumont's treatise of 1833, can be added to the list of literary firsts. *The*

Garland of the West, 1842, is a remarkable first—the first literary magazine in the entire Northwest Territory. The first memoir is clearly that of Rev. Mazzuchelli even though written in Italian and published in Italy in 1844. Mrs. Mears loses two firsts attributed to her, for a book of verse and for the "epic," but gains another, the first play by a Wisconsinite presented in the state. Mrs. Kinzie loses one first, that of autobiography or memoir, but gains a new one, the first novel by a Wisconsinite, *Mark Logan,* published in 1871. And humorist/governor, George Wilbur Peck, appears to have title to the first short story collection published in the state.

With literary antecedents such as these stretching back into the earliest years, how could Wisconsinites fail to recognize and to honor such auspicious beginnings and the prodigious outpouring of writing that has ensued in the last century and more in their state? Perhaps there is no better way to acknowledge such a rich literary heritage than to take note of, and to honor, our present day writers and to search out, read, and cherish good books by Wisconsin authors of whatever era.

Endnotes

[1] As quoted by Clarice Chase Dunn, in "Wisconsin Writes," *Wisconsin Academy Review,* June 1983, pp. 26–27.

[2] The best source to begin such a review is Orrilla T. Blackshear's *Wisconsin Authors and Their Books: 1836–1975* (Madison: Wisconsin Department of Public Instruction, 1976).

[3] "The Cass Manuscripts," republished in *Wisconsin Historical Collections,* Vol. III., (Madison: The State Historical Society, 1856), pp. 152-53, contain short speeches by Fox, Sauk, and Winnebago spokesmen at a parley with the French in 1726.

[4] See, for example, the speech of Sau-sa-man-nee in *Wisconsin Historical Collections,* Vol. X, pp. 143–45. Native American orations are scattered throughout the volumes of this invaluable collection.

[5] "After a moment's pause, and a quick survey of the troops, and with a composed observation of his people, he spoke, looking at Major Whistler, and said: 'I am ready.' Then, advancing a step or two, he paused and said, 'I do not wish to be put in irons. Let me be free. I have given away my life—(stooping and taking some dust between his finger and thumb and blowing it away)—like that' (eyeing the dust as it fell and vanished), then adding, 'I would not take it back. It is gone.'" From Moses M. Strong, "Indian Wars," *Wisconsin Historical Collections,* Vol. VIII (Madison: The State Historical Society, 1879), pp. 262-63. Red Bird died in prison soon after his surrender.

[6] See Henry Rowe Schoolcraft, Algic Researches, 1839; Walter James Hoffman, "The Menomini Indians," *The Fourteenth Annual Report of the Bureau of American Ethnology,* 1896; Paul Radin, numerous books, selections of which form the volume, *The Winnebago Tribe* (Bison Books: University of Nebraska Press, 1970); and Francis Densmore, *Chippewa Music I & II,* Bureau of American Ethnology Bulletin 53, 1913, and *Menomonee Music,* Bureau of American Ethnology Bulletin 102, 1932.

[7] The booklet is referred to in the biography of Rev. Samuel Mazzuchelli by Jo and J. Alderson, *The Man Mazzuchelli: Pioneer Priest* (Madison: Wisconsin House, 1974), Chapter 5 (no page nos.), and again in the Aldersons' article on Mazzuchelli in the *Wisconsin Academy Review,* Summer, 1998. Only one copy of the booklet is known to exist; it is located in the Library of Congress. The only other reference to its being the first published in Wisconsin is found in footnote 13,

page 87, of the *Positio,* or *A Documentary Account of His Life, Virtues and Reputation for Holiness* used as the basis for consideration in the Roman Catholic Church for Rev. Mazzuchelli's beatification, published in Rome in 1989.

[8] See Henry Eduard Legler, "Early Wisconsin Imprints: A Preliminary Essay," *Wisconsin Historical Society Proceedings,* 1904, p. 119; See also Paul G. Hayes, "Increase A. Lapham: A Useful and Honored Life," *Wisconsin Academy Review,* Spring, 1995, pp. 10–15. Of course, it still is assumed to be the first scientific treatise published in Wisconsin.

[9] Legler, 119.

[10] See Legler, p. 120: Increase A. Lapham, *Geographical and Topological Description of Wisconsin* (Milwaukee: P.C. Hale, 1844). This was popularly known as the Wisconsin Gazetteer.

[11] William Beaumont, *Experiments and Observations on the Gastric Juice and the Physiology of Digestion* (Plattsburgh, New York: Allen, 1833). Dr. Beaumont was stationed at Mackinac Island in 1822 when he began to treat St. Martin's wound. Dr. Beaumont then served at Fort Howard, Green Bay, from 1826–28, and at Fort Crawford, Prairie du Chien from 1828–1832, where, from 1829 on, the majority of his experiments were carried out.

[12] See M. M. Quaife, "Wisconsin's First Literary Magazine," *Wisconsin Magazine of History,* Vol. 5, 1, 1921–22, 43.

[13] Quaife, 47.

[14] Quaife, 47.

[15] See Oscar Wegelin, "Historical Fragments: Wisconsin's First Versifiers," *Wisconsin Magazine of History,* Vol. 1, 1921–22, pp. 64-67. The book, written in German, was published in Germany (by J. Badecker of Elberfeld and Iserlohn); it's possible that Schults never lived in Wisconsin or that he visited here for a short time only.

[16] "Hiram Alvin Reid, *The Heartlace and Other Poems* (the author, 1856)" according to Blackshear, but the book was published in Davenport, Iowa, that year, and he claimed many years later that it was the first book of poetry printed in Iowa, not Wisconsin. "Orpheus Everts, *Onawequah, An Indian Legend and Other Poems,* (Hudson: Times Printing Office, 1856)" according to Blackshear, but the book was published that year in La Porte, Indiana, not in Wisconsin. He was a member of the law firm of Tuttle, Reymart & Everts in Hudson from 1859 to 1861. Though Reymart became prominent in Wisconsin, Everts disappeared from sight.

[17] Among many others over the years, Legler, p. 121. But even as recently as Janet Ela's "Sculptor Helen Farnsworth Mears" in *Wisconsin Academy Review,* March, 1986, that claim was repeated. The Helen Farnsworth Mears of the article title was one of Mrs. Mears's three talented daughters.

[18] See Oscar Wegelin, "Historical Fragments: Wisconsin's First Versifiers," *Wisconsin Magazine of History,* Vol. 1, No. 1, 1918. Written "by a Western Tourist" this book was published in New York in 1848 and was the one Legler discounted because he did not think the author had residency in Wisconsin. But in an interesting aside, the whole story of the "Wisconsin Bard" is rendered in *The Chronicles of Milwaukee* by A. C. Wheeler, 1861. Smith, a teacher in a rural school near Southport, took himself seriously as a poet. He was apparently led on by others in what they intended as a massive joke which boomeranged when Smith began to profit from his "epic."

[19] Oscar Wegelin, "An Early Wisconsin Play," *Wisconsin Magazine of History,* Vol. 1, No. 4, pp. 307–8.

[20] This is all very curious. Wegelin was apparently aware of the "true" Mrs. Partington because he mentions Shillaber, though Wegelin de-

cides Shillaber had nothing to do with the piece. Since there is no other information available, we can only conjecture: the manuscript was written by Shillaber and printed by a friend; the manuscript was pirated; the manuscript was written and printed by persons unknown who might or might not have lived in Wisconsin.

[21] Publius V. Lawson, "Mary Elizabeth Mears: 'Nellie Wildwood,'" *Wisconsin Historical Society Proceedings,* 1916, p. 255. The claim is actually made by her daughter, Mary Mears, in a letter she wrote to Lawson shortly after her mother's death.

[22] *Memorie Istoriche ed Edificanti d'un Missionario Apostolico del'Ordine dei Predicatori fra Varie Tribu di Selvaggi e fra I Cattolici e Protestanti negli Stati-Uniti d'America* (Milano: Bonardi-Pogliani, 1844).

[23] Alderson, Chap. 10 and "Sources," at the end of the book. His *Memoirs* were essentially unknown to Wisconsinites until their translation in 1915 by Sister Mary Benedicta Kennedy, O.S.D., the order that Rev. Mazzuchelli founded, headquartered at Sinsinawa. The book was reprinted in 1967. Rev. Mazzuchelli founded many parishes in southwest Wisconsin, eventually settling in Benton, Wisconsin, where he served as pastor until his death in 1864.

[24] Warren Chase, *The Life-Line of the Lone One; or Autobiography of the World's Child* (Marsh, 1857).

[25] For a succinct account of his life see *Dictionary of Wisconsin Biography* (Madison: The State Historical Society of Wisconsin, 1960).

[26] See Richard Boudreau, "Wisconsin's First Novel," *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 86, 1998. Two other books in Blackshear appear to be possibilities: *Teone* by Rusco (Mary Ann Smith, Milwaukee, 1862), and *The Friar's Curse* by Michael Quigley (Milwaukee, 1870). But neither is a novel; both are long narrative poems in the style of medieval romances.

[27] But in Publius V. Lawson's article, "Mary Elizabeth Mears: 'Nellie Wildwood,'" in *Wisconsin Historical Society Proceedings* for 1916, daughter Mary Mears claims that her mother "was the author of many fugitive poems and stories which appear in editions of the early newspapers of Wisconsin." If so, Elizabeth Farnsworth Mears may hold another first: the writer of the first Wisconsin short story.

[28] The first collection of short stories about which there would be no argument is that of Capt. Charles King: *Starlight Ranch, and Other Stories of Army Life on the Frontier* (Lippincott, 1890).

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Richard Boudreau

Wisconsin's First Novel

What was the first "Wisconsin" novel? The answer to that question has traditionally been *Bachelor Ben,* by Ella Augustus Giles, published in 1875. That assumption has gone unchallenged for years, even in two lengthy books published for the state's centennial in 1948: *The Story of Wisconsin Women* by Ruth de Young Kohler (76) and *The Wisconsin Story* by H. Russell Austin (478). But in this year of Wisconsin's sesquicentennial, it's time to set the record straight: The Giles novel clearly is not the first. A close review of *Wisconsin Authors and Their Books, 1836–1975,* by Orilla Blackshear, turns up around 20 possible candidates for that honor. A few of these can be eliminated for various reasons when cross-checked in *The National Union Catalogue,* but ten possibilities survive.

Even with the shorter list, however, there are still difficulties; it is not a simple task to define what a "Wisconsin" novel should be. Though any definition will probably prove less than satisfactory, let us try one that is at least simple and workable. This would be two-fold: (1) that the writer at the time of composition was or had been a resident of the area and (2) that some part of the novel be set in the area and/or draw to some extent on experiences from that residency, however tangential. In other words, that both the writer and his/her artistic production reflect a Wisconsin connection. With this in mind let us take a closer look at the possibilities.

Two books from the final list turn out not to be novels. The entry in the Blackshear bibliography for Mary Ann Smith's book, *Teone; or, The Magic Maid,* published in Milwaukee in 1862 by the pseudonymous "Rusco," is a long narrative poem in the style of the medieval masterpiece, *The Pearl.* Strange enough to be published in frontier Milwaukee, but even stranger is that it purports to be told around the bunkhouse stove in a Maine logging camp by one of the loggers. And its story of magic, involving the lovely maid, Teone, a prince, a Green Knight, a time frame of a year and a day, and a three days waiting period before the final settlement of accounts, echoes the famous long poem, *Sir Gawain and the Green Knight.* But this story in book form stretches to over 5,000 lines, double that of its model. And the rest is silence: Who was Mary Ann Smith? How did this book come to be written? How did it come to be published on a Wisconsin press?

The second non-candidate is *Trimsharp's Account of Himself,* published originally in 1873, and including a handful of poems at its end. The book is not poetry, however, nor is it finally fiction, but, as its title suggests, an autobiography, though published under a pseudonym. Not an autobiography of an ordinary man—at the time of its writing its author, Harvey A. Fuller, was only 38 years old. Born in upstate New York near Lake Ontario, he grew up on the frontier, first in New York, then in Ohio and Indiana. At the age of 20 he became deathly ill with cholera, and through complications and lingering illness, lost sight in both eyes. After his recovery he attended the newly opened Institution for the Blind in New York City, where he became acquainted with the inspirational Laura Bridgman, who though blind, deaf and mute, lived a full life (Fuller quotes an extensive passage from Charles Dickens's *American Notes* concerning this remarkable woman). After several more adventures he entered Hillsdale College in Michigan, graduating in 1868. At the urging of his friend, Wisconsin poet Will Carleton, Fuller moved to Milwaukee a few years after his autobiography appeared, and lived the rest of his life there, publishing a play and three books of poetry.

With *Amanda: A Tale for the Times,* by W. H. Brisbane, M. D., we begin our look at bona fide novels. Published in Philadelphia in 1848, it is the tale of a beautiful young woman of Cincinnati who exchanges promises with her brother's college friend, James Ballou of Charleston, South Carolina. Along the way she unknowingly arouses lust in one of his classmates, Jack Dundas—the villain. He arranges an elaborate plot of drugging, kidnapping, and transportation to enslavement in New Orleans to achieve his ends. Amanda herself is led to believe she is part Negro, daughter of a slave. But both brother and betrothed, each separately, discover her whereabouts, free her, and have Dundas arrested. Though the preface suggests an attack on "the wickedness of certain Federal and State laws and Judicial Decrees," the story is merely an adventure-romance. And though published as a book, at 12,500 words it is hardly a long short story. William Henry Brisbane (1803–1878) was an active abolitionist in the 1840s, a member of the American and Foreign Anti-Slavery Society. In later years, well after the publication of his tale, he lived in Arena, Wisconsin.

Julia, or Sister Agnes, is certainly a novel, but it is also a tract, first on living a good Christian life and more narrowly a Catholic life (with strong overtones of Jansenism), written by the Rev. John W. Vahey of Milwaukee. Two Irishmen with their young families emigrate to America in 1844, settling as farmers in central Illinois. But the heart of the story is the wooing of Julia, the properly raised daughter of Richard Burke, by John, the atheistic son of James Moran. He is headed for a bad end—corrupted by the public schools, by the university (where he worked on a law degree), and by his inheritance of money. Her God-fearing parents see what he is and will be and forbid Julia further contact with him. Frustrated, Julia elopes to St. Louis, and with his promise to become a Catholic, she marries him. Of course it does not work out: he submits her to a life of misery, heightened by his drunkenness, his hypocrisy, his rages, and his dissipation of the inheritances of both his parents and hers. After five years of hell, Julia is delivered—her husband expires in the throes of delirium tremens. Penniless, she becomes a laundress, eventually enters the convent she had considered entering long before, and dies there at the age of 45. Discerning readers will note that since she was born just prior to her family's departure for America, she must have died in 1889, 14 years after the time of the appearance of the book. That's writing for the eternities! The narrative is not well told: characters, particularly Julia, are manipulated beyond belief. Dialogues are stilted and often turn into diatribes. Even so, the story is a novel, and it appeared in the same year as Ella Giles's *Bachelor Ben.*

Charles Herbert Richards's novel, *Will Phillips, or, The Ups and Downs in Christian Boy-Life,* appeared in 1873. The publisher—not listed in Blackshear (505)—was D. Lothrop of Boston, and the book, categorized as juvenile fiction, was one of 32 titles in the company's Young Folks series. The Union Catalogue contains no entry for the book, though it does for other of his writings. Of the two libraries with copies, neither would release it for interlibrary loan. Oddly enough, there is no copy of it registered in the Library of Congress. A Congregational minister, Richards (1839–1925) lived his last years in Madison, quite likely well after this book was published. In any case the exact year of his move to the state raises the question of whether he could be considered a Wisconsin author at the time of the book's publication.

Several Lives by Thomas Marshall, was published in 1874 under the strange pseudonym, Fasyl Stamford. It is an out and out temperance tract—common enough in that era—and at first sight seems to be a collection of such stories. But it is more than that—or less. It contains the parallel lives of two Chicago men from birth to death. Each chapter contains two parts, one devoted to one man at a particular time in his life, the other to the other man at the same time, the chapter ending, usually ironically, with items from the local newspapers. Albert Smythe, son of a successful businessman, grows up to live the good life, then through his own success becomes an alcoholic. Dick Donner, the son of a drunkard, doomed to alcoholism, late in life after his health has been destroyed by drink, becomes a reformer. The book ends up qualifying as a novel, somewhat unusual in its telling and always with the failings of character and motivation found in tracts, temperance or otherwise. It also contains a curious appendix: a collection of reports for the first months of 1874 of the women's crusade against drink throughout the United States, particularly in the upper Midwest. Thomas Marshall was a resident of Milwaukee at the time of its publication.

Minnie Hermon: or, The Night and Its Morning by Thurlow W. Brown, published in 1854, would seem to be a prime candidate for the first Wisconsin novel. Though it is a temperance tract, a cautionary tale, it is for all that clearly a novel. Thurlow W. Brown was a New York native, a fervid "dry" who edited the temperance newspaper, *Cayuga Chief,* beginning in 1849, when he was 30. In 1854 he moved to Hebron, Wisconsin, for his health, and two years later began editing his paper in Fort Atkinson. In 1857 he changed its name to *Wisconsin Chief* and began including abolitionist fulminations as well. His style of delivery both written and spoken was "vehement, sarcastic, and vitriolic" (Dictionary, 53), and perhaps for that reason he was successful in reviving the ailing temperance movement in the state. The setting for the novel was upstate New

York; that would not disqualify it, but Brown notes in the preface that the story "was commenced two years ago in the *American Temperance Magazine,* but abandoned," and further that "detached chapters . . . appeared in the Chief"—all of this prior to his move to Wisconsin.

There is only one Tucker noted in the Blackshear listing: Mary Eliza Perine Tucker, followed by various pseudonyms and a reference to La Crosse (596). Her novel, *Confessions of a Flirt: "An Over True Tale,"* under the pen-name of Ella Leigh, published in 1865, would seem to qualify as an early Wisconsin novel. The citation, however, does not show that the place of publication was Milledgeville, Georgia. Further research reveals that she was married first to a John M. Tucker and later to a James H. Lambert. Her second husband worked for "Brick" Pomeroy on his New York *Democrat,* and for a few months on Pomeroy's La Crosse *Democrat* as well. The La Crosse city directory for 1868–69 lists Lambert as assistant editor of the *Democrat.* It was Mrs. Lambert's 1868 biography, *Life of Mark M. Pomeroy,* editor of the La Crosse *Democrat* and a leader of the Copperheads during the Civil War, that led to complex confusion. David O. Coate, English professor at the La Crosse normal school, assumed that the author of the Pomeroy biography was the La Crosse Mrs. Tucker who had published the book, *Hawthorne Dale,* in 1869 (71).

But the La Crosse Mrs. Tucker's given names were Elizabeth Letitia, and it is certain that she was the mother of Blanche Roosevelt, a moderately successful opera singer and writer, who was born in 1854 in Ohio, shortly before they moved to La Crosse. Thus if she was "Ella Leigh," she would have been scarcely 16 at the time of the birth of her daughter and lived not only in Ohio and Wisconsin but also in Georgia—not impossible, but certainly improbable. The evidence seems overwhelming: Mary Eliza Perrine Tucker, "Ella Leigh," cannot be considered a Wisconsin author. But Elizabeth Letitia Tucker of La Crosse can be. Her book, *Hawthorne Dale,* is, however, neither fish nor fowl, spending 200 pages on English country life and another 200 pages on Masonry (including a description of the first Masonic funeral in La Crosse). The book, not listed in Blackshear at all, is certainly not a novel and so must be disqualified.

Another writer not mentioned by Blackshear and not included in the list of ten referred to earlier is Mrs. E. D. E. N. Southworth, an enormously popular novelist of the mid-nineteenth century. As a young bride she lived in Prairie du Chien from 1841 to 1844 and taught school in Platteville during that time (Campbell, 187). She seems to have used the three year experience on the frontier in only one novel, *India, or The Pearl of Pearl River,* 1856. Serialized three years earlier in *The National Era* (the magazine in which Harriet Beecher Stowe's *Uncle Tom's Cabin* appeared), it originally bore the title, *Mark Sutherland, or Power and Principle.* Though the frontier setting provides the background for about a third of the novel, Mrs. Southworth did not locate the site in Wisconsin but along the Mississippi in Illinois somewhere above Rock Island. Neither her residency nor the setting of her novel, then, are adequate to mark her book as the first Wisconsin novel.

Stronger candidates are two novels written by Juliette Magill Kinzie, who is well known to Wisconsin readers. Her husband was appointed Indian Agent at the Portage in 1830, and the couple lived there for two and a half years. Her memories of that era are beautifully told in her book, *Wau-Bun,* *the Early Day in the Northwest,* first published in 1856 and republished many times since. Following the years at the Portage, they lived in Chicago, and Mrs. Kinzie, besides raising a family, continued her writing. The novel, *Walter Ogilby,* appeared in 1869; *Mark Logan the Bourgeois,* in 1871 (the 1887 edition in Blackshear is a reprint, 342), a year after Mrs. Kinzie's death. The first was set in New York state (not "at Fort Winnebago" as the *Dictionary of Wisconsin Biography* has it, 208); the second, an adventure novel, is set in what was then Michigan territory—in Green Bay, along the Fox River, and at the Portage. The narrative is competently written, though the story, concerning an affluent young man masquerading as a voyageur is derivative. Mrs. Kinzie makes good use of her knowledge of the settings. Is two and half years enough to qualify a writer as a native? We would certainly balk at not calling *Wau-Bun* anything other than a Wisconsin book.

But the strongest candidate for the honor of the first "Wisconsin" novel seems to be the book, *Garangula, the Ongua-Honwa Chief: A Tale of Indian life Among the Mohawks and Onondagas Two Hundred Years Ago.* Published in Milwaukee in 1857, its title page claims that it was written by a citizen of that city. The book is certainly a novel—about 60,000 words in length. Commentary about the book in an article, "Early Wisconsin Imprints," in *Wisconsin Historical Society Proceedings* for 1903 (120–21) reveals nothing further about the author. The subject matter and setting are obviously New York, but in the early days of Dutch settlement. It is, primarily, a love story involving Katrine, "a beautiful, plump, rosy-cheeked, black-eyed" girl, and Diedrich, a stalwart Dutch boy. They are caught up in the border wars, allies of the Mohawk but enemies of the French. Through all the misunderstandings and hair-raising adventures, love finally wins out, and handsome Diedrich in the end marries the beautiful Katrine, and they all live happily ever after. Because of his/her intimate knowledge of the area around Schenectady, the author must have been raised there. So important questions remain: When did he/she write the book? When did he/she move to Wisconsin?

And then there is *Bachelor Ben.* That, too, is set in New York, but in the city. Benjamin Grant, a bachelor of about 30, finds an abandoned babe on his doorstep at midnight. The following day he adopts the little girl, naming her Bertha. Later he befriends a young boy by the name of Harry, takes him under his wing and sends him to school. Of course love develops between the two youngsters, and following college Harry will marry Bertha. Then there are revelations: Bertha and Harry are said to be brother and sister! A few bad moments—but the confusion is finally cleared up. They marry and live happily ever after with Bachelor Ben helping them set up an orphanage in the mansion of his former partner, the real father of Bertha. That was the first, but not the only novel by Ella Giles, later Ruddy. She continued her career in writing, both fiction and poetry, but the date of that first novel is finally too late to stand unchallenged as the first in Wisconsin.

What we have left after this curious—and curiouser—walk-about among the musty pages of the past are six possibilities: *Garangula,* 1857, is the earliest published—if only we knew something definitive about the author. *Walter Ogilby,* 1869, and *Mark Logan,* 1871, were the next earliest, and though it is a book for boys, we can't just ignore Will Phillips, whose date of publication, 1873, puts it midway among these survivors. *Several Lives,* 1874, is another possibility, but it just barely qualifies as a novel.

Julia shares the publication date of 1875 with *Bachelor Ben,* but like that novel, it is not set in the state, though both Rev. Vahey and Ella Giles are certainly Wisconsin authors. Not one is a perfect candidate.

Garangula should, without question, be cited at the first novel published in Wisconsin, but since it seems likely that its author wrote the story before coming to the state, it cannot be considered the first "Wisconsin" novel. That leaves the novels of Juliette Magill Kinzie, whose ties to Wisconsin were short though strong. Her first novel, *Walter Ogilby,* set elsewhere, does not reveal any ties to the state, and so misses on one of our criteria. But her second novel not only takes place primarily in what would become Wisconsin, but makes vivid use of her actual experiences in the area. *Mark Logan,* then, seems the best and firmest candidate for the honor of being called the first "Wisconsin" novel.

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Keith R. McCaffery, James E. Ashbrenner, and Robert E. Rolley

Deer Reproduction in Wisconsin

Abstract *White-tailed deer* (Odocoileus virginianus) *reproductive information was obtained during 1982–87 from 1,686 does. About two-thirds of all does were pregnant in all regions except the Southern Farmland Region where about three-quarters were pregnant. The incidence of fawn pregnancy ranged from 3% in the Northern Forest Region to 51% in the Southern Farmland Region and appeared to vary with deer density relative to estimates of maximum carrying capacity. Statewide, the number of fetuses per pregnant doe averaged 1.65 ± 0.02 (S.E). Mean litter size of yearlings and adults was generally lower in the forested regions than in the farmland regions. The sex ratio for all fetuses observed was 109 males per 100 females. In utero productivity of does increased with age until 2.5 years old and declined after does reached 8.5 years of age. Estimates of in utero productivity for regional populations ranged from 1.10 fawns per doe in the Northern Forest Region to 1.26 in the Southern Farmland Region and correlated with the percentage of yearlings among does and with antler development of yearling bucks.*

The Wisconsin Department of Natural Resources (WDNR) is responsible for balancing the positive benefits (hunting and non-hunting recreation, economic expenditures, etc.) and negative impacts (deer-vehicle accidents, crop damage, etc.) of Wisconsin's white-tailed deer resource. The WDNR uses regulated harvests to manage deer populations at established population goals. Proper harvest management involves balancing mortality rates with reproduction. However, deer reproductive potential has not been well documented in Wisconsin. Earlier research had limited sample size (Dahlberg and Guettinger 1956:84) or restricted geographic distribution (Hale 1959). Additionally, reproductive rates of white-tailed deer are density-dependent (McCullough 1979), and deer densities in the farmland regions have increased considerably since these earlier studies.

Our objectives were to determine age-specific reproductive rates and fetal sex ratios for the major physiographic regions in the state. Additionally, we compared estimates of the productivity of regional deer populations to several indices that are currently used to monitor deer reproduction.

Physiographic Regions

Wisconsin is divided into over 120 deer management units. For our analyses, deer management units were grouped into 5 physiographic regions based mainly on land use (Figure 1).

Northern Forest Region

This region lies above 45° latitude in the east and 46° in the west. Severe winters (causing significant direct mortality of deer) occur on average once per 3 to 4 years (Kohn 1972, McCaffery 1987). Most units within this region are 75 to 95% deer range (patches > 4 ha [10 acres] of commercial and noncommercial forest land, reverting brushy old fields, plus a 100 m [330 ft] perimeter extending from this permanent cover into agricultural fields [McCaffery 1988, Wisconsin Department of Natural Resources 1994]) and forested mainly with northern hardwoods (mostly *Acer* spp.), aspen (*Populus* spp.), balsam fir (*Abies balsamea*), pines (*Pinus* spp.), and swamp conifers (mostly *Picea mariana, Thuja occidentalis,* and balsam fir) (Spencer et al. 1988). Topography is gently to moderately rolling. Soils include stoney glacial till, pitted outwash sands, and peat.

Deer densities from 1982 to 1987 averaged about 6.7 deer/km^2 (17/mi^2) of deer range, which is close to the established goal of 6.9 (18/mi^2). Winters are the main variable affecting annual variation in carrying capacity in northern Wisconsin. The winter severity index for northern Wisconsin (Creed et al. 1984:256) averaged 62 for the 6 years of the study compared to the long term (1960–89) average index of 68 (Wisconsin Department of Natural Resources 1994:12). Severe conditions for deer occur when the index exceeds 80. Thus, sampling occurred under representative deer densities and winter conditions.

Central Forest Region

This region experiences severe winters for deer an average of once in 6 years (Kubisiak 1979). The primary landuse is forestry and cranberry production, although dairy and truck farming exists on the perimeter of this region. The land is generally flat and is 70 to 88% deer range, which includes open marshes and forests that are mostly oaks (*Quercus* spp.), pines, and aspen. Soils are mainly sands, sandy loams, and shallow peats. Deer populations in the Central Forest Region averaged about 12.3 deer/km^2 (32/mi^2) of deer range during the study, which is somewhat above the goal of 10.6 (28/mi^2).

The Farmland Regions

The Eastern and Western Farmlands, separated by the Central Forest Region, lie above latitude 44° and below the Northern Forest. These regions experience significant winter losses of deer infrequently (1967 and 1979 from 1960–90), whereas winter losses are even less frequent (only 1979 from 1960–90) in the Southern Farmland Region which is between 42°30" and 44° latitude. In all 3 regions, upland forests are mainly central hardwoods (oaks, maples, hickories [*Carya* spp.]) and pines, while

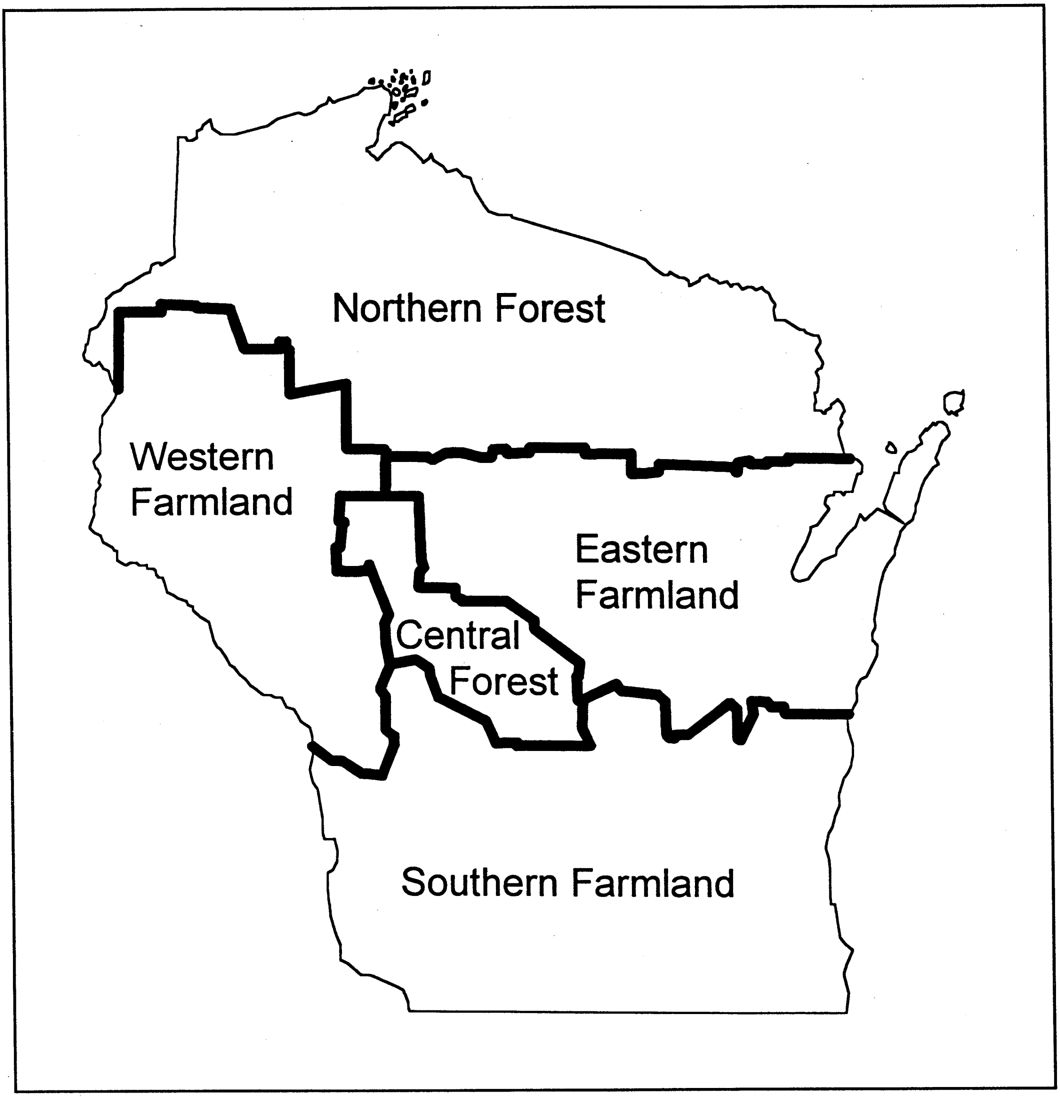

Figure 1. Regions sampled during the 1982–87 deer reproduction survey in Wisconsin. The Northern Region lies north of a line from the cities of Grantsburg to Spooner in the west and from Cornell to Marinette in the east. The Southern Farmland Region lies generally south of a line from LaCrosse to Oshkosh.

wetlands are represented by marshes, shrub-carr, and lowland hardwoods (mainly *Fraxinus* spp. and *Acer saccharinum*). Deer range comprises 25 to 75% of most units, lower in the southeast. Topography varies from gently rolling in the east to steep-walled valleys (mostly 100–200 m [330–660 ft] of relief) in the west. Soils are mainly silt loams and sandy loams. Dairy farming is the primary land use. Overwinter deer populations during this study averaged close to the 1986 goal of about 9 deer/km^2 (23/mi^2) of deer range (Wisconsin Department of Natural Resources 1994:28).

Methods

Wildlife managers throughout the state were provided instructions for collection of reproductive observations from dead deer (mostly road-killed). Observers removed the uterus to determine presence, number, and sex of fetuses. Presence or absence of lactation was noted when fetuses were absent. Observations were restricted to 1 February through 1 June to facilitate determination of sex of fetuses. Observers were instructed to examine deer systematically and not to choose only those that were obviously pregnant.

Ages of deer were initially assigned in the field as fawn, yearling, or adult using a modification of tooth wear and replacement criteria (Severinghaus 1949). The age assigned was the age at the time the deer would have been bred. To confirm field assigned ages and to obtain specific ages of adult does, incisors were collected from each doe, and cementum annuli were counted on thin sections (Low and Cowan 1963, Gilbert 1966, Kuehn 1970). When annuli on tooth sections of young deer were indistinct, the field assigned age was used as suggested by Howe (1980).

In utero productivity of regional populations was estimated by multiplying the estimated proportion of the doe population in each age class by the respective pregnancy rate and fetuses per pregnant doe. The proportion of yearlings and adults for each region was determined using age data obtained from harvested animals (Wisconsin Department of Natural Resources, unpublished data). The proportion of fawns was estimated from summer roadside observations of fawns and does in the forested regions, an assumed fawn:doe ratio of 1.2 for the farmland regions, and the observed fetal sex ratio of 109 males per 100 females. The resulting age distribution of females ranged from 28% fawns, 20% yearlings, and 52% adults in the Northern Forest Region to 36% fawns, 27% yearlings, and 37% adults in the Southern Farmland. Estimates of in utero herd productivity were compared to 3 potential indices of reproductive performance: (1) summer roadside observations of fawns per doe (Rusch 1986), (2) antler development of yearling bucks (percentage with forked antlers), and (3) the percentage of yearlings among does ≥ 1.5 years old (Wisconsin Department of Natural Resources, unpublished data).

Regional pregnancy rates of fawns were compared to regional deer densities relative to estimated maximum deer carrying capacity. Estimates of regional deer carrying capacity were based on observed rates of population increase (post-harvest to subsequent preharvest or Lambda$_2$) relative to deer population size (Keith 1988; Wisconsin Department of Natural Resources 1994, 1995); i.e., $K = D/2\text{-}L$ where D is the 13-year (1981–93) mean deer density, L is the mean (1981–93) Lambda$_2$, and 2 was assumed to be the maximum instantaneous rate of increase for any region (McCullough 1979, Keith 1988, McCaffery 1989, Wisconsin Department of Natural Resources 1995: Appendix C).

We used two-way ANOVA to test for age and region effects on mean litter size and made multiple-comparisons with the Duncan's Multiple Range Test. Because litter size is count data, we used a square root transformation (Snedecor and Cochran 1967). These procedures were also used to test for effects of doe age on in utero productivity. Log-linear analyses of three-way contingency tables and chi-square analysis of two-way contingency tables were used to examine the effect of age and region on pregnancy rate. The relationship of pregnancy rate and relative population density was assessed with Spearman rank correlation as were the relationships of estimated herd productivity with the 3 indices of reproduction. Fetal sex ratios were tested for deviation from a 1:1 ratio using a chi-square goodness of fit test, and chi-square contingency tables were used to compare fetal sex ratios among age classes and litter size.

Results

During 1982–87, 1,686 does and 1,895 fetuses were examined. Though not specifically solicited, no observers reported discovering mummified or decaying fetuses. Over 94% of the deer were killed by vehicles on roads. Although samples were sought throughout the state, almost three-fourths of the total sample came from farmland regions (Table 1) because of the high frequency of roadkills there.

Pregnancy Rate

Pregnancy rates differed among age classes in all 5 regions (χ^2 = 68.01-215.12, 2 df, P = 0.001), much lower for fawns than for yearlings and adults (Table 1). Among yearlings and adults, the effect of age was consistent among regions (χ^2 = 1.42, 4 df, P = 0.84), lower for yearlings than adults (χ^2 = 23.71, 1 df, P < 0.001).

The effect of region on pregnancy rate differed among age classes (χ^2 = 31.92, 8 df, P < 0.001). Pregnancy rate did not differ among regions for adults (χ^2 = 2.22, 4 df, P = 0.70) or yearlings (χ^2 = 3.56, 4 df, P = 0.47). However, pregnancy rate of fawns differed among regions (χ^2 = 85.41, 4 df, P = 0.001); lowest in the Northern Forest, intermediate in the Central Forest and Eastern and Western Farmland regions, and highest in the Southern Farmland. Regional fawn pregnancy rate was negatively correlated (r = -1.00, n = 5, P < 0.001) with relative

Table 1. In utero productivity of female white-tailed deer by age class (when bred) for 5 regions of Wisconsin, 1982–87. Values shown ±1 standard error.

Region	*Age Class*	*No. of Does*	*Percent Pregnant*	*No. of Fetuses*	*Fetuses per Pregnancy*	*Fetuses per Doe*
Northern Forest	Fawns	79	3 ± 3	4	2.00 ± 0	0.05
	Yearl	58	81 ± 5	65	1.38 ± 0.07	1.12
	Adult	163	95 ± 2	268	1.75 ± 0.04	1.64
Central Forest	Fawns	42	17 ± 6	8	1.14 ± 0.14	0.19
	Yearl	34	85 ± 6	37	1.28 ± 0.08	1.09
	Adult	45	96 ± 3	80	1.86 ± 0.17	1.78
Western Farmland	Fawns	182	29 ± 3	62	1.17 ± 0.05	0.34
	Yearl	106	86 ± 3	148	1.66 ± 0.05	1.40
	Adult	135	96 ± 2	249	1.95 ± 0.04	1.84
Eastern Farmland	Fawns	68	19 ± 5	14	1.08 ± 0.08	0.21
	Yearl	31	94 ± 4	48	1.66 ± 0.09	1.55
	Adult	74	99 ± 1	143	1.96 ± 0.07	1.93
Southern Farmland	Fawns	288	51 ± 3	165	1.15 ± 0.03	0.57
	Yearl	207	88 ± 2	302	1.66 ± 0.04	1.46
	Adult	172	95 ± 2	302	1.90 ± 0.04	1.76
Statewide		1,684	69	1,895	1.65 ± 0.02	1.13

population density (percent of estimated regional carrying capacity) and positively correlated with regional carrying capacity ($r = 0.90$, n = 5 , $P = 0.04$, Table 2).

Mean Litter Size

Among the 1,152 litters examined, 39% contained a single fawn, 57% contained twins, and 3% contained triplets. Only two sets of quadruplets were encountered during the study, both from farmland regions.

Statewide, the mean (± SE) litter size (number of fetuses per pregnant doe) was 1.65 ± 0.02 (Table 1). The effect of region on mean litter size differed among age classes (F = 2.61; 8, 1,136 df; $P = 0.008$). For adult (≥ 2.5 yrs when bred) does, mean litter size varied among regions (F = 3.46; 4, 551 df; $P < 0.008$), lower in the Northern Forest than in the Eastern and Western Farmland regions. Mean litter size of yearlings also differed among regions (F = 6.03; 4, 371; $P < 0.001$), lower in the Northern and Central Forests than in the 3 farmland regions. Because of the low fawn pregnancy rate in the Northern Forest, sample size was too small (n = 2) for reliable estimation of mean litter size. Therefore, we excluded the Northern Forest from the regional comparison. Mean litter size for fawns did not differ among the 4 remaining regions (F = 0.24; 3, 213 df; $P = 0.87$).

Productivity versus age

In utero productivity (fetus/doe, including does that were not pregnant) varied among ages (F = 168.88; 9, 1,653 df; $P < 0.001$), increasing with age for fawns, yearlings, and 2 year old does (Figure 2). Productivity did not differ among 2–8 year old does ($P > 0.05$), but productivity of 9+ year old does was lower than for 3–6 year old does ($P < 0.05$). The oldest doe observed during the present collection was 18 years old and was carrying one fetus.

Fetal Sex ratios

Sex was determined for 1,803 of the 1,895 fetuses examined. The sex ratio was 109 males per 100 females, which was nearly different from 1:1 ($\chi^2 = 3.29$, 1 df, $P = 0.07$). Fetal sex ratios did not vary among doe age class ($\chi^2 = 1.62$, 2 df, $P = 0.45$), litter sizes ($\chi^2 = 1.14$, 3 df, $P = 0.77$), or region ($\chi^2 = 3.16$, 4 df, $P = 0.53$).

Regional Population Productivity

Estimates of in utero productivity for regional populations ranged from 1.10 fawns per doe in the Northern Forest to 1.26 fawns per doe in the Southern Farmland (Table 3) and correlated well with the subsequent percentage of yearlings among does ≥ 1.5 years ($r = 0.97$, n = 5, $P = 0.005$) and the percentage of yearling bucks with forked antlers ($r = 0.90$, n = 5, $P = 0.04$). The percentage of yearling does and the percentage of yearling bucks with forked antlers also were correlated ($r = 0.97$, n = 5, $P = 0.005$, Table 3). However, the mean fawn:doe ratio from roadside observations did not correlate with regional in utero productivity ($P = 0.28$), percent yearling does ($P = 0.22$), or antler forking ($P = 0.19$).

Discussion

Among the reproductive parameters we measured, fawn pregnancy rate showed the strongest regional differences. The low fawn pregnancy rate in the Northern Forest (3%) during our study was similar to that reported for northern Wisconsin by Hale (1959), for northern Michigan by Friedrich and Hill

Table 2. Incidence of fawn pregnancy and recent deer herd status (deer/km^2) relative to estimated maximum average carrying capacity (K) in 5 regions of Wisconsin.

Region	*K*[a]	*Mean Density*[b]	*Percent K*	*Percent of fawns Pregnant*[c]
Northern forest	10.8	6.7	62	3
Central forest	22.3	12.3	55	17
Western farmland	25.4	7.9	31	29
Eastern farmland	26.2	9.3	35	19
Southern farmland	33.5+	8.7	<25	51

[a] Average (1981–94) biological carrying capacity (K) by zone: K = D/2-Lambda$_2$, where D is the average overwinter deer density (1981–94), 2 is the assumed maximum instantaneous rate of increase for any region, and Lambda$_2$ is the average (1981–94) observed rate of herd increase from postharvest to subsequent preharvest. Note that 2 - Lambda$_2$ = %K/100.

[b] Mean overwinter deer density estimate (1981–87) by region from Wisconsin Deer Database (WDNR 1989).

[c] Percent of fawns pregnant from Table 1.

Table 3. Comparative indices to deer reproduction in the 5 regions of Wisconsin.

Region	*Fawns/doe in Regional Population*[a]	*Roadside Fawn:doe Ratios*[b]	*Yearling Doe Percent*[c]	*Percent Forks on Yearl. Bucks*[c]
Northern forest	1.10	0.81	28	55
Central forest	1.11	1.15	33	59
Western farmland	1.20	1.11	38	86
Eastern farmland	1.22	0.96	38	85
Southern farmland	1.26	1.21	45	94

[a] In utero productivity of regional population based on age-specific fetuses per doe and age composition of females.

[b] Six-year means (1982-87) of fawns/doe from Summer Deer Observation Survey (McCaffery 1992).

[c] Percent yearlings among does ≥1.5 yr. (1983–88) and percent of yearling bucks with forked antlers (1982-87) from WDNR unpublished data.

(1982), and for northern Minnesota by Bill Berg (Minnesota Department of Natural Resources, unpublished data).

We estimated a 17% fawn pregnancy rate in the Central Forest; however, our sample size was relatively small. Prior research in this region found only 3 of 40 fawns (8%) necropsied during late-winters of 1968–72 contained fetuses, and only 3 of 38 yearling does (8%) with corpora albicantia (indicating prior pregnancy) between 1979–84 (John Kubisiak, Wisconsin Department of Natural Resources, unpublished data). Hale (1959) reported 16% fawn breeding in his West Central Area, which included both Central Forest and farmland counties. We retabulated his data for our Central Forest Region, and only 6 of 79 fawns (8%) were bred. Our estimate of fawn pregnancy rate for this region was not statistically different from these earlier estimates ($\chi^2 = 2.88$, 2 df, $P = 0.24$).

Fawn pregnancy rates were at intermediate levels in the Eastern and Western Farmland and highest in the Southern Farmland Region. The 51% fawn pregnancy rate in the Southern Farmland Region was lower than the 65 to 74% reported for Iowa (Haugen 1975), but similar to southern Minnesota (45%, Ingebrigtsen 1988) and

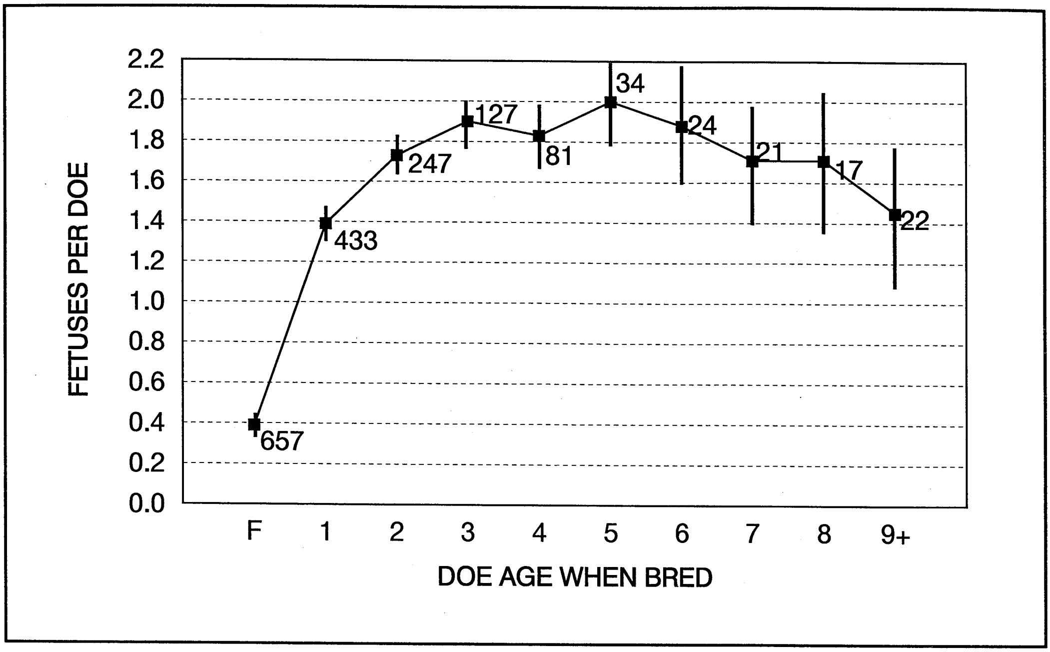

Figure 2. Average fetuses per doe by age class in Wisconsin during 1982–87. Numbers denote total does in sample and vertical bars show 95% confidence limits.

southern Michigan (51%, Friedrich and Hill 1982:Table B, and Verme 1991).

Deer reproductive performance is affected by nutritional condition, which in turn is influenced by density relative to carrying capacity (McCullough 1979 and 1984, Verme 1983, Teer 1984:274). Fertility of the youngest does (fawns and yearlings) is most affected by environmental variables (Hesselton and Jackson 1974). McCullough (1979:61) and Downing and Guynn (1983) indicated that fawn breeding would not generally occur when population densities exceed 60% of carrying capacity.

Local deer carrying capacity is affected by habitat quality, but on a larger scale it is also affected by climate (Strickland et al. 1994:451). The incidence of fawn breeding in Wisconsin increased with decreasing latitude (climatic effect of milder winters and longer growing seasons). Also, the availability of agricultural crops, with high nutrient quality, increases with decreasing latitude. Thus, carrying capacity was much higher in the southern regions of the state. Deer population goals are roughly similar across regions (~7–10 deer/km^2, 18–28/mi^2). As one moved south, the lower deer densities relative to carrying capacity resulted in increased fawn breeding. Regional differences in mean litter size of yearlings and adults also suggested lower reproduction in the forested regions than the farmland regions.

In utero productivity increased with age through 2 years of age, was stable for 2- to 8-year-old does, and then declined (Figure 2). This pattern was very similar to that reported for the eastern United States by Sileo (1966:Figure 2) and a large dataset from Michigan (Friedrich and Hill 1982).

Our statewide fetal sex ratio (109 males/ 100 females) was similar to other sex ratio estimates for the Lake States, which range from 107 to 119 males/100 females (Mc-

Cullough 1979, Verme 1985, Ingebrigtsen 1988, Paul Friedrich, Michigan Department of Natural Resources, unpublished data). A number of factors have been hypothesized to influence in utero sex ratios including age of the doe (Severinghaus 1984), litter size (Verme 1983), nutritional status (Verme and Ullrey 1984:99, Verme 1985), deer density (McCullough 1979:68), and timing of breeding (Verme and Ozoga 1981). Verme (1983) and Ozoga and Verme (1986) also indicate that primiparous (first pregnancy) does, whether fawns or yearlings, have disproportionately more male offspring. Despite considerable variation in regional carrying capacity and relative population density, we detected no regional variation in fetal sex ratio. Likewise, we found no effect of maternal age or litter size on fetal sex ratio.

The factors that affect sex ratio may vary by region and year, and some factors may be compensatory. But precise and accurate measurement of sex ratio differences requires huge sample sizes. Following their review of the literature, Woolf and Harder (1979) concluded that many observed departures from a near 1:1 ratio may be "mere localized aberrations." Based on our findings and other research in the region, it seems reasonable to believe that the fetal sex ratio tends to favor males in Wisconsin.

Despite the large regional differences in some age-specific reproductive parameters, estimates of population productivity (fawns/all does) were relatively similar among regions ranging only from 1.10 fawns/doe in the Northern Forest Region to 1.26 in the Southern Farmland Region. This similarity was caused by the higher proportion of fawn and yearling does in the population, which produce at lower rates than adults, in the South. Although population productivity was relatively similar among regions, southern herds had a much higher rate of population increase (mean Lambda$_2$ of 1.72 for the Southern Farmland Region vs. 1.33 for the Northern Forest Region when herds are at goals [Wisconsin Department of Natural Resources 1995:191–92]). This was due in part to the higher proportions of does in the population in the South as a result of higher harvest rates of bucks. In addition, recruitment of fawns to the fall population is a function of both reproduction and neonatal survival. Neonatal survival is likely lower in the North due to inadequate maternal nutrition (Verme 1977).

Regional estimates of population productivity were strongly correlated with the percentage of yearlings among does, which is routinely measured in harvested samples. However, variable over-winter mortality associated with winter severity may limit the usefulness of yearling age composition for evaluating annual variation in fawn production, especially in the forested regions. Antler development of yearling bucks has been demonstrated to correlate with production in New York (Severinghaus and Moen 1983) and was significantly correlated with both population productivity and yearling age composition of does. Yearling antler development is annually monitored through mandatory registration of harvested deer and shows promise for monitoring annual as well as regional variation in reproduction.

The Wisconsin Department of Natural Resources has collected roadside observations of fawns and does since the early 1960s. Kohn (1976) reported a negative relationship between fawn:doe ratios in the Northern Forest and an index to winter severity. The lack of correlation between roadside fawn:doe ratios and regional population productivity, percentage of yearlings among does, and antler development of yearling bucks in this study raises questions about the usefulness of this index. Additional research should assess the validity of this index of deer reproduction, especially in the farmland regions.

Recently, some have expressed concern about the effect of high adult buck harvest rates on deer social behavior and herd productivity (Miller et al. 1995). Hale (1959) indicated that the annual firearm hunting season in November did not seem to impair pregnancy rates in Wisconsin at the time of his study. Deer populations and adult buck mortality rates in Wisconsin farmland have increased during the past 30 years. The high incidence of pregnancy among farmland does suggests that pregnancy rates are near normal (Harder 1980) despite adult buck mortality rates of 85 to 90% in many units due mostly to late November gun hunting (Wisconsin Department of Natural Resources 1989:IV). The peak of conceptions tends to occur in mid-November prior to Wisconsin's firearm hunt, however much of the fawn breeding occurs during December (Hale 1959) by surviving adult bucks or pubertal buck fawns (L.J. Verme, pers. comm.).

The results of this study have led to two modifications to WDNR's deer population model. First, the fawn sex ratio is now assumed to be 110 males per 100 females statewide rather than the region-specific estimates of 111–135:100, based on harvested samples of fawns that were used prior to 1986. Second, we have suspended the use of annual data from the summer roadside fawn/doe index in farmland regions, using long-term constants instead.

Since these data were collected, deer populations have increased substantially in the Northern Forest and farmland regions (ratio of mean 1994–96 population estimates:mean 1982-87 population estimates = 1.66, 0.93, 1.36, 1.49, and 1.45 for the Northern Forest, Central Forest, Eastern Farmland, Western Farmland, and Southern Farmland, respectively). While we suspect that fawn pregnancy rates have declined in some regions with the increases in deer density, direct measures of deer reproduction (in utero fetal counts) are not available for recent years. Other indices of reproduction (roadside fawn:doe ratios, percentage of yearlings among does, and antler development of yearling bucks) do not show consistent declines that can be attributed to these higher deer densities. But roadside observations and age composition of harvested does combine data from all age classes of does masking the contribution of fawn does. Because yearlings and adults are affected less by nutritional stress than are fawns, these indices are relatively insensitive to changes in density. Additionally, annual variation of all 3 indices in the forested regions is strongly affected by variation in winter severity, which complicates the detection of density-dependent declines in reproduction within these regions (McCullough 1990).

Deer populations during 1994–96 were well above prescribed population goals. Aggressive harvest strategies and back-to-back severe winters (1996 and 1997) in the North have greatly reduced herd levels. We expect that the reproductive rates observed during this study would be representative of populations near goal.

Acknowledgments

Special thanks are due to all field personnel who did the sometimes unpleasant task of necropsying bloated dead deer. Thanks are also offered to Dr. Lyle Nauman (UW-Stevens Point) for coordinating the preparation and reading of tooth sections by students. We also acknowledge Harry Hill and Paul Friedrich (Michigan DNR) for providing tabulations of Michigan data to compare to our own. This manuscript was improved following reviews and comments on earlier drafts by W.A. Creed, L.J. Verme, G.A. Bartelt, R.T. Dumke, and anonymous referees. The study was funded in part by Federal Aid to Fish and Wildlife Restoration, Pittman-Robertson Project W-141-R.

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Black Bear Food Items in Northern Wisconsin

Abstract *We identified 68 black bear* (Ursus americanus) *food items in 967 scats collected during May through August 1976–79. Frequency of occurrence and volume composition indicate that seasonally important foods were grasses (Gramineae), sedges* (Carex *spp.*), *sweet cicely* (Osmorhiza claytonii), *and quaking aspen* (Populus tremuloides) *in May; grasses, sedges, ants (Formicidae), jack-in-the-pulpit* (Arisaema triphyllum), *and sweet cicely in June; ants, tree and shrub fruit, and wild sarsaparilla* (Aralia nudicaulis) *in July; ants and tree and shrub fruit in August. Plants were found in 100% of the scats, insects in 47%, and other animals in 15%. Of 13 forest communities examined, important bear foods appeared to be more abundant in boreal, aspen, wet mesic, and wet communities.*

Black bear food habits have been reported elsewhere in recent studies (Beeman and Pelton 1980, Irwin and Hammond 1985, Rogers 1987, Hellgren and Vaughan 1988, MacHutchon 1989, McClinton et al. 1992, Hellgren 1993, Boileau et al. 1994). Seasonal changes in diets of black bears are related to availability of foods, preference, and physiological needs (Tisch 1961, Landers et al. 1979, Beeman and Pelton 1980). Availability of foods has been reported to influence reproductive success and the localization of activities within home ranges (Rogers 1976, 1987; Lindzey and Meslow 1977; Novick 1979; Beecham 1980; Young 1980). Thus, the identification of principal and alternate food sources is an important aspect of black bear ecology.

This paper is the compilation of 2 studies (Norton 1981, Bertagnoli 1986) designed to identify the important summer (May–August) food items for black bears. The compilation provides the most comprehensive list of black bear foods for

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[1] Deceased, June 20, 1993, at age 43 from Lou Gehrig's disease. This paper is dedicated to him and the memory of his sense of humor and his professionalism, especially his contribution to black bear biology.

Wisconsin. The information can be used to help understand differences in bear productivity within the Great Lakes region and to identify potential impacts of forest management activities on bear habitat quality.

Study Area

The 995-km^2 study area was located in western Iron County, Wisconsin, which borders Lake Superior and the Upper Peninsula of Michigan (Figure 1). Kohn (1982) estimated a population of 255 black bears (1 bear/3.9 km^2) in the study area. A series of hills (the Penokee Range) divides the area into northern and southern zones. The northern zone comprises 25% of the study area and has moderately fertile loams and sandy loams (Soil Conservation Service 1972), with forestry and agriculture the major land uses. The southern zone soils are typically clay or sandy loams representing the Gogebic and Wakefield series (Curtis 1959), with forestry and forest-related recreation the major land uses.

Hardwood and coniferous forest types (Curtis 1959) dominate the study area. Forest reconnaissance data from 1978 (Wisconsin Department of Natural Resources files) showed a composition of 43% northern hardwoods, 25% aspen (*Populus* spp.), 21% conifers, and 8% cleared land. Municipalities and lakes comprise 3% of the study area. Dominant tree species include sugar maple *(Acer saccharum)*, yellow birch *(Betula lutea)*, and American basswood *(Tilia americana)* in the northern hardwood type. Quaking aspen *(Populus tremuloides)* and big-tooth aspen *(P. grandidentata)* constitute the aspen type. Coniferous forests consist of 3 associations: (1) white spruce *(Picea glauca)* and balsam fir *(Abies balsamea)* are dominant in the boreal or upland type; (2) northern white cedar *(Thuja occidentalis)* and balsam fir dominate in the wet-mesic, or swamp conifer type; (3) black spruce *(P. mariana)* and tamarack *(Larix laricina)* dominate in the wet forest type (Curtis 1959). Cleared land includes areas under active cultivation and abandoned farmlands. Both provide sodded openings and a source of domestic apples (*Pyrus* spp.). Common crops are corn, oats, potatoes, and hay. Many streams, lakes, ponds, and bogs occur in the area.

Weather patterns in the area are influenced by Lake Superior. Summer temperatures are lower and precipitation is generally higher than in other areas of the state. Snow cover usually exists from mid-November until mid-April with an annual accumulation of over 279 cm. Length of the growing season is 110–120 days.

Methods

This study was conducted in conjunction with a bear population study by the Wisconsin Department of Natural Resources (Kohn 1982). Food habits were determined by analyzing fresh scats (fecal droppings) collected daily during May through August, 1976–1979. Scats were placed in plastic bags, labeled (date, location), and frozen to maintain color, texture, and aroma of food items.

Laboratory procedures described by Adams (1957) and Korschgen (1969) were used to analyze the scats. Food items were identified by comparing scat fragments with plates in Symonds (1963) and Montgomery (1977), reference materials collected on site, plant keys, and herbarium specimens. Mammal remains were identified with the hair key developed by Adorjan and Kolenosky (1969) and by comparing bone and hair samples with museum specimens. An ocular estimate of the percent composition of solid material in each scat was recorded: trace, 2–5%, 6–15%, 16–50%, 51–75%,

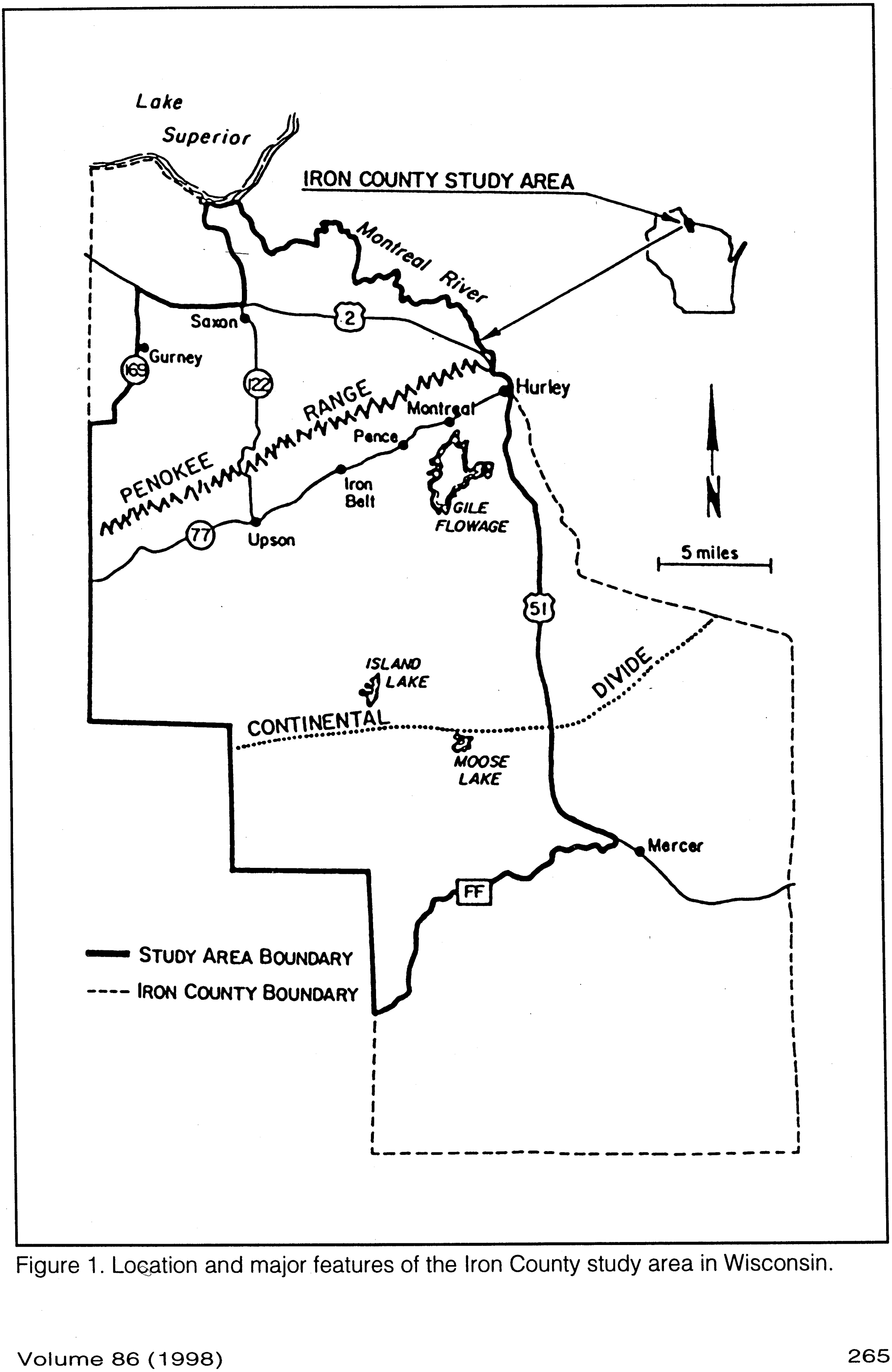

Figure 1. Location and major features of the Iron County study area in Wisconsin.

76–100% (Clark 1957, Tisch 1961, Beeman 1971). Food use was summarized monthly by percent composition and frequency of occurrence in the scats. Forage importance values (frequency of occurrence x percent composition) also were determined for each food item (McCaffery et al. 1974). Percent composition values for all food items eaten each month were compared among all years by using *Z*-tests (Neu et al. 1974).

Availability of bear foods within forest types was estimated by using data from the original field sheets of Curtis (1959) in the Plant Ecology Laboratory, Department of Botany, University of Wisconsin-Madison. The percentage of study plots in which Curtis (1959:79) observed a plant species in each forest community was used to estimate availability of that plant species. Similarities between forest communities relative to availability of plant foods were determined by using indices of similarity (Curtis 1959:83). In 1978 and 1979, the relative importance of a forest community as a source of plant foods for black bears was estimated from the percent occurrence of each plant food found in the community and from the forage importance value (determined by scat analysis) for that food.

Results

Sixty-eight black bear food items were identified from analysis of 967 scats collected during May through August 1976–79. Nineteen percent of the scats were collected in May, 38% in June, 23% in July, and 20% in August. Plants occurred in 100% of the scats, insects in 47%, and other animals in 15%.

Foods of black bears were identified and ranked by their forage importance (FI) values (Table 1). Plant material dominated the diet in frequency and volume, with grasses and sedges having the greatest forage importance value (1,151). Grasses and sedges were combined and identified as 1 food item because of the difficulty in separating families, genera, and species. Of the black bear foods identified from scats, 32 had low (<10) forage importance values. Some unidentifiable material occurred in all scats examined.

Members of the Rosaceae had relatively high forage importance values: apple (*Pyrus malus* and *Pyrus* spp.), raspberry (*Rubus* spp.), cherry (*Prunus* spp.), juneberry (*Amelanchier* spp.). So did blueberry (*Vaccinium* spp.). Excluding fruit, quaking aspen leaves and catkins were the most important tree parts used by black bears in this area.

Colonial insects (mainly ants) were the most important of the animal remains identified. Snowshoe hares *(Lepus americanus)* had the highest forage importance value of all other animal foods. The remains of hares, consisting of small amounts of hair and bone, could have represented scavenging or predation. White-tailed deer *(Odocoileus virginianus)* remains were observed at low levels. The remains consisted of hair and bone chips, the result of scavenging or predation. We observed 12 occurrences of black bear remains in black bear scats.

In all months a variety of foods was eaten, but only a few had high monthly forage importance values (Table 2). The general pattern in food habits for bears in northern Wisconsin was as follows: (1) In May, grasses, sedges, sweet cicely, and aspen catkins and leaves were most important. Ants, skunk cabbage *(Symplocarpus foetidus)*, common dandelion *(Taraxacum officinale)*, cow parsnip *(Heracleum maximum)*, clover (*Trifolium* spp.), hemlock *(Tsuga canadensis)* needles, and cranberries (*Vaccinium* spp.) were important as some of the diet for most bears or most of the diet for some bears. (2) In June, grasses, sedges, ants, jack-in-the pulpit, and sweet cicely were most important. Skunk cabbage, common dandelion, and aspen leaves and catkins were important as some of the diet for most bears or most of the diet for some bears. (3) The diets of black bears seemed to be the most diverse in July. Ants, tree and shrub fruits (especially Rosaceae: *Rubus* spp., blueberry [*Vaccinium* spp.], wild sarsaparilla, and apple) and jack-in-the-pulpit were most important. Common dandelion, grasses, sedges, and sweet cicely were important as some of the diet for most bears. (4) In August, ants, tree and shrub fruit (especially *Rubus* spp., cherry, mountain holly *[Nemopanthus mucronatus]*, red-osier dogwood *[Cornus stolonifera]*, and apple) were most important. Grasses, sedges, clover, wild sarsaparilla, jack-in-the-pulpit, and bees (Vespidae) were important as some of the diet for most bears or most of the diet for some bears. The occurrence of Vespidae in scats probably indicates the use of honey and honey bees *(Apis mellifera)*, both wild and commercial, in the diet. In Wisconsin, bears often raid apiaries, resulting in nuisance complaints.

Type and pattern of food use were similar during all 4 years, but differences ($P <$ 0.05) were noted in the number of occurrences of some foods. The use of apples, blueberries, blackberries (*Rubus allegheniensis*), and juneberries and the farm crops of corn and oats reflected annual differences in their availability. Jack-in-the-pulpit, skunk cabbage, red-osier dogwood, sweet cicely, wild sarsaparilla, and common dandelion were important in the diet in 1976 and 1977, but were not eaten in 1978 and 1979. Only 10 of the 68 bear food items were present all 4 years.

Of those foods common all years, ants ($Z = -5.19$), buds ($Z = -11.45$), blackberries ($Z = -2.87$), clover ($Z = -3.95$), grasses ($Z = -8.41$), juneberries, raspberries, and snowshoe hares occurred more ($P < 0.05$) in 1978 and 1979 than in 1976 and 1977. Occurrences of aspen catkins ($Z = 2.26$), cherries ($Z = 4.08$), and mountain holly ($Z = 2.60$) were greater ($P < 0.05$) in 1976 and 1977 than in 1978 and 1979.

Plant foods used by black bears were present in every forest community of the study area in 1978 and 1979 (Table 3). With > 26 food items in wet mesic, > 25 in boreal, and > 25 in aspen communities, these communities appeared to contain the greatest number of plant foods and have the greatest community forage importance values (Table 4). Most (> 65%) of the plant foods in the wet mesic, boreal, and aspen communities occurred in > 25% of the stands examined by Curtis (1959).

Although sample sizes were low, differences ($P < 0.05$, 12 df) existed between availability and use of grasses ($\chi^2 = 79.8$), red-osier dogwood ($\chi^2 = 64.8$), sweet cicely ($\chi^2 = 134.1$), raspberry ($\chi^2 = 102.2$), cherry ($\chi^2 = 75.0$), wild sarsaparilla ($\chi^2 = 183.2$), juneberry ($\chi^2 = 84.2$), aspen leaves ($\chi^2 = 76.8$), blueberry ($\chi^2 = 115.7$), clover ($\chi^2 = 69.9$), water arum ($\chi^2 = 63.2$), blackberry ($\chi^2 = 74.7$), moss (Lycopodiales, $\chi^2 = 137.2$), and gooseberry (*Ribes* spp., $\chi^2 =$ 75.0) throughout the 13 forest communities. A chi-square test of frequency indicated a positive relationship ($P < 0.05$) between availability of plant foods and use by black bears in the forest communities studied (Table 5). Dry mesic, mesic, wet mesic, wet, aspen, sedge, and bracken communities provided more ($P < .05$) grasses than other communities. Similarly, wet mesic, wet, aspen, and alder communities provided more ($P <$ 0.05) red-osier dogwood than other communities. In general, of the 13 forest communities examined, important bear foods appeared to be more abundant in boreal, aspen, wet mesic, and wet communities.

Discussion

Plants and insects were the most important bear food items found in this study. The importance of plant material for black bears has long been recognized (Cottam et al. 1939). The relatively small number of important plant foods indicates that black bears rely on certain key foods to meet their nutritional needs (Rogers 1976, 1987).

Grasses and sedges, sweet cicely, and the catkins and leaves of quaking aspen were the most important bear food items from the time of den emergence until 30 June. Early fruiting shrubs (*Ribes* spp. and *Vaccinium* spp.) also were important food items during this period.

Ants (Formicidae) had the highest forage importance value of all food items in July and were important in all 4 months. Fruits of raspberry, blueberries, and wild sarsaparilla also were important food items in July. Although jack-in-the-pulpit is mildly toxic (Gleason and Cronquist 1963), it too was eaten often in July.

Tree fruits (*Prunus* spp. and *Pyrus* spp.) constituted a major portion of the August diet. Tree fruits were dominated by a single species—black cherry *(Prunus serotina)*. When abundant, black cherries were preferred to other fruits. Bears foraged for black cherries on the forest floor or climbed the trees for them. Branches of fruiting trees along opening edges and roadsides often were broken by bears. Preference for black cherries might be responsible for the reduced frequency of shrub fruits in the diet. Bears in the nonagricultural portion of the study area appeared to supplement their diet with mountain holly when black cherries were not abundant.

Domestic oats also provided an alternate food source. Farmers in the study area reported that bear damage to oats crops was highest when black cherries and blueberries were scarce; damage was nonexistent or low when the fruits were abundant.

White-tailed deer were not an important food item of bears during this study. But Anderson and Fleming (1994) reported that 7 of 12 radio-tagged fawns killed by predators in their study area (only 40 km west of ours) were killed by bears. They thought that most of the bear predation was due to chance encounters with fawns less than 2 weeks old, but noted that bears were known to be purposely hunting fawns on several occasions.

Most of the principal foods used by bears in this study were produced by shade intolerant plants as defined by Curtis (1959). In Wisconsin, these are abundant in grassy forest openings, road rights-of-way, recent cutovers, canopy gaps, natural wetlands, pine openings, and the aspen and aspen-balsam forest types. In addition, all of the rotting logs in the sodded forest openings on the study areas were visited by bears in search of insects. Except for sweet cicely and a few mature black cherry trees, northern hardwood stands provided limited amounts of bear food items in the study area.

Wisconsin's black bears are among the largest and most productive in the country (Reneau and Reneau 1993, Kessler 1994). This undoubtedly reflects the quality of the current habitat.

Table 1. Annual black bear food habits in northern Wisconsin as determined from 967 scats collected during 4 summers (May, June, July, August) 1976–79.

	1976			*1977*			*1978*			*1979*			*Average*		
Food Item[a]	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*
Monocots															
Gramineae and Cyperaceae	41.2	25.2	1038	48.4	19.0	920	71.6	12.0	859	73.7	22.0	1621	58.7	19.6	1151
Arisaema triphyllum	16.2	36.7	595	11.0	31.5	347	0.0	0.0	0	0.0	0.0	0	6.8	17.1	116
Symplocarpus foetidus	4.0	46.0	184	3.1	27.2	84	0.0	0.0	0	0.0	0.0	0	1.8	18.3	33
Zea mays	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	2.3	22.0	51	0.6	5.5	3
Alisma spp.	2.1	18.4	39	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.5	4.6	2
Acorus calamus	0.8	28.0	22	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.2	7.0	1
Juncus spp.	0.5	49.1	25	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	12.3	1
Avena sativa[b]	—	—	—	—	—	—	0.5	3.0	2	0.0	0.0	0	0.1	0.8	<1
Equisetum spp.	0.5	3.0	2	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	0.8	<1
Unidentified monocots	1.6	19.7	32	3.2	19.2	61	3.4	1.0	3	5.3	1.0	5	3.4	10.2	35
Dicots															
Osmorhiza claytonii	19.7	24.8	489	16.2	18.3	297	13.2	11.0	145	15.8	22.0	348	16.2	19.0	308
Trifolium spp.	4.5	13.6	61	7.5	13.2	99	13.2	2.0	26	12.8	9.0	115	9.5	9.5	90
Taraxacum officinale	9.6	17.2	165	16.5	21.5	355	0.0	0.0	0	0.0	0.0	0	6.5	9.7	63
Fragaria spp.	0.3	5.0	2	0.8	10.0	8	1.5	1.0	2	1.5	45.0	68	1.0	15.3	15
Heracleum maximum	1.8	17.7	32	4.0	18.2	73	0.0	0.0	0	0.0	0.0	0	1.5	9.0	14
Calla palustris	0.0	0.0	0	0.0	0.0	0	25.0	2.0	50	27.8	2.0	56	13.2	1.0	13
Unidentified Umbelliferae	1.6	5.0	8	11.9	6.1	73	0.0	0.0	0	0.0	0.0	0	3.4	2.8	10
Hieracium spp.	1.1	11.0	12	0.8	10.3	8	0.0	0.0	0	0.0	0.0	0	0.5	5.3	3
Lycopodium spp.	0.0	0.0	0	0.0	0.0	0	9.8	1.0	10	9.0	1.0	9	4.7	0.5	2
Urtica spp.	0.0	0.0	0	0.5	30.0	15	0.0	0.0	0	0.0	0.0	0	0.1	7.5	1
Polygonum cilinode	0.0	0.0	0	1.2	18.2	22	0.0	0.0	0	0.0	0.0	0	0.3	4.6	1
Unidentified Compositae	0.0	0.0	0	0.0	0.0	0	2.0	1.0	2	4.5	1.0	5	1.6	0.5	1
Viola spp.	0.0	0.0	0	0.4	25.0	10	0.0	0.0	0	0.0	0.0	0	0.1	6.3	1
Unidentified ferns	0.0	0.0	0	0.0	0.0	0	1.5	1.0	2	3.0	1.0	3	1.1	0.5	1
Potentilla spp.	0.3	5.0	2	0.4	1.0	1	0.0	0.0	0	0.0	0.0	0	0.2	1.5	<1
Sonchus spp.	0.2	1.0	1	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	0.3	<1
Cornus canadensis	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	1.5	1.0	2	0.4	0.3	<1
Lactuca spp.	0.0	0.0	0	0.0	0.0	0	1.0	1.0	1	1.5	1.0	2	0.6	0.5	<1
Unidentified dicots	4.1	27.0	111	5.5	28.1	155	9.8	1.0	10	6.8	1.0	7	6.6	14.3	94

Table 1, continued.

	1976			1977			1978			1979			Average		
Food Item[a]	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*
Tree fruit															
Prunus serotina [c]	12.2	45.0	549	30.3	60.4	1830	0.0	0.0	0	0.0	0.0	0	10.6	26.4	280
Pyrus spp.[d]	5.8	49.3	286	2.4	38.0	91	0.0	0.0	0	0.0	0.0	0	2.1	21.8	46
Pyrus malus [d]	0.0	0.0	0	0.0	0.0	0	9.8	40.0	392	3.8	7.0	27	3.4	11.8	40
Prunus spp.[c]	0.0	0.0	0	0.0	0.0	0	13.2	18.0	238	8.3	8.0	66	5.4	6.5	35
Sorbus americana	0.8	37.2	30	4.7	36.5	172	0.0	0.0	0	0.0	0.0	0	1.4	18.4	26
Prunus virginiana [c]	3.2	33.4	107	1.2	6.6	8	0.0	0.0	0	0.0	0.0	0	1.1	10.0	11
Pyrus coronaria [d]	0.0	0.0	0	0.0	0.0	0	0.5	1.0	1	0.0	0.0	0	0.1	0.3	<1
Shrub fruit															
Rubus spp. (raspberry)	8.2	1.1	9	2.8	41.6	117	18.6	11.0	205	21.8	12.0	262	12.9	16.4	212
Aralia nudicaulis	20.0	14.2	284	5.9	13.5	80	15.7	11.0	173	18.8	5.0	94	15.1	10.9	165
Vaccinium spp. (blueberry)	8.0	30.9	247	4.7	24.2	114	12.8	8.0	102	3.0	2.0	6	7.1	16.3	116
Cornus stolonifera	0.0	0.0	0	0.0	0.0	0	13.2	31.0	409	6.8	24.0	163	5.0	13.8	69
Nemopanthus mucronatus	7.4	35.9	266	0.8	48.5	39	2.5	5.0	13	0.0	0.0	0	2.7	22.4	60
Ribes spp.	3.2	12.2	39	2.0	45.7	91	5.4	1.0	5	3.0	1.0	3	3.4	15.0	51
Amelanchier spp.	0.3	5.0	2	0.0	0.0	0	6.4	1.0	6	17.3	18.0	311	6.0	6.0	36
Vaccinium spp. (cranberry)	1.9	10.4	20	3.1	12.3	38	1.0	1.0	1	5.3	1.0	5	2.8	6.2	17
Rubus allegheniensis	2.1	57.1	120	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.5	14.3	7
Viburnum spp.	0.0	0.0	0	1.2	25.3	30	1.5	1.0	2	0.8	1.0	1	0.9	6.8	6
Rubus spp.	0.0	0.0	0	0.0	0.0	0	6.9	11.0	76	0.0	0.0	0	1.7	2.8	5
Sambucus pubens	0.3	5.0	2	0.0	0.0	0	2.0	2.0	4	4.5	2.0	9	1.7	2.3	4
Vitis spp.	0.0	0.0	0	0.4	25.0	10	0.0	0.0	0	0.0	0.0	0	0.1	6.3	1
Cornus alternifolia	0.0	0.0	0	0.0	0.0	0	1.0	2.0	2	0.8	1.0	1	0.5	0.8	<1
Unidentified	3.5	13.3	47	2.4	21.6	52	4.9	3.0	15	17.3	7.0	121	7.0	11.2	78
Other tree and shrub parts															
Populus tremuloides (leaves)	2.1	18.0	38	7.1	37.0	263	4.9	1.0	4.9	5.3	42	223	4.9	24.5	120
Populus tremuloides (catkins)	7.2	30.6	220	2.0	39.0	78	0.5	1.0	1	4.5	30.0	135	3.6	25.2	91
Thuja occidentalis (leaves)	1.8	4.4	8	0.0	0.0	0	0.5	1.0	1	6.1	52.0	317	2.1	14.4	30
Tsuga canadensis (needles)	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	2.3	51.0	117	0.6	12.8	8
Rhamnus alnifolia	0.0	0.0	0	0.0	0.0	0	3.9	5.0	20	1.5	12.0	18	1.4	4.3	6
Ulmus americana (seeds)	0.0	0.0	0	3.1	21.0	65	0.0	0.0	0	0.0	0.0	0	0.8	5.3	4
Tsuga canadensis (cones)	0.3	75.0	23	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	18.8	2
Corylus spp.	0.0	0.0	0	0.0	0.0	0	1.5	1.0	2	3.8	1.0	4	1.3	0.5	1
Pinaceae (cone scales)	0.0	0.0	0	0.0	0.0	0	2.5	1.0	3	3.0	1.0	3	1.4	0.5	1

Table 1, continued.

Food Item[a]	1976 F	1976 C	1976 FI	1977 F	1977 C	1977 FI	1978 F	1978 C	1978 FI	1979 F	1979 C	1979 FI	Average F	Average C	Average FI
Corylus spp.	0.0	0.0	0	0.0	0.0	0	1.5	1.0	2	3.8	1.0	4	1.3	0.5	1
Pinaceae (cone scales)	0.0	0.0	0	0.0	0.0	0	2.5	1.0	3	3.0	1.0	3	1.4	0.5	1
Thuja occidentalis (cones)	0.0	0.0	0	0.0	0.0	0	0.5	1.0	1	0.0	0.0	0	0.1	0.3	<1
Picea glauca (needles)	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.8	1.0	1	0.2	0.3	<1
Abies balsamea (needles)	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	3.8	1.0	4	1.0	0.3	<1
Unidentified buds	0.5	3.0	2	0.0	0.0	0	19.6	1.0	20	21.8	3.0	65	7.3	1.9	14
Unidentified plants	32.7	17.1	559	41.4	14.6	604	85.8	34.0	2917	75.9	25.0	1898	59.0	22.7	1339
Insects															
Formicidae	36.2	11.1	402	37.5	14.0	525	52.0	3.0	156	57.1	9.0	514	45.7	9.3	425
Vespidae	7.2	7.8	56	1.2	11.0	13	2.5	1.0	3	3.8	9.0	34	3.7	7.2	27
Orthoptera (grasshopper)	0.5	30.0	15	0.3	5.0	2	0.0	0.0	0	0.0	0.0	0	0.2	8.8	2
Bombidae	0.0	0.0	0	0.0	0.0	0	1.0	1.0	1	4.5	1.0	5	1.4	0.5	1
Coleoptera	0.3	1.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	0.3	<1
Unindentified	0.9	3.9	4	0.4	10.0	4	1.0	1.0	1	1.5	1.0	2	1.0	4.0	4
Mammals															
Lepus americanus	0.3	45.0	14	0.4	20.0	8	7.8	1.0	8	4.5	1.0	5	3.3	16.8	55
Ursus americanus	0.0	0.0	0	5.0	59.5	298	3.4	1.0	3	1.5	1.0	2	2.5	15.4	39
Procyon lotor	0.5	38.3	19	0.4	35.0	14	0.0	0.0	0	0.0	0.0	0	0.2	18.3	4
Other animal	0.0	0.0	0	0.0	0.0	0	12.3	1.0	12	18.8	1.0	19	7.8	0.5	4
Castor canadensis	0.3	10.0	3	1.2	9.1	11	0.0	0.0	0	0.0	0.0	0	0.4	4.8	2
Marmota monax	0.5	8.0	4	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	2.0	<1
Ondatra zibethicus	0.3	5.0	2	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	1.3	<1
Odocoileus virginianus	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	6.0	1.0	6	1.5	0.3	<1
Unidentified	3.7	41.0	152	2.0	28.2	56	3.4	1.0	3	6.8	1.0	7	4.0	17.8	71
Total plants	98.9	69.1	6834	98.4	67.5	6642	100.0	53.0	5300	100.0	57.0	5700	99.3	61.7	6127
Total insects	43.1	10.7	461	39.0	13.9	542	54.9	3.0	165	58.6	9.0	527	48.9	9.2	450
Total mammals	6.1	34.0	207	5.2	33.0	172	0.0	0.0	0	0.0	0.0	0	2.8	16.8	47
Birds	1.9	3.9	7	0.0	0.0	0	0.0	0.0	0	1.5	1.0	2	0.9	1.2	1
Fish	0.3	2.0	1	0.0	0.0	0	1.0	1.0	1	0.0	0.0	0	0.3	0.8	<1
Debris and fine materials	95.5	17.9	1709	97.6	18.4	1796	100.0	36.0	3600	100.0	11.0	1100	97.6	20.4	1991

[a] F = % frequency, C = % volume composition, FI = forage importance value (FI = F X C).

[b] Domestic oats was present all 4 years, but included with grasses in 1976 and 1977.

[c] In 1976 and 1977, 2 species of *Prunus* were identified; in 1978 and 1979, these were combined as *Prunus* spp.

[d] In 1978 and 1979, 2 species of *Pyrus* were identified; in 1976 and 1977, these were combined as *Pyrus* spp.

Table 2. Monthly black bear food habits[a] in northern Wisconsin as determined from 967 scats collected during 4 summers, 1976–1979.

	May			June			July			August		
Food Item	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*
Monocots												
Gramineae and Cyperaceae	88.5	37.0	3275	62.0	10.0	620	37.0	6.0	222	30.0	9.0	270
Symplocarpus foetidus	5.5	24.0	132	3.2	62.0	198	0.0	0.0	0	0.0	0.0	0
Arisaema triphyllum	3.7	12.0	44	14.0	40.0	560	14.0	30.0	420	4.2	37.0	155
Juncus spp.	0.4	99.0	40	0.0	0.0	0	4.4	1.0	4	0.0	0.0	0
Acornus calamus	1.4	2.8	4	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Equisetum spp.	1.0	3.0	3	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Alisma spp.	0.0	0.0	0	2.5	21.0	53	4.4	1.0	4	0.0	0.0	0
Zea mays	0.0	0.0	0	3.0	1.0	3	0.8	32.0	26	0.0	0.0	0
Avena sativa[b]	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.4	3.0	1
Unidentified monocots	4.6	8.4	39	1.4	25.7	36	7.0	34.5	242	3.0	14.0	42
Dicots												
Osmorhiza claytonii	32.2	23.3	750	23.0	20.0	460	10.0	15.3	153	2.5	23.3	58
Taraxacum officinale	3.6	30.0	108	8.0	22.0	176	16.0	21.0	336	4.6	12.0	55
Heracleum maximum	5.0	20.0	100	0.3	1.0	<1	1.3	22.0	29	0.8	10.5	8
Trifolium spp.	8.7	9.5	83	9.0	5.0	45	7.7	2.4	19	7.5	17.0	128
Calla palustris	3.2	1.0	3	14.3	2.0	29	7.7	3.0	23	5.4	1.0	5
Polygonum cilinode	0.4	5.0	2	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Fragaria spp.	0.0	0.0	0	1.4	2.0	3	1.7	25.0	43	0.0	0.0	0
Hieracium spp.	0.4	1.0	<1	0.0	0.0	0	1.7	15.0	26	0.4	5.0	2
Urtica spp.	0.0	0.0	0	0.4	30.0	12	0.0	0.0	0	0.0	0.0	0
Viola spp.	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.4	25.0	10
Sonchus spp.	0.0	0.0	0	3.1	1.0	3	0.0	0.0	0	0.0	0.0	0
Potentilla spp.	0.0	0.0	0	0.7	3.0	2	0.0	0.0	0	0.0	0.0	0
Lactuca sp.	0.0	0.0	0	0.0	0.0	0	1.3	1.0	1	0.4	1.0	<1
Cornus canadensis	0.0	0.0	0	0.0	0.0	0	0.4	1.0	<1	0.4	1.0	<1
Unidentified Umbelliferae	0.9	7.5	7	2.1	5.0	11	0.8	8.0	6	0.0	0.0	0
Unidentifed Compositae	0.0	0.0	0	0.7	1.0	1	0.8	1.0	1	2.5	1.0	3
Lycopodiales	1.4	1.0	1	5.0	1.0	5	4.7	1.0	5	2.1	1.0	2
Unidentified ferns	0.0	0.0	0	0.7	1.0	1	1.7	1.0	2	0.4	1.0	<1
Unidentified dicots	3.2	15.6	50	11.3	14.0	158	6.2	15.0	93	2.5	13.0	33

Table 2, continued.

Food Item	May F	May C	May FI	June F	June C	June FI	July F	July C	July FI	August F	August C	August FI
Tree fruit												
Prunus serotina [c]	0.0	0.0	0	0.7	1.0	1	5.1	17.0	87	45.4	17.5	795
Pyrus malus [d]	0.4	1.0	<1	0.3	1.0	<1	0.8	1.0	1	8.7	40.0	348
Prunus spp.[c]	0.0	0.0	0	0.0	0.0	0	2.1	1.0	2	13.7	12.0	164
Prunus virginiana [c]	0.0	0.0	0	0.0	0.0	0	4.0	15.0	60	2.5	47.5	119
Pyrus spp.[d]	1.4	23.0	32	0.0	0.0	0	5.2	62.0	322	0.8	40.0	32
Sorbus americana	0.0	0.0	0	0.7	1.0	1	4.7	19.0	89	0.8	40.0	32
Pyrus coronaria [d]	0.004	1.0	<1	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Shrub fruit												
Rubus spp. (raspberry)	0.0	0.0	0	2.2	1.0	2	22.4	26.5	594	19.6	46.0	902
Nemopanthus mucronatus	0.0	0.0	0	0.3	1.0	<1	2.1	17.0	36	12.0	36.0	432
Cornus stolonifera	0.0	0.0	0	0.0	0.0	0	3.4	2.0	7	11.7	32.0	374
Rubus spp.	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	16.0	11.0	176
Aralia nudicaulis	0.0	0.0	0	4.0	4.0	16	40.0	13.0	520	13.3	11.0	146
Vaccinium spp. (blueberry)	0.0	0.0	0	0.7	1.0	1	23.3	23.4	545	6.6	11.0	73
Amelanchier laevis	0.0	0.0	0	1.0	2.0	2	7.7	18.0	139	6.6	7.0	46
Rubus allegheniensis	0.0	0.0	0	0.3	4.0	1	0.8	14.3	11	2.1	20.0	42
Ribes spp.	0.0	0.0	0	2.5	27.0	68	7.7	8.0	62	3.0	9.4	28
Vitis sp.	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.4	25.0	10
Viburnum sp.	0.0	0.0	0	0.0	0.0	0	1.3	20.0	26	1.6	6.0	10
Cornus alternifolia	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	1.2	2.0	2
Vaccinium spp. (cranberry)	3.2	14.0	45	4.0	7.0	28	4.3	1.0	4	0.8	1.0	1
Sambucus pubens	0.0	0.0	0	0.7	3.0	2	3.4	1.2	4	0.4	1.0	<1
Unidentified	0.4	1.0	<1	4.0	1.4	6	7.3	15.0	110	4.6	6.0	28
Other tree and shrub parts												
Populus tremuloides (catkins)	16.1	28.0	451	2.2	39.0	86	0.0	0.0	0	0.0	0.0	0
Populus tremuloides (leaves)	12.4	30.0	372	5.4	22.0	119	0.0	0.0	0	0.0	0.0	0
Ulmus americana (seeds)	3.7	21.0	78	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Tsuga canadensis (needles)	1.4	51.0	71	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Rhamnus alnifolia	0.0	0.0	0	0.0	0.0	0	2.2	7.0	15	1.9	2.0	4
Thuja occidentalis (leaves)	6.5	3.9	25	1.8	1.0	2	0.0	0.0	0	0.0	0.0	0
Abies balsamea (needles)	1.4	1.0	1	0.7	1.0	1	0.0	0.0	0	0.0	0.0	0
Picea glauca (needles)	0.4	1.0	<1	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0

Table 2, continued.

	May			June			July			August		
Food Item	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*	*F*	*C*	*FI*
Thuja occidentalis (cones)	0.0	0.0	0	0.3	1.0	<1	0.0	0.0	0	0.0	0.0	0
Tsuga canadensis (cones)	0.0	0.0	0	0.3	1.0	<1	0.0	0.0	0	0.0	0.0	0
Corylus spp.	0.0	0.0	0	0.4	1.0	<1	0.9	1.0	1	2.0	1.0	2
Pinaceae (cone scale)	1.4	1.0	1	1.8	1.0	2	0.4	1.0	<1	0.0	0.0	0
Unidentified buds	9.7	1.0	10	12.6	2.0	25	8.6	1.0	9	1.7	1.0	2
Insects												
Formicidae	30.0	6.0	180	59.3	11.0	652	69.0	9.4	649	22.0	67.0	1474
Vespidae	0.9	1.0	1	0.3	1.0	<1	2.1	2.0	4	13.3	9.0	120
Orthoptera	0.0	0.0	0	0.0	0.0	0	0.8	30.0	24	0.4	5.0	2
Bombidae	0.0	0.0	0	0.0	0.0	0	1.7	1.0	2	0.0	1.0	1
Coleoptera	0.5	1.0	1	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Unidentified	1.4	7.0	10	0.7	5.5	4	8.6	1.0	9	1.7	1.0	2
Mammals												
Ursus americanus	1.3	27.3	36	0.7	1.0	1	2.1	4.0	8	1.2	1.0	1
Procyon lotor	0.0	0.0	0	0.3	35.0	11	4.4	5.0	22	0.4	71.0	28
Lepus americanus	3.2	4.0	13	4.0	6.0	24	1.7	1.0	2	0.8	1.0	1
Castor canadensis	1.4	12.0	17	0.0	0.0	0	0.0	0.0	0	0.4	1.0	<1
Ondatra zibethicus	0.4	30.0	12	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Marmota monax	0.0	0.0	0	0.0	0.0	0	0.9	8.0	7	0.0	0.0	0
Odocoileus virginianus	1.4	1.0	1	0.3	1.0	<1	2.0	1.0	2	0.0	0.0	0
Unidentified	5.5	19.0	105	4.3	8.5	37	2.1	5.0	11	2.5	8.2	21
Total plants	98.6	67.7	6675	98.9	53.1	5252	100.0	60.6	6060	99.2	75.1	7450
Total insects	18.9	5.2	98	60.1	10.6	637	70.7	16.0	1131	32.9	8.0	263
Total mammals	15.2	22.5	342	9.4	10.7	101	9.1	20.1	183	4.2	13.9	58
Birds	0.0	0.0	0	1.0	4.0	4	2.6	3.0	8	0.0	0.0	0
Fish	1.4	1.3	2	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
Debris and fine material	100.0	21.3	2130	100.0	22.0	2200	100.0	20.9	2090	100.0	16.7	1670

[a] F = % frequency, C = % volume composition, FI = forage importance value (FI = F X C).

[b] Domestic oats was present all 4 years, but included with grasses in 1976 and 1977.

[c] In 1976 and 1977, 2 species of *Prunus* were identified; in 1978 and 1979, these were combined as *Prunus* spp.

[d] In 1978 and 1979, 2 species of *Pyrus* were identified; in 1976 and 1977, these were combined as *Pyrus* spp.

Table 3. Percent of stands in each forest community in northern Wisconsin (Curtis 1959 and Plant Ecology Laboratory, University of Wisconsin-Madison) in which black bear foods were observed in summer 1978 and 1979.

Food	*Dry Mesic*	*Mesic*	*Wet Mesic*	*Wet*	*Boreal*	*Aspen*	*Alder*	*Sedge Meadow*	*Bog*	*Bracken Grassland*	*Dry Weed*	*Northern Pasture*	*Mesic Weed*
Gramineae and Cyperaceae	91.4	95.1	97.1	100.0	89.7	95.0	91.7	100.0	86.7	100.0	71.4	100.0	100.0
Cornus stolonifera	—	—	41.2	21.6	17.9	35.0	50.0	18.5	—	—	—	—	—
Osmorhiza claytonii	44.4	72.5	32.4	—	39.3	15.0	—	—	—	—	—	—	—
Rubus spp. (raspberry)	47.2	20.0	58.8	27.5	64.3	50.0	8.3	—	—	—	—	—	—
Prunus spp.	54.3	17.5	14.3	6.0	46.4	75.0	8.3	—	6.7	25.6	—	—	—
Arailia nudicaulis	94.4	90.0	94.1	41.2	96.4	80.0	—	—	13.3	—	—	—	—
Amelanchier spp.	50.0	7.5	8.8	—	50.0	60.0	8.3	—	—	18.5	—	—	—
Populus tremuloides	71.4	10.0	31.4	16.0	64.3	100.0	—	—	20.0	40.7	—	—	—
Vaccinium spp. (blueberry)	63.9	12.5	38.2	94.1	50.0	75.0	—	—	66.7	74.1	—	—	—
Trifolium spp.	—	—	—	—	28.6	10.0	—	—	—	44.4	95.2	85.7	100.0
Calla palustris	—	—	8.8	21.6	10.7	5.0	—	7.4	53.3	—	—	—	—
Rubus allegheniensis	58.3	17.5	17.6	—	25.0	70.0	—	—	—	—	—	—	—
Tsuga canadensis	40.0	80.0	48.6	2.0	25.0	5.0	—	—	—	—	—	—	—
Fragaria spp.	66.7	30.0	44.1	—	64.3	95.0	—	11.1	—	85.2	52.4	42.9	30.0
Rhamus alnifolia	—	—	17.6	23.5	7.1	—	—	—	—	—	—	—	—
Lycopodium spp.	82.9	80.0	57.1	58.0	96.4	80.0	—	—	6.7	7.4	—	—	—
Nemopanthus mucronatus	2.8	2.5	26.5	56.9	7.1	15.0	8.3	—	33.3	—	—	—	—
Sambucus pubens	25.0	55.0	8.8	—	32.1	20.0	—	—	—	—	—	—	—
Ribes spp.	38.9	40.0	76.5	35.3	75.0	55.0	50.0	22.1	—	—	—	—	—
Vaccinium spp. (cranberry)	—	2.5	20.0	74.4	—	—	—	—	100.0	3.7	—	—	—
Corylus spp.	83.3	57.5	44.1	—	71.4	90.0	8.3	—	—	40.7	—	14.3	—
Thuja occidentalis	20.0	25.0	91.4	42.0	64.3	15.0	8.3	—	—	—	—	—	—
Abies balsamea	51.4	60.0	80.0	38.0	100.0	95.0	—	—	6.7	7.4	—	14.3	—
Cornus alternifolia	34.3	30.0	20.0	—	10.7	30.0	—	—	—	—	—	—	—
Lactuca spp.	8.6	7.5	28.6	8.0	14.3	40.0	—	—	—	37.0	28.6	—	20.0
Viburnum spp.	72.2	25.0	32.4	—	28.6	65.0	16.7	3.7	—	—	—	—	—
Cornus canadensis	54.3	40.0	71.4	76.0	96.4	90.0	—	3.7	53.3	11.1	—	—	—
Picea glauca	17.1	7.5	20.0	—	89.3	35.0	—	—	—	—	—	—	—
Average[a]	49.2	32.9	39.7	37.8	49.0	52.2	18.5	11.1	36.0	33.0	58.7	39.3	50.0
Number food items[a]	22	24	26	17	26	25	9	6	10	12	3	4	3

[a] Excludes Gramineae and Cyperaceae.

Table 4. Forage importance values[a] indicate the relative importance of each forest community in northern Wisconsin for black bear foods comprising ≥ 2% frequency of occurrence in scats collected during summer 1978 and 1979.

		Community Importance Values												
Food Item	*Forage Importance Value*	*Dry Mesic*	*Mesic*	*Wet Mesic*	*Wet*	*Boreal*	*Aspen*	*Alder*	*Sedge Meadow*	*Bog*	*Bracken Grassland*	*Dry Weed*	*Northern Pasture*	*Mesic Weed*
Gramineae and Cyperaceae	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4	1158.4
Cornus stolonifera	311.4	—	—	311.4	311.4	311.4	311.4	311.4	311.4	—	—	—	—	—
Osmorhiza claytonii	228.6	228.6	228.6	228.6	—	228.6	228.6	—	—	—	—	—	—	—
Rubus spp. (raspberry)	220.9	220.9	220.9	220.9	220.9	220.9	220.9	220.9	—	—	—	—	—	—
Prunus spp.	170.6	170.6	170.6	170.6	170.6	170.6	170.6	170.6	—	170.6	170.6	—	—	—
Arailia nudicaulis	138.6	138.6	138.6	138.6	138.6	138.6	138.6	—	—	138.6	—	—	—	—
Amelanchier spp.	129.5	129.5	129.5	129.5	129.5	129.5	129.5	129.5	—	129.5	—	—	—	—
Populus tremuloides	88.5	88.5	88.5	88.5	88.5	88.5	88.5	—	—	88.5	88.5	—	—	—
Vaccinium spp. (blueberry)	66.8	66.8	66.8	66.8	66.8	66.8	66.8	—	—	66.8	66.8	—	—	—
Trifolium spp.	60.3	—	—	—	—	60.3	60.3	—	—	—	60.3	60.3	60.3	60.3
Calla palustris	52.2	—	—	52.2	52.2	52.2	52.2	—	52.2	52.2	—	—	—	—
Rubus allegheniensis	47.9	47.9	47.9	47.9	—	47.9	47.9	—	—	—	—	—	—	—
Lycopodium spp.	9.5	9.5	9.5	9.5	9.5	9.5	9.5	—	—	9.5	9.5	—	—	—
Ribes spp.	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	4.5	—	—	—	—	—
	Sum	2263.8	2263.8	2627.4	2350.9	2687.7	2687.7	1995.3	1526.5	1814.1	1554.1	1218.7	1218.7	1218.7

[a] Forage importance value = % frequency multiplied by % volume composition of food items in scats.

Table 5. Communities in northern Wisconsin where a positive relationship ($P < 0.05$) existed between availability and use of plant foods comprising ≥ 2% frequency of occurrence in black bear scats, summer 1978 and 1979.

Graminae	*Cornus stolonifera*	*Osmorhiza claytonii*	*Rubus spp. (raspberry)*	*Prunus* spp.	*Aralia nudicaulis*	*Amelanchier* spp.	*Populus tremuloides*	*Vaccinum* spp.	*Trifolium* spp.	*Calla palustris*	*Rubus allegheniensis*	*Lycopodium* spp.	*Ribes* spp.
Dry mesic	Wet mesic	Dry mesic	Dry mesic	Dry mesic	Dry mesic	Dry mesic	Dry mesic	Dry mesic	Boreal	Bog	Dry mesic	Dry mesic	Dry mesic
Mesic	Wet	Mesic	Wet mesic	Boreal	Mesic	Boreal	Wet mesic	Wet mesic	Bracken grassland		Mesic	Mesic	Mesic
Wet mesic	Aspen	Wet mesic	Boreal	Aspen	Wet mesic	Aspen	Wet	Wet	Dry weed		Wet mesic	Wet mesic	Wet mesic
Wet	Alder	Boreal	Aspen	Bracken grassland	Boreal		Boreal	Boreal	Pasture		Boreal	Wet	Wet
Aspen					Aspen		Aspen	Aspen	Mesic weed		Aspen	Boreal	Boreal
Sedge							Bog	Bog				Aspen	Aspen
Bracken grassland							Bracken grassland	Bracken grassland				Bog	Alder
												Bracken grassland	Sedge

Appendix A. Forest community terminology used in this study for northern Wisconsin.

Curtis (1959) Terminology	*Dominant Species*	*WDNR[a] Terminology*
Dry mesic forest	*Pinus strobus* *Acer rubrum* *Quercus borealis*	White pine/oak
Mesic forest	*Acer saccharum* *Fagus grandifolia* *Tsuga canadensis* *Betula lutea*	Northern hardwoods
Wet mesic forest	*Thuja occidentalis* *Abies balsamea* *Fraxinus nigra*	Swamp conifer
Wet forest	*Picea mariana* *Larix laricina*	Black spruce
Boreal forest	*Picea glauca* *Abies balsamea*	Fir – spruce
Aspen forest	*Populus tremuloides* *Populus grandidentata*	Aspen
Alder	*Alnus rugosa*	Alder
Sedge meadow	*Carex* spp. *Calamagrostis canadensis* *Aster simplex*	Marsh/muskeg
Bog	*Andromeda glaucophylla* *Chamaedaphne calyculata* *Kalmia polifolia*	Muskeg – bog
Bracken grassland	*Pteridium aquilinum* *Bromus kalmii* *Danthonia spicata*	Herbaceous vegetation
Dry weed	*Conyza canadensis* *Oenothera biennis* *Agropyron repens*	Noncommercial herbaceous vegatation
Northern pasture	*Poa pratensis* *Taraxacum officinale* *Trifolium repens*	Heavily grazed
Mesic weed	*Phleum pratense* *Trifolium pratense* *Plantago major*	Grass

[a] Wisconsin Department of Natural Resources.

Acknowledgments

The Wisconsin Department of Natural Resources and the Wisconsin Trappers Association provided funding. R. W. Freckman, University of Wisconsin-Stevens Point, helped identify food items. G. Cottam, University of Wisconsin-Madison, helped identify forest communities. W. A. Creed and K. R. McCaffery, WDNR, provided advice. M. J. Lovallo and T. Ryan, graduate students at University of Wisconsin-Stevens Point, combined tables of data from the 2 studies involved. B. Howe and referees reviewed the manuscript.

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Effects of Trapping on Colony Density, Structure, and Reproduction of a Beaver Population Unexploited for 19 Years

Abstract *A trapline system for beaver* (Castor canadensis) *occurred on Sandhill Wildlife Area during 1981, 1982, and 1983 to harvest populations unexploited for at least 19 years. We censused 48 beaver colonies (1.30/km²) in 1981, 38 (1.03/km²) in 1982, and 18 (0.49/km²) in 1983. Ground counts indicated that 22% of the colonies were missed in aerial counts. A winter harvest of 3.9 beaver/colony in 1981 resulted in a 21% decline in active colonies in 1982; subsequent harvest of 3.2 beaver/colony in 1982 caused a 53% decline in 1983. In 1981 and 1982, 89% of the beaver harvest was achieved during the first 16 days of the season and involved 64% of the trapping effort. Mean age decreased after harvest began, from 2.9 years in 1981 to 2.2 years in 1982. Average colony size was 4.2 in 1981 and 3.1 in 1982. Single and pair colonies occurred as 9% of all colonies trapped in 1981 and 22% in 1982. Family colonies averaged 5.6 beaver in 1981 and 5.2 in 1982. Lack of exploitation might have delayed sexual maturation and dispersal and increased the number of nonbreeding adults. In 1981, 35% of the females (N = 51) had placental scars, fewer than the 80% (N = 25) found in 1982. Breeding females averaged 3.1 placental scars in 1981 (N = 56) and 3.6 in 1982 (N = 72). Yearlings reproduced after 1 year of harvest when about 79% of the available colony sites were occupied. The estimated 34% mortality for the unharvested population seemed high, perhaps due to dispersal and tularemia.*

Some effects of trapping have been reported for beaver *(Castor canadensis)* colonies experiencing short (4- or 5-year) season closures (Parsons 1975, Parsons and Brown 1978, Boyce 1981*a*, Payne 1982). No combined effects of trapping on colony density, structure, and reproduction have been studied on beaver populations with long-term season closures.

Nordstrom (1972) and Boyce (1981*a*) compared the population dynamics and density between trapped and untrapped beaver populations. Parsons (1975) and Parsons and Brown (1978) investigated effects of a 4-year closure on beaver trapping in New York, as did Payne (1982) after a 5-year closure in Newfoundland. This study was undertaken to determine the influence of trapping on colony density, structure, and reproduction of a beaver population unexploited for at least 19 years.

Study Area

Sandhill Wildlife Area, in central Wisconsin, has a 2.5-m high deer-proof fence enclosing 37 km^2. The area is managed by the Wisconsin Department of Natural Resources as an experimental and demonstration area with emphasis on wildlife habitat and managed hunting. No furbearer trapping occurred on the area since the state bought the land in 1962; historical furbearer harvest records were unavailable. Habitat composition and forest management on Sandhill were described by Kubisiak et al. (1980). The property has 419 ha of surface water, including 16 impoundments, 39 km of drainage ditch and a 0.8-km segment of stream, which enters and leaves Sandhill. Five drainage ditches, remnants of farming attempts of the early 1900s (Grange 1949), drain out of Sandhill. Drainage ditches and impoundments are major sources of permanent water. Not all are suitable beaver habitat because annual freezeouts occur commonly in many shallow impoundments, which are 0.6-0.9 m deep; drainage ditches average 1.2 m deep. Low marsh fertility was reported by Baldassarre and Nauman (1981), who described vegetation cover types of emergent and submergent species in 2 major impoundments on Sandhill.

Methods

A trapline system for beaver (Payne 1980) occurred on Sandhill during December 1981, 1982, and 1983. Each year, 8 trappers were assigned exclusive traplines and required to report numbers of trapnights and beaver caught in each colony daily. Carcasses were tagged through the tail with self-locking, numbered tags, and returned skinned the next day.

Tag numbers were attached to or placed with the jawbones and reproductive tracts. Reproductive tracts were preserved in 10% formalin and examined (Hodgdon 1949, Leege and Williams 1967). Ages of beaver were determined by basal closure and cementum annuli of teeth (van Nostrand and Stephenson 1964, Klevezal' and Kleinenberg 1967, Larson and van Nostrand 1968).

In fall 1981 before the first trapping season, we conducted an aerial census with a Cessna 337 Skymaster to determine the number of active beaver colonies on Sandhill and an adjacent harvested area of 31 km^2 (Hay 1958, Payne 1981). We conducted an aerial census again in fall 1982 after the first trapping season. In fall 1983, after the second trapping season, the census consisted of complete ground coverage alone, without aerial census. Ground checks also were conducted on Sandhill in 1981 and 1982 to assure complete coverage and to verify colony sites on Sandhill, but ground checks were not conducted on the adjacent area. We used the correction factor between aerial and ground censuses on Sandhill to estimate overall colony density on the adjacent harvested area. Beaver population density was expressed in colonies/km^2 due to the relatively flat terrain and numerous wetlands and impoundments (Hill 1982).

Selection of beaver colonies to be completely trapped each year was based on nuisance activities associated with the colony site. Wisconsin prohibits beaver trapping within 4.6 m of the lodge and/or dam. This restriction was lifted on these selected colonies to facilitate removal of all beaver from the colony to determine colony size, age, and sex structure. Complete removal was determined by placing a piece of quaking aspen *(Populus tremuloides)* through the ice near the lodge entrance; evidence of gnawing on the branch indicated the presence of additional beaver (Payne 1982). Trappers provided additional information regarding presence of beaver activity.

We used chi-square analyses to test for difference between data sets. P values ≤ 0.05 were considered significant.

Results

Colony Density and Harvest

We observed 48 colonies (1.30/km^2) in 1981, 38 (1.03/km^2) in 1982, and 18 (0.49/km^2) in 1983 on Sandhill. In 1981 and 1982 our aerial census missed 22% of the colonies on Sandhill counted on the ground. Thus, the 13 colonies aerially censused on the adjacent harvested area were adjusted 22% higher, i.e., to 15 colonies (0.48/km^2). After the second trapping season on Sandhill, the colony density was similar to that on the adjacent harvested area.

The beaver harvest was 182 in 1981, 116 in 1982, and 4 in 1983. In 1981 and 1982, 89% of the beaver harvest was achieved during the first 16 days of the season and involved 64% of the trapping effort, although the season was 31 days long and each of the 8 trappers had an exclusive trapline. All beaver were removed from 11 of 23 colonies scheduled to be completely trapped in 1981, and from 12 of 25 colonies in 1982. During 1983, only 2 colony sites were recolonized after all beaver were removed from them in 1981 and 1982. In 1981, 137 beaver were removed from 35 incompletely trapped colonies ($\bar{x}$ = 3.9/colony), and 81 were removed from 25 incompletely trapped colonies in 1982 ($\bar{x}$= 3.2/colony).

Colony Size and Structure

In 1981 and 1982 the sex ratio of 75 beaver (97 males:100 females) from 23 completely trapped colonies, and 223 beaver (85 males:100 females) from incompletely trapped colonies, did not differ. Mean age decreased after harvest began, from 2.9 years in 1981 to 2.2 years in 1982 (Table 1).

Average colony size was 4.2 from 11 colonies trapped out in 1981 and 2.9 from 12 colonies trapped out in 1982, averaging 3.5 both years (Table 2). But in 1982, more beaver/colony were trapped from the 25 incompletely trapped colonies (3.2) than from the 12 completely trapped colonies (2.9). (One colony was not trapped in 1982.) Thus, the average colony size on Sandhill in 1982 was at least 3.1 ([81beaver trapped from incompletely trapped colonies + 35 beaver trapped from completely trapped colonies] ÷ 37 total colonies trapped). More single (1 beaver) and pair (2 beaver) colonies existed in 1982 than in 1981 (Table 3). Single or pair colonies occurred as 9% of all colonies trapped in 1981 (N = 46) and 22% in 1982 (N = 37). The average size of completely trapped family colonies was 5.6 beaver from 7 colonies in 1981 and 5.3 from 4 colonies in 1982, averaging 5.5 both years.

Of 35 family colonies incompletely trapped, at least 26% had 2.5-year-olds in 1981 (N = 35) and 0% in 1982 (N = 25). In 1981, 2 family colonies completely trapped had ≥ 4 beaver ≥ 2.5 years old. Each of these colonies had 2 or 3 beaver 2.5 years old. Of the 11 family colonies completely trapped, 3 (27%) had 3 beaver ≥ 2.5 years

Table 1. Age structure of beaver trapped after 19 years of no harvest (1981) and 1 year after harvest (1982) on Sandhill Wildlife Area.

Age	*1981*		*1982*	
(years)	*N*	*%*	*N*	*%*
0.5	62	43	67	58
1.5	42	23	11	9
2.5	23	13	8	7
3.5	12	7	6	5
≥ 4.5	43	24	24	21
Total	**182**	**100**	**116**	**100**
≥ 1.5	120	66	49	42
≥ 2.5[a]	78	43	38	33
≥ 3.5	55	30	30	26

[a] Beaver normally disperse at age 2.5 years.

Table 2. Average colony size from beaver colonies completely trapped on Sandhill Wildlife Area, 1981–82.

Colony Type	*1981*[a]	*1982*	*Both*
Family (≥ 3 beaver)			
Beaver	39	21	60
Colonies	7	4	11
Beaver/colony	5.6	5.3	5.5
Single and pair			
Beaver	7	14	21
Colonies	4	8	12
Beaver/colony	1.8	1.8	1.8
Combined			
Beaver	46	35	81
Colonies	11	12	23
Beaver/colony	4.2	2.9	3.5

[a] No beaver were harvested during the previous 19 years; in 1981, in addition to the 46 beaver trapped from these 11 colonies, another 136 beaver were trapped from 37 other colonies.

old. Yearlings occurred in 8 of the 9 pair colonies completely trapped both years.

In 1981, one colony had 14 beaver removed. Six age classes were present: three kits, four yearlings, three 2.5-year-olds, two 3.5-year-olds, one 8.5-year-old, and one 10.5-year old. Reproductive tracts from two females indicated previous parturition.

Reproduction

All 11 completely trapped family colonies contained kits. In 1981, all 7 family colonies completely trapped had 15 kits (2.14 kits/colony); in 1982, all 4 family colonies had 12 kits (3.00 kits/colony). Of the beaver trapped from all colonies, kits comprised 34% in 1981 and 58% in 1982.

In 1981, 35% of the females ($N = 51$) had placental scars, fewer than the 80% ($N = 25$) found in 1982. Number of breeding female yearlings was 0 in 1981 and 2 in 1982. Excluding yearlings, 58% ($N = 31$) had placental scars in 1981, fewer ($P < 0.05$) than the 86% ($N = 25$) in 1982. Breeding females averaged 3.1 placental scars in 1981 ($N = 56$) and 3.6 in 1982 ($N = 72$). A difference existed between the 2 means when the breeding yearlings were excluded.

Logarithmic regression of female age (kits and other barren females omitted) and mean number of placental scars/female resulted in a correlation coefficient of 0.563 ($N = 51$) in 1981 and 0.579 ($N = 25$) in 1982. No females younger than 3 years bred in 1981; yearlings and 2-year-olds bred in 1982.

Mortality

In 1981, the average colony size (4.2) times the number of colonies (48) indicated a population of 202 beaver, of which 182 (90%) were harvested. In 1982, the average colony size (at least 3.1) times the number of colonies (38) indicated a population of at least 118 beaver, but 116 were harvested, probably indicating some inaccuracy in population estimates and almost 100% removal, although 18 colonies were censused in 1983.

If the population were stationary in 1981 because no previous harvesting or other unusually high mortality occurred, then life table analysis (Payne 1984*a*) of the sample

Table 3. Number of single, pair, and family beaver colonies trapped on Sandhill Wildlife Area, 1981–82.

	Single		*Pair*		*Family*		*Number Colonies*	*Number Colonies*
Year	*N*	*%*	*N*	*%*	*N*	*%*	*Trapped*	*Present*
1981[a]	1	2.2	3	6.4	42	91.3	46	48
1982	2	5.4	6	16.2	29	78.4	37	38
1981–82	3	3.6	9	10.7	71	85.5	83	86

[a] No beaver were harvested the previous 19 years; in 1981, 46 beaver were trapped from 11 completely trapped colonies, and another 136 beaver were trapped from the other 37 colonies.

from 1981 indicated an annual mortality of 34%. Because the population in 1981 had been unharvested previously, the 34% annual mortality represents the natural mortality of previous years, when no harvest mortality occurred, assuming balanced rates of ingress and egress. In 1981, the 2.1 kits/colony and the 3.1 placental scars/breeding female indicated a mortality rate of 32% for kits from parturition until the trapping season.

Discussion

Colony Density and Harvest

Beaver colony density throughout North America varies widely, from 0.15 to 4.6/km^2 (Novak 1987), and depends on habitat quality, trapping intensity (Larson and Gunson 1983), and mutually exclusive territories (Semyonoff 1951, Nordstrom 1972, Bergerud and Miller 1977, Busher et al. 1983, Buech 1985, Nolet and Rosell 1994). Availability of suitable sites for lodge and cache construction, adequate forage, and geomorphology influence distribution of colonies (Boyce 1981*b*, Johnston and Naiman 1990, Fryxell 1992). For example, beaver populations increased in Ontario when active forest management replaced conifers with deciduous trees (Ingle-Sidorowicz 1982).

After 19 years of closure, the beaver colony density of 1.30 colonies/km^2 was high on Sandhill compared to an adjacent trapped area (0.42/km^2). Unexploited populations in Alberta indicated 1.06 colonies/km^2 in 1976, 1.07/km^2 in Manitoba during 1973–80 (Larson and Gunson 1983), and 0.34/km^2 in Newfoundland (Payne 1984*b*) where habitat quality for beaver is marginal (Payne 1984*a*, 1984*b*). Comparison of trapped and untrapped populations indicated higher densities without trapping in New Brunswick (Nordstrom 1972) and New York (Parsons and Brown 1978).

Parsons and Brown (1981) reported a harvest of 2.0 beaver/colony, resulting in a 39% decline of active colonies with a 37-day February–March trapping season in New York. Similar seasons appeared to stabilize the population at the reduced level. During a 14- to 16-day February season resulting in a harvest of 1.8 beaver/colony in New York, number of colonies declined 27% initially; similar seasons increased the original beaver population level (Parsons and Brown 1981). Trapping season length accounted for annual variation in Missouri beaver harvests (Erickson 1981). Reduced season length would reduce the harvest, but the reduction must be substantial, perhaps greater than 50%, to compensate for harvest effort concentrated into the shorter season (Erickson 1981). On Sandhill, for example, the harvest would have had to have been less than 16 days long, because 89% of the harvest occurred in the first 16 days.

After 19 years of closure, winter harvest intensity of 3.9 beaver/colony in 1981 reduced the colony density by 21% in 1982; winter harvest intensity of 3.1 beaver/colony in 1982 reduced the colony density by 53% in 1983. Colony density during 1983 was reduced to levels found in the trapped population censused outside Sandhill in 1981, which had similar habitat.

Ground counts of colonies exceeded aerial counts with a Cessna by 22% on Sandhill, compared to a Newfoundland survey (Payne 1981) in which ground counts exceeded aerial counts with Super Cubs by 39% and with helicopters by 19%. Cache surveys are reliable in indicating population size or trend of beaver when the average colony size is known (Swenson et al. 1983).

Colony Size and Structure

Exploitation of beaver on Sandhill reduced the mean age and number of adults. The mean age of 2.9 years for the 11 completely trapped colonies in 1981 is similar to the 2.98 years that Boyce (1974) found for 11 completely trapped colonies in Alaska, but differs from the 3.81 years that Payne (1982) found for 11 completely trapped colonies previously unharvested in Newfoundland. Nordstrom (1972) found that untrapped populations contained more adults than trapped populations did and that higher beaver density in untrapped populations results in reduced productivity and fewer beaver in the younger age classes.

Social organization of beaver colonies seems more variable than often assumed (Busher et al. 1983). More single and pair colonies were found on Sandhill the year after trapping than the previous year, as Payne (1982) found, but the proportions varied from the 14–19% single, 13–24% pair, and 59–68% family colonies in populations reported by Gunson (1970), Payne (1982), and Peterson and Payne (1986). Changes in the proportion will affect census results based on colony counts (Swenson et al. 1983). Young populations will have a smaller average colony size because more pair and single colonies occur, and family colonies are smaller. Also, nuisance colonies often are smaller than normal because they are trapped out repeatedly, leaving no time to expand (Peterson and Payne 1986). This situation might have occurred on Sandhill, resulting in a smaller than average colony size, after some nuisance colonies were trapped out.

More yearlings occurred in pair colonies on Sandhill the first year, a possible result of high colony density (Payne 1982). The average colony size decreased after exploitation due to harvest mortality and dispersal of beaver ≥ 2.5 years old. Family colonies normally do not contain 2.5-year-olds due to normal dispersal of juveniles when they are 2 years old (Leege 1968), although 2.5-year-olds usually are found in colonies further north (pers. comm. M. Boyce, University of Wisconsin-Stevens Point). Failure to disperse has been attributed to lack of colonization sites and high colony density (Novakowski 1965, Nordstrom 1972, Bergerud and Miller 1977, Payne 1982). Individuals delaying dispersal could be larger and behaviorally more prepared for future dispersal (Novakowski 1965). Delayed dispersers could therefore have a selective advantage over younger dispersers at high population densities when suitable colony sites are limited (Boyce 1981*a*, Molini et al. 1981).

Reproduction

An increase in the pregnancy rate, mean litter size, and percentage of kits trapped suggests compensatory reproduction in beaver on Sandhill after 1 year of exploitation. The adult (≥ 2.5 years) pregnancy rate (86%) in 1982 after 1 year of harvest on Sandhill was similar to the 87% in north-central Wisconsin reported by Peterson and Payne (1986) for a regularly harvested population. The pregnancy rate (58%) in 1981 was similar to that of a lightly harvested beaver population in South Dakota (62%) in 1986 (Dieter 1992), but low compared to unexploited populations in Newfoundland (71%) (Payne 1984*b*), Massachusetts (87%) (Lyons 1979), and New York (86%) (Parsons and Brown 1978). In Newfoundland, pregnancy rates of exploited (70%) and unexploited (71%) beaver populations were similar (Payne 1984*b*). Reduced pregnancy rates after fall harvest have been reported in Idaho (Leege and Williams 1967), Maine (Hodgdon and Hunt 1955), and Minnesota (Longley and Moyle 1963) due to potential disruption of the dominant breeding pair. The increased pregnancy rate on Sandhill during 1982 suggests replacement of a dominant breeder by a delayed disperser (Brooks et al. 1980, Payne 1984*b*), because the percentage of colonies with such breeders was high and probably density dependent (Molini et al. 1981). Correlation coefficients suggest a weak relationship between progressive age of females and increased productivity, as Payne (1984*b*) found.

Delayed sexual maturation might have reduced reproduction of beaver before exploitation. After exploitation, yearlings bred and the number of non-breeding adults decreased. Lack of exploitation of beaver can delay age at first reproduction (Lyons 1979, Boyce 1981*a*) and increase the number of non-breeding adults (Nordstrom 1972). No yearlings bred in a lightly harvested population in South Dakota (Dieter 1992). Parsons and Brown (1979) found little or no yearling reproduction when more than 40% of the potential colony sites were occupied. Unexploited populations have available colony sites saturated with territorial adults; fewer dispersers can colonize them (Boyce 1981*a*). Payne (1975) found about 6% of the yearlings bred on a 179-km^2 island in Newfoundland, which contained 60 colonies after 5 years of no harvest, of which 90% occurred on only 27% of the 190 lakes and ponds (Payne 1989). But Payne (1984*b*) found that 24% of the yearlings bred from exploited populations. Probably most or all available colony sites were occupied on Sandhill in 1981 after 19 years of unexploited growth. In 1982, yearling reproduction was found after 1 year of harvest when about 79% of the available colony sites was occupied. Although uncommon in beaver, if many yearlings disperse and establish colonies, yearling reproduction can be important to beaver population growth (Payne 1982, 1984*b*). Beaver productivity is characterized by low average litter size and pregnancy rates for young and old beaver, with peak production during middle years (Payne 1984*b*). Despite increased reproduction in older and potentially more productive beaver, the population declined after 2 years of intensive harvest on Sandhill when harvest mortality apparently exceeded the capability for compensatory reproduction and immigration.

Mortality

Estimated population levels and the heavy harvest intensity indicated substantial immigration of beaver into Sandhill in 1982 and 1983, as well as the documented increase in reproduction. Although colony density appeared substantially lower in the adjacent trapped area, dispersal probably occurred into the heavily trapped Sandhill area. Although only 11 colonies were definitely documented to have been trapped out, with

46 beaver removed, 136 beaver, or 3.8/colony, were trapped from the other 36 colonies trapped. (Two additional colonies were untrapped.) Because colony size of the 11 trapped out colonies was 4.2, the 3.8 beaver trapped/colony from the other 36 colonies indicates most of the 36 colonies also were trapped out in 1981. Yet in 1982, 38 colonies occurred.

The estimated annual mortality (34%) before 1981 for the unharvested beaver population on Sandhill seems higher than the 28% from unharvested and 27% from harvested populations in Newfoundland (Payne 1984*a*), and the 31% calculated from those exploited in Saskatchewan (Gunson 1970). The higher rate on Sandhill might be due to higher egress than ingress of dispersing juveniles from an unharvested population on Sandhill to adjacent harvested populations. During winter 1981, tularemia *(Francisella tularensis)* was identified in beaver on Sandhill and might have increased mortality above normal. Four beaver colonies were eradicated by tularemia in 1981. Tularemia epizootics have been linked to overpopulation in beaver (Banfield 1954). Tularemia outbreaks were not documented on Sandhill before 1981. If the beaver population were decreasing from tularemia before 1981, then the population would not have been stationary, and the mortality estimate of 34% would have been low (Caughley 1977).

Many of the shallower impoundments and associated wetlands freeze solid in winter on Sandhill, resulting in inaccessible browse piles and possible starvation of the colony, which might be limiting. Other studies in the Northwest Territories (Aleksiuk 1968) and Alaska (Boyce 1974) found that winter starvation might be limiting or at least it might limit sites that can be occupied longer than 1 season.

Management Implications

Beaver populations often attain nuisance status with human encroachment of beaver habitat, which usually results in efforts to control beaver populations. However, the number of beaver trappers in Wisconsin has declined because pelt prices have declined. Reduced competition also has resulted in more nuisance beaver complaints (Payne and Peterson 1986), as fewer beaver are trapped, and some trappers "farm" their areas to leave breeding stock for future years. With interested, dedicated trappers, a trapline system of harvest can be effective in achieving population control and a high annual harvest of beaver (Payne 1980).

Beaver trapping in Wisconsin in late fall-early winter, when pelts are less prime but still valuable, could increase trapping effort and beaver harvest due to milder temperatures, open water or less ice, and more beaver activity around the lodge compared to later or long beaver seasons. A harvest of more than 3.0 beaver/colony might be needed in saturated populations to exceed capability for compensatory mortality and reproduction the first year; perhaps lower harvests thereafter would then produce reduced beaver populations (Payne 1989). Eliminating trap restrictions that prohibit trapping near the lodge would facilitate complete removal of nuisance colonies. Removal of an adult after freeze-up but before the breeding season will reduce pregnancy rates. Replacement of a dominant breeder by a subadult probably will result in smaller litters and lower survival of offspring.

Maintaining beaver populations at reduced levels would lower the minimum breeding age and would prevent females from reaching ages of optimal productivity (Payne 1984*b*). Regular harvest without complete removal would maintain territories and prevent dispersers from recolonizing vacant colony sites. Colonization can be inhibited by constructing artificial scent mounds around potential beaver sites (Welsh and Müller-Schwarze 1989). Maintaining conifers or advanced seral stages of vegetation along water would deter colony site selection, spacing, and reproduction (Boyce 1981*b*). Other methods can be used to reduce beaver populations (Hammerson 1994).

Acknowledgments

J. W. Hardin, S. D. Van Horn, M. S. Boyce and anonymous referees reviewed the manuscript. The Wisconsin Department of Natural Resources supported and cooperated throughout the study, especially J. C. Haug, J. F. Kubisiak, N. C. Norton, and others. This project would not have been possible without the cooperation and knowledge of the participating trappers.

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