PRAIRIE AND SAVANNA IN SOUTHERN LOWER MICHIGAN: HISTORY, CLASSIFICATION, ECOLOGY

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ABSTRACT

Tallgrass prairie and associated savanna were at their continental boundary in southern Michigan when white settlers arrived and had largely disappeared before scientists could describe them. The historical extent of upland prairie, wet prairie and savanna in Michigan was estimated to be 930,000 ha (2.23 million ac), with savanna constituting 78 percent. In 1830 there were 54 separate locations of upland prairie in Michigan. Historical and modern sources were consulted to locate and visit 66 relict prairies and savannas in 1979–1980. Ordination of these 66 remnants identified several prairie and savanna communities (and a distinct fen community) which varied along three environmental gradients. A moisture gradient ranging from soils of low to high water-retaining capacity formed the series of sand prairie/oak barrens; oak openings; mesic prairie; wet prairie; and fen. A soil texture gradient separated mesic and wet prairies on loams and silt loams (with some sandy loams) from those on sandy loams and sands (with some loams). Soil texture differences generally corresponded to glacial parent material differences: coarser-textured soils were associated with glacial lake plains and to a lesser extent with outwash plains, while finer-textured soils were associated with outwash plains and moraines. A third but weak gradient divided oak openings on south- to west-facing hillsides from those on rolling to level ground. Summaries of species presence, indicator species, and environmental characteristics are provided for each community type (except fens, which were used solely for the purpose of ordinating stands).

Michigan's extensive savannas defined much of southern Lower Michigan and were characterized by a complex interaction of fire, tree canopy cover, and herbaceous plant diversity. Soils, landscape setting, drought, and other disturbances influenced these interactions. The oak grubs found in Michigan's savannas and described by early writers are now understood as essential for perpetuating the tree canopy of fire-maintained savannas.

These remnants represent less than 0.1% of Michigan's historical prairie and savanna acreage. In view of this loss any remnant should be protected, but especially the oak openings, which were a dominant ecological feature of southern Lower Michigan. Since oak openings existed on a large scale, small reserves are insufficient to represent former ecological processes and encompass the majority of animal and plant species characteristic of oak openings. Consequently, conservation groups and natural resource agencies should identify, protect, and restore large blocks of oak openings in southern Michigan, especially those that contain other prairie and savanna plant communities.

KEY WORDS: tallgrass prairie, oak savanna, classification, ecology, environmental history

INTRODUCTION

Michigan's extensive prairies and savannas disappeared in the 1800s before scientists could fully describe them (Chapman 1984), yet early 20th century

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ecologists understood that southern Lower Michigan formed the northeastern continental edge of tallgrass prairie and savanna (Gleason 1917; Transeau 1935; Curtis 1959). Tallgrass prairie extended from the Great Plains at 98 degrees longitude eastward to central Illinois (Risser et al. 1981; Sims 1988), Michigan, Ohio, and Indiana (Transeau 1935; Küchler 1975). Savanna co-occurred with tallgrass prairie (Küchler 1975, Nuzzo 1986). Savanna, a fire-maintained plant community co-dominated by herbaceous plants and trees, was called oak openings or oak barrens by European settlers, depending on the type of soil and tree species (Cooper 1848; Peters 1970a).

Beginning about 1830 in Michigan (Peters 1970b) and later farther west, settlers claimed prairies and savannas before other land and transformed them by plowing, stopping annual wildfires, and initiating season-long grazing. After 1945 residential and other development increasingly displaced agriculture (Risser et al. 1981; Nuzzo 1986; Noss et al. 1995). By 1980 nearly all of Michigan's prairies and savannas were destroyed or drastically altered by agriculture, fire cessation, and development (Chapman 1984).

Given the historical abundance and modern rarity of prairie and savanna in Michigan, their ecological status is of great scientific and conservation interest. This paper classifies Michigan's prairie and savanna communities, describes their history and ecology, and presents the most complete account of Michigan's prairies and savannas to date in order to assist future scientific studies and conservation efforts.

HISTORICAL ACCOUNTS

Settlers, travelers, and scientists reported that upland prairies, wet prairies, and savannas were distinct, prominent, and extensive features of southern Lower Michigan in the 1800s (e.g., Hubbard 1838, Douglas 1839; for a full account see Chapman 1984). Historical documents available from the 1830s to early 1900s ranged from settlers' journals to early scientific accounts. We quote selected passages at length because they are the only source for information about key ecological aspects of the original prairies and savannas and are more useful to the reader when directly encountered rather than filtered by a modern ecologist.

Treeless Prairies and Bur Oak Plains

Michigan's prairies disappeared so quickly that Butler (1947) complained the state gazetteer failed to mention them. Some (e.g., Prairie Ronde at Schoolcraft) are still obvious today due to their flatness and relative treelessness (Figure 1), and their ghosts are encountered in place names such as Youngs Prairie Road and Grand Prairie Cemetery (Figure 2). Most early observers agreed that Michigan's prairies were treeless (Taylor 1855; Anonymous 1877; Coffinberry 1880; Brown 1881; Van Buren 1884; Geib 1907; Wheeting & Berquist 1923).

> The prairie [Prairie Ronde] . . . seemed wondrously beautiful and grand. It was simply in a state of nature, covered with a pretty rank growth of grass, then dry and sere, no tree except the Big Island grove and one or two other small groves (Brown 1881).

FIGURE 1. Land use in 1971 on historical Prairie Ronde. The flat, treeless aspect differs sharply from most of Michigan's rural landscape and resembles central Illinois. View is to the east from 8th St. near V Ave., Kalamazoo Co. (Photo by Richard Brewer.)

> Ascending slightly from the circumference to the center, yet so as to seem full rather than elevated; surrounded with a noble forest whose sharp-cut and perfect line was nowhere so distant as to be indistinct . . . (Van Buren 1884).

Others (primarily early 20th century soil scientists) stated that Michigan's prairies contained scattered bur oak saplings and hazelnut brush (Rogers & Smith 1916; Perkins & Tyson 1926; Deeter & Trull 1928; Moon et al. 1932; Peters 1970a).

These conflicting accounts were due to prairie's early destruction and the existence of bur oak plains, now extirpated from Michigan. Bur oak plains were a type of open savanna often fringing prairies but also located on level plains lacking prairies, notably in Calhoun and western Jackson County (Kenoyer 1940; Wood 1964; Peters 1970a; Hodler et al. 1981; Brewer et al. 1984; Michigan Department of Natural Resources 2003). Those who witnessed Michigan before 1850 agreed that prairies were distinct from bur oak plains and that the prairies were treeless.

> On the one hand stretched bur-oak plains, spread with a verdant carpet, variegated with dazzling wild flowers, without an obstacle to intercept the view for miles, save the somber trunks of the low oaks, sparsely spreading their shadows across the lawn; on the other hand arose the undulations of the white oak openings, with picturesque outlines of swells and slopes, gracefully sweeping and sharply defined in the distance. Then, there lay the majestic prairie, grand in expansive solitude, its fringe of timber, as seen in the distance, resembling a diligently trained and well-trimmed garden parterre (Coffinberry 1880).

Further evidence that prairies and bur oak plains were distinct is seen in the pattern of initial settlement. As Peters (1970b) showed, most of the earliest land claims by settlers in Kalamazoo County were prairie but almost always at the edge so as to include adjacent oak savanna, in which they built their house. Prairie was valued because it required no tree cutting before cultivation; the savanna added wood for fuel, lumber, and fences and acorns for the farmers' pigs. Property combining the two types of vegetation was optimal; nearly all of it was occupied between 1828 and 1830, before land was officially open for sale.

FIGURE 2. Harrison Cemetery in fall 1968, on historical Prairie Ronde, Kalamazoo Co. Michigan's floristically diverse blacksoil prairies survived only in rights-of-way and cemeteries. After the last mowing of the season, stalks of big bluestem, *Andropogon gerardii*, are visible, emerging from persistent roots to overtop the headstones. (Photo by Richard Brewer.)

Types of Savannas

The term "savanna" encompasses several plant communities described by early travellers and settlers: openings, barrens, plains. Savanna simply means a plant community where herbaceous and woody plants co-dominate.

"Opening" as a term for a sparsely wooded area in a landscape also containing forest was used in New England in the 18th century, according to the 1971 edition of the Oxford English Dictionary. In the first third of the 19th century as a flood of settlers encountered the savannas of the Midwest, the combination "oak openings" probably became widely used. Frederick Marryat (1960), an English traveler in America, used the term in its current sense in 1838, describing lightly treed portions of the landscape southwest of Lake Winnebago in Wisconsin. James Fenimore Cooper gave the term national currency with his 1848 novel Oak Openings set in southwestern Michigan (Figure 3).

> The trees . . . were what is called the "burr-oak" . . . and the spaces between them, always irregular, and often of singular beauty, have obtained the name of "openings;" the two terms combined giving their appellation to this particular species of native forest, under the name of "Oak Openings" (Cooper 1848).

Oak openings were savanna, a plant community where woody and herbaceous plants co-existed in more equal amounts than in forest or grassland. Dispersed groves of oaks or continuous tracts of oaks whose crowns barely touched, grew with a dense groundcover of grasses, sedges, and wildflowers. Depending

FIGURE 3. Bur oak plains might have resembled this stand of bur oak (*Quercus macrocarpa*) near Madison, Wisconsin, but with smaller trees. No intact example of this plant community survives in Michigan. Groundcover in all remnants consists primarily of Eurasian forage grasses, goldenrod, and weedy plants. The open architecture of oak tree crowns lets sunlight reach the ground; light patches move with the sun, producing various light levels that allow species of deep shade to co-exist with species needing full sun. (Photo by Kim Chapman.)

on soils and location, settlers called savanna "oak openings," "barrens," or "bur oak plains" (Peters 1970a, 1970b). Oak openings were the common savanna condition, while oak barrens dominated by species in the black oak group were located on sandy soils, and bur oak plains were a savanna on heavier soils, often next to prairies as discussed above (Higgins 1840; Brewer et al. 1984).

> The oak openings are of two types, that characterized by the bur oak, whence the adjacent village of Burr Oak gets its name, and that in which black oak species predominate. The former lies next to the prairies and has a rich, heavy soil, the latter . . . is of a lighter and even sandy soil, though the land is seldom pronouncedly barren (Daniels 1904).

White oak (*Q. alba*) and hickories (*Carya* spp.) were the common trees of oak openings on rolling topography of sandy loam and loam soils. Chinkapin oak (*Q. muhlenbergii*) also was reported as common in oak openings of southwest Michigan by GLO surveyors, who called it yellow oak. The species is now rare in southern Michigan and its dramatic decrease remains unexplained.

Fire in Savannas

Early accounts agree that large portions of southern Lower Michigan presented the impression of an "Englishman's park," a garden, or an orchard. The early observers concluded that the open forest conditions and absence of woody understory and debris in these savannas were due to annual fires set by Potawatomi and other Indians. They speculated that the fires killed the above-ground portion of oak trees but left the roots alive, creating oak grubs which could quickly grow into trees when fires ceased. They witnessed fire burning the prairies, perceived that fire stimulated the blooming of wildflowers, and took the increase in woody plants after cessation of fire as evidence that prairies were maintained by annual burning (Cooper 1848; Clapp 1881; Brown 1881; Van Buren 1884; Glidden 1892; Geib 1907; Turner 1911). Curtis (1959) presented early accounts which confirm that annual fires also occurred in Wisconsin savannas. The following accounts are from southern Lower Michigan.

> Clumps of the noblest oaks, with not a twig of underwood, extending over a gently undulating grassy surface as far as the eye can reach: here clustered together in a grove of tall stems supporting one broad canopy of interlacing branches, and there rearing their gigantic trunks in solitary grandeur from the plain . . . (Hoffman 1835).

> . . . travelers might wind at will through the superb natural park, trampling down only the flowers that in many places created glowing parterres . . . (Hubbard 1872).

> . . . On entering these vast plains a traveller is led to believe that it has been Cleard [sic] by the hand of man. These openings are a sandy loom [sic] and are covered with grass & flowers of various descriptions and hues (Everett 1956).

> The annual fires burnt up the underwood, decayed trees, vegetation, and debris, in the oak openings, leaving them clear of obstructions. You could see through the trees in any direction . . . for miles around you, and you could walk, ride on horse-back, or drive in a wagon wherever you please in these woods, as freely as you could in a neat and beautiful park (Van Buren 1884).

> To-day, for the first time, I saw the meadows on fire. . . . they are burnt over thus annually to make it tender. These fires, traveling far over the country, seize upon the largest prairies, and consuming every tree in the woods, except the hardiest, cause the often-mentioned oak openings, so characteristic of the Michigan scenery (Hoffman 1835).

> Though our mode of conveyance for a few years was by ox-team, we could expedite by taking a bee-line (nearly) to the different points, as there was no underbrush (the Indians kept them burned down). . . . In the spring the fire would run through the woods, which warmed up the ground and caused the vegetation to spring up. . . . The flowers covered the earth . . . (Clapp 1881).

The annual fires which prevented a woody understory from developing beneath the oak canopy created savannas with few obstacles to travel and, consequently, the first travel routes between the early white settlements of southern Lower Michigan passed through savannas (Higgins 1840; Van Buren 1884; Peters 1970a; Peters 1970b; Chapman 1984).

Succession of Savanna to Forest

The federal government's removal from Michigan of most Potawatomi Indians by 1840, and the creation of fire breaks by cropland, roads, railroads, and settlements, stopped the annual fires. Michigan's savannas quickly became oak thickets and then forests. The grubs mentioned by Geib, Glidden, and Hoppin are, in effect, a form of long-lived tree seedling which, owing to its large root mass, can grow and reach a fire-proof size more quickly than an acorn seedling.

The word grub in this sense seems to be a 19th century American invention, probably derived from the same word used as a verb, meaning "to dig up" and known from England several centuries earlier.

> The ordinary character of the "openings" is that of a majestic orchard of stately oaks, which is frequently varied by small prairies, grassy lawns, and clear lakes. These magnificant groves were, until within a few years, kept free from underbrush by the passage through them of annual fires, allowing successive growths of herbage to spring up luxuriantly, covering the surface with a profusion of wild flowers and verdure . . . (Hubbard 1838).

> As the periodical fires had now ceased for many years, underbrush was growing in lieu of the natural grass, and in so much these groves are less attractive than formerly; but one easily comprehends the reason . . . (Cooper 1848).

> . . . though the rural beauty of the country is still unrivaled, little remains of the original character of the openings. This is a result partly of the progress of civilization, and partly of the thick growth of small timber that has covered all the uncultivated portions since the annual fires have ceased, which kept down the underbrush (Hubbard 1872).

> The practice of the Indians was to burn the land over every fall, which had the effect not only of keeping the annual vegetation burned off but the young tree growth also. The "grubs" thus formed grew laterally into stools, the tops of which were hardly perceptible among the prairie grasses (Geib 1907).

> After the very best job of breaking, a live grub would be left upon every square rod of ground [i.e., a density of 395/hectare or 160/acre]. . . . The enlargement at the surface about the tap root increased with each year's growth of sprouts, until the cap was formed, a foot or more in width, like an underground toadstool. . . . The whole under-surface of this cap was filled with dormant buds, that awoke into activity at once when the standing ones were cut or were burned away. Nature reasserted itself when the annual burnings had ceased and the fittest stem survived and became the tree, or young oak, as we see them today . . . (Glidden 1892).

Formerly a defining feature of southern Lower Michigan, savanna is now one of the rarest of plant communities. The flora of savannas persists at the edges of forests instead of in the interiors; in field corners and in railroad rights-of-way; and at other locations that experience disturbances which prevent trees from forming a closed canopy. All evidence suggests that the flora of the savannas was diverse and contained species today considered to belong in prairies and woodland edges, as well as many that now are considered characteristic of oak forest.

At a meeting of the Pioneer Society at Centreville, Michigan, in 1893, Ruth Hoppin, an experienced naturalist who taught taxonomic botany at Smith College and what is now Eastern Michigan University, was asked to describe "a Michigan oak openings." The plant life she described is now rarely found under the oaks of Michigan's woodlands. Probable identities of plants named by Hoppin are given in brackets.

> Your secretary has requested me to describe the appearance of a Michigan oak openings in its primeval beauty. Such a description would require the eye of an artist and the pen of a poet. Much as I loved those forest scenes, I have not words sufficient to give you an adequate picture of them. The fires had not run through the woods for years, so the wild flowers had been given full possession, and the underbrush, grubs, we called it, had not had time to grow up. The result was, that the woods looked more like an old orchard than a forest. Roads wound at will among the trees making the most graceful curves and pleasing turns. In early summer the grass was overtopped with wild flowers surpassing in beautiful effects the most skillful landscape gardening and city park scenery.

> Blue lupines [*Lupinus perennis*], variegated phlox [*Phlox pilosa*], scarlet painted cups [*Castilleja coccinea*], purple and white erigerons [*Erigeron philadelphicus, E. pulchellus, E. strigosus*], purple cranes' bills [*Geranium maculatum*], blue spider worts [*Tradescantia ohiensis*], yellow cynthias [*Krigia biflora*], senecios [*Senecio plattensis*] and rock roses [*Helianthemum canadense*], tall golden Alexanders [*Zizia aurea*, *Taenidia integerrima* or *Thaspium trifoliatum*] and white meadow rue [*Thalictrum dioicum*], dainty galiums [*Galium boreale, G. pilosum*, etc.] and coarse columbo [*Frasera caroliniensis*], medicinal lady slippers [*Cypripedium calceolus* var. *pubescens*], Seneca snake root [*Polygala senega*] and culver root [*Veronicastrum virginicum*], all these came on together in rapid succession, co-mingling in the wildest profusion, and stretching as far as the eye could reach under the delicate oak foliage. Why try to describe the earlier growth of violets, asters and all their sisters, their cousins, and their aunts. The now nearly exterminated fringed gentian [*Gentiana crinita*] then flourished in abundance. The farmers, in their eagerness to subdue the soil, have destroyed whole families of these harmless plants and have let in others, many of them not pleasing to look at, and much more hurtful than the native species. I see the day coming when there will not be a patch of forest where the child may see the flowers which charmed his parents' eyes. Like buffalo, the deer, the wild pigeon, the Whip-poor-will and the prairie hen, these, too, will soon be things of the past. The last pioneer will soon be gone and with him many of the native plants and animals will soon disappear (Hoppin 1893).

MATERIALS AND METHODS

Location and Extent

We produced two estimates of prairie and savanna location and extent. The first inferred vegetation boundaries from soil and geological maps and historical accounts (Fippin & Rice 1901; Geib 1907; Rogers & Smith 1916; Wheeting & Bergquist 1923; Perkins & Tyson 1926; Kerr et al. 1927; Deeter & Trull 1928; Veatch 1930; Deeter & Matthews 1931; Moon et al. 1932; Moon et al. 1933; Deeter et al. 1934; Veatch 1934; Mick et al. 1951; Veatch 1959; Farrand and Bell 1982). The resulting map (Chapman 1984) was checked for accuracy against maps based on General Land Office (GLO) survey records (such as Kenoyer 1934, Trygg 1964 and Brewer et al. 1984). The second estimate inferred vegetation boundaries from GLO surveyor field notes that were digitized and available from the Michigan Center for Geographic Information, Lansing, Michigan (Comer et al. 1995). These data were compiled from survey records taken at section corners and on section lines during land surveying prior to settlement (1816–1856). Information from the surveys, including identities of witness trees and locations of such features as prairies and wetlands, was mapped and interpreted by ecologists to produce the digital data layer. The GLO survey data were digitized as polygons, checked by ecologists and formatted in ArcInfo 7.2.1. Location accuracy is 80–186 meters. We assembled these data in ArcView 3.1 and aggregated acreages in four classes: black oak barrens, mixed oak savanna, mesic prairie, and wet prairie.

Field Methods

Journal articles, unpublished theses, and local experts were consulted to locate prairie and savanna stands in Michigan. New stands were discovered during field work. Sixty-six prairie and savanna stands were visited in 1979 and 1980 (Chapman 1984). Tree canopy cover in stands was <51%, a level that has been used to separate savanna from forest (Curtis 1959, Brewer et al. 1984). Stands had not been excavated, filled, graded, grazed, or similarly disturbed, and contained <1% non-native species cover (excepting *Agrostis gigantea*, *Phalaris arundinacea*, *Poa pratensis*, and *Poa compressa*) We included fens in the study because differences with wet prairies were not understood. Five stands classified as fens—a plant community on organic soil saturated by calcium- and magnesium-rich groundwater (Curtis 1959) and found in prairie and savanna regions of Michigan—were used in the ordination but are described in detail elsewhere (Chapman 1984).

All vascular plant species, the mosses *Polytrichum juniperinum* and *P. piliferum*, and *Cladonia* lichens were recorded. Sampling avoided forest edges and vegetation transitions created by elevation, soil moisture, or flooding, as recommended in phytosociological studies (Mueller-Dombois & Ellenberg 1974). Species recorded by experts in 23 stands, but not found in our field work owing to the timing of visits, were added. For 13 stands, these additions represented <10% of the total species and for 10 other stands 10–50% of total species. Species names are consistent with Voss (1972, 1985, 1996).

Ordination and Classification

With the goal of identifying modern prairie and savanna plant communities, relationships among stands were determined by calculating Jaccard's coefficient of similarity and constructing a polar ordination of stands along three ordination axes (Bray & Curtis 1957; Mueller-Dombois & Ellenberg 1974). Stands that shared the fewest species were placed farthest apart along the axes. Stands near each other shared a greater number of species. This technique is appropriate for presence-absence data when the underlying environmental gradients are not known (Beals 1973). Endpoints of axes were selected using a manual method (Bray & Curtis 1957; Mueller-Dombois & Ellenberg 1974). The x-axis endpoints were chosen as two stands which were most different (i.e., they had the smallest coefficient of similarity) but which had high coefficients of similarity with other stands. Subsequent axis endpoints were chosen from remaining stands in the same way.

A computer program was written to calculate coefficients of similarity among stands, calculate the ordination position on three axes, and evaluate the performance of the ordination. The performance was analyzed with a Student's t-test of the correlation between stand locations in ordination space (interstand distance) and stand differences based on plant composition (coefficients of similiarity). A subset of 25 stand pairs (about 1% of stand pair combinations in the ordination) was selected and a linear combination of factors for those stands was calculated for each axis and compared to the average coefficient of similarity for those stands.

To aggregate stands into plant communities, clusters of similar stands were identified and compared to other clusters. A reference stand at the center of evident clusters was chosen, an ordination distance was calculated from the reference stand to all other stands, and stands were assigned to the cluster containing the nearest reference stand.

Plant Community Characteristics

For the resulting prairie and savanna plant communities, we calculated the total species found; a mean number of species per stand; the percent presence of each species (i.e., number of stands a species occurs in divided by number of stands in the community); and the percentage of frequent species (i.e., species found in 50–100% of all stands in that community). Sorensen's similarity index (Mueller-Dombois and Ellenberg 1974) was calculated among pairs of plant species as confirmation of community differences (see Chapman 1984).

We selected indicator species for each prairie and savanna plant community to aid in future field identification (Mueller-Dombois & Ellenberg 1974) and restoration efforts. Indicator species were ranked as high – restricted to the community and 80–100% presence; medium-high—restricted to the community and 50–79% presence; medium—restricted to the community and <50% presence; medium-low—80–100% presence and <20% presence in another community; low—50–79% presence and <20% presence in another community.

The environment of prairie and savanna plant communities was described by soil pH, texture, and water retaining capacity (WRC), a measure of the weight of water a soil type can hold when saturated. The pH was measured in the top 5–10 cm of the soil surface using a LaMotte-Morgan field test kit. Soil texture was determined by feel (Thein 1979). To determine WRC, soil cores of 5cm diameter and 8cm depth were obtained and soaked in water for 24 hours, drained for 24 hours, weighed, oven dried at 120^{o} C. for 48 hours, then weighed again and the container tared. WRC was calculated as: [(wet soil – dry soil)(100)]/(dry soil – tare). For each plant community, the mean pH and WRC were calculated and the prevalent soil textures listed. Percent slope, aspect, geological substrate, and land use were also recorded (see Chapman 1984).

RESULTS

Location and Extent

Historical and modern accounts and the soil and GLO survey data agree that prairie and savanna plant communities once dominated large areas of southern Lower Michigan (Figure 4; Table 1). The acreage estimated from soils and geology (Chapman 1984) was less than half the acreage obtained from digitized GLO

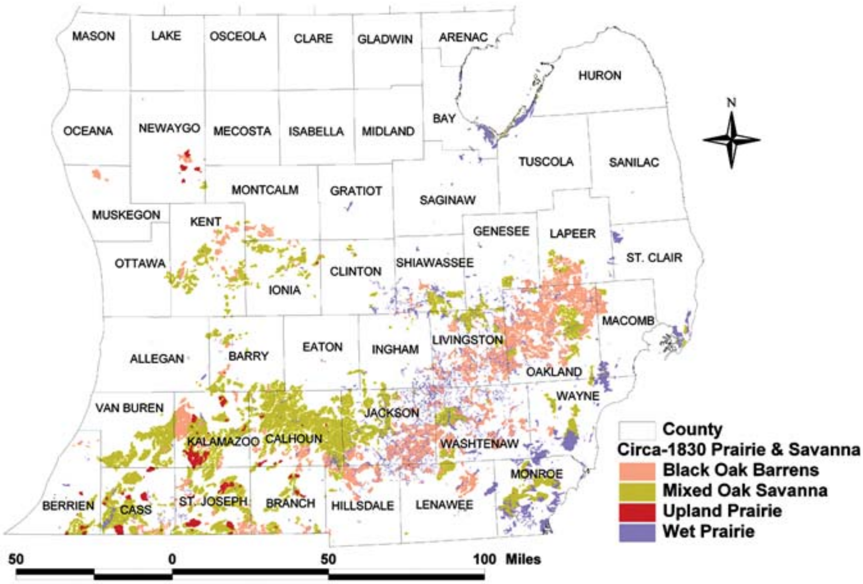

FIGURE 4. Distribution circa 1830 of prairie and savanna in southern Lower Michigan (Comer et al. 1995). Black oak barrens was a savanna on low fertility soils; mixed oak savanna occurred on richer soils.

survey data. The digitized GLO data estimate of Michigan's savannas and prairies was 902,300 ha (2,229,630 ac), with savanna comprising 77.9%. Historical sources identified 54 locations likely to have been upland prairie in 1830, totaling 35,600 ha (88,000 ac) (Figure 5; Chapman 1984). The largest at 5,100ha (12,600 ac) was Prairie Ronde in Kalamazoo County. The GLO digital data estimate for upland prairie was less than Chapman's soils-geology estimate, but also was less accurate because it was calculated from section line data which infer community boundaries beyond section lines, while Chapman's was calculated from soil units on soil survey maps. Wet prairie occupied more area than upland prairie but may have included sedge meadows, fens, and sedge-dominated marshes.

Environmental Characteristics of Prairies and Savannas

The ordinated prairie and savanna plant communities exhibited the greatest variation in species and environment along a soil moisture gradient from sand prairie/oak barrens (see cover), to oak openings, mesic prairie, wet prairie, and fen (Table 2). (A photograph of the ordination and a list of sites are available from the senior author.) This dominant soil moisture gradient also defined the prairies of Wisconsin (Curtis 1959; Umbanhowar 1992), Ontario (Faber-Langendoen and Maycock 1987), and Illinois (White and Madany 1981). Soil moisture and pH were correlated; low pH was associated with low water-retaining capacity soils, high pH with high water-retaining capacity soils.

TABLE 1. Estimated acreage of Michigan prairie and savanna circa 1830.

	Total Acres[1]	Total Acres[2]	Mean Acres[2]
Black Oak Barrens	185,000	722,049	1,668
Mixed Oak Savanna	475,000	1,058,557	1,819
Upland Prairie	88,000	66,192	919
Wet Prairie	112,000	382,832	271
Total	860,000	2,229,630	—

[1]Chapman 1984
[2]Comer et al. 1995; mean acres is of polygons

On a second gradient, soil texture was associated with floristic differences within mesic and wet prairie categories. Soil texture differences generally corresponded to parent material differences. Fine-textured, loamy soils on moraines and outwash plains supported mesic and wet prairie communities, whereas coarse-textured, sandier soils of glacial lake plains and to a lesser extent outwash plains supported mesic sand prairie and lakeplain wet prairie. Umbanhowar (1992) and Faber-Langendoen and Maycock (1987) also demonstrated that soil characteristics (and to a lesser extent geographic location) played a significant role in determining the plant composition of prairie types in Wisconsin and Ontario.

A third but weak gradient separated oak openings on south- to west-facing hillsides from those on rolling to level ground.

The ordination of stands on the x-axis was highly correlated with coefficients of similarity among 25 stands selected for testing ($p < 0.001$), with a mean coef-

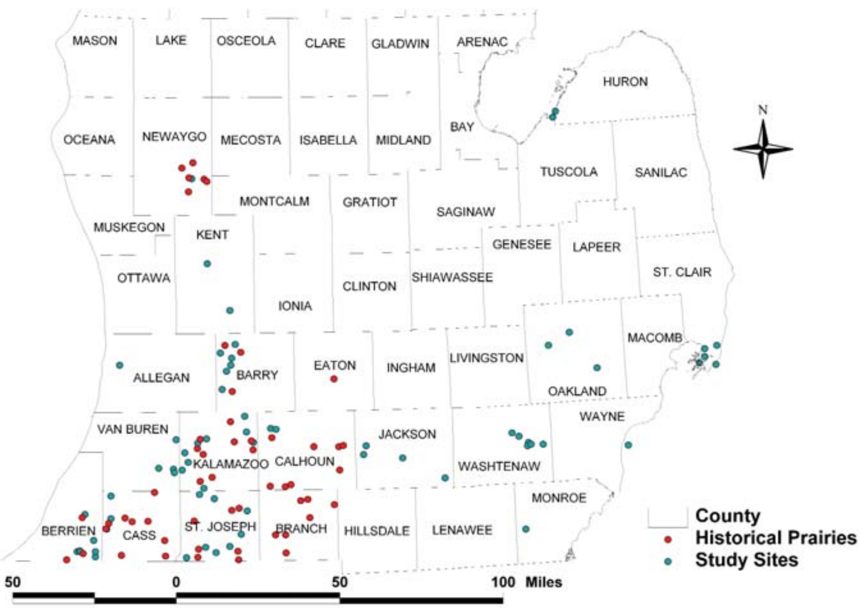

FIGURE 5. Locations of historical prairies identified by early settlers and travellers and in soil surveys; and of study sites used in the ordination of prairie and savanna plant communities.

TABLE 2. Soil characteristics of Michigan prairie and savanna plant communities. (Fen is included for reference as the endpoint of the first ordination gradient.)

Plant Community	Mean pH	Range in pH	Mean WRC[1] (%)	Range in WRC (%)	Common Soil Textures	Other Soil Textures
Dry Sand Prairie/ Oak Barrens	5.1	4.6–5.7	38	28–48	loamy sand	sandy loam
Mesic Sand Prairie	5.5	5.4–5.9	43	31–62	sandy loam	loamy sand, sand
Oak Openings (Hillsides)	5.5	4.5–7.8	51	30–85	loamy sand, sandy loam	none
Oak Openings	5.8	5.2–6.7	54	43–94	sandy loam	loamy sand, sand
Mesic Prairie	6.2	4.9–7.5	64	37–106	loam, sandy loam	silt loam
Wet Prairie	6.9	5.5–7.7	100	43–170	loam	sandy loam, silt loam
Lakeplain Wet Prairie	8	7.7–8.2	60	50–68	sandy loam, loamy fine sand	loam
Fen	7.6	6.8–8.2	432	220–745	sapric muck	none

[1]Water retaining capacity (see Methods).

ficient of similarity of 75.1 (standard deviation 23.3) for the selected stands used in the test. The x-axis endpoint stands had a very low coefficient of similarity (2.7 of a possible 100). The y- and z-axes individually were not significantly correlated with coefficients of similarity for the 25 stands tested. The endpoint stands on the y- and z-axes were more similar than those on the x-axis (coefficient of similiarity 24.1 and 26). Although a linear regression test of variance was not performed, it can be concluded from these simple tests that the x-axis represented the greatest amount of variation among stands, while the y- and z-axes represented a lesser amount of variation. However, the y-axis probably represented significantly more variance than the z-axis judging from the physical separation of stands at the right side of the ordination.

Vegetation Characteristics of Prairies and Savannas

The 66 stands supported 495 plant species and were grouped into seven plant communities which varied in species composition along the three environmental gradients just described: moisture, soil texture, and a gradient related to slope and aspect (Table 2; Appendix 1).

Plant communities varied in the degree of internal species homogeneity, distinctness from one another, and number of indicator species (Table 3; Appendix 1 & 2). Plant communities near each other on the environmental gradients shared more species than plant communities farther apart on those gradients. Sand prairie/oak barrens, wet prairie, lakeplain wet prairie, and fen were the most internally homogeneous and distinctive plant communities and contained the most indicator species. Oak openings was the least internally homogeneous plant community and had the fewest indicator species. Though oak openings supported 237 plant species, only 16.8% of them were encountered frequently and a single plant, *Aster pilosus*, qualified as an indicator species. Oak openings had a

TABLE 3. Plant species statistics in Michigan prairie and savanna plant communities.

Plant Community	Total Species	Mean Species Per Stand	% Frequent Species[1]	Number of Indicators
Dry Sand Prairie/Oak Barrens	182	77	41.8	33
Mesic Sand Prairie	241	79	24.5	20
Oak Openings (Hillsides)	148	49	27.7	14
Oak Openings	237	65	16.8	1
Mesic Prairie	172	81	29.1	25
Wet Prairie	177	69	36.1	24
Lakeplain Wet Prairie	157	76	37.6	26

[1]Frequent species have a presence of 50–100% among all stands of a plant community.

large number of species in common with other upland prairie and savanna communities. Oak openings on hillsides was less internally homogeneous than dry sand savanna/oak barrens and wet prairies, but had a high number of indicator species. Mesic prairie and mesic sand prairie had few restricted indicators but a large number that were at low presence in other plant communities.

DISCUSSION

The prairie and savanna plant communities derived from field data and ordination are consistent with historical accounts, to the extent that comparisons can be made. Adding stands to the ordination and employing a finer level of analysis (e.g., ordinating only the upland prairies and savannas) may reveal finer patterns in species presence among stands. For example, Faber-Langendoen and Maycock (1987) described a wet-mesic sand prairie type in southwest Ontario which exists on Michigan's coastal lakeplains but was not revealed by the ordination. Current ordination software with greater computing power and flexibility (e.g., McCune and Mefford 1999) might also improve the ordination results.

With 495 plant species recorded out of about 2500 vascular plants statewide (including non-native species), Michigan's prairie and savanna flora is large. We think it likely that these species, and others of prairie and savanna affinities, arrived at various times after glacial recession and also that some sites of appropriate parent material and physiography supported vegetation recognizable as prairie well before the mid-postglacial hypsithermal period of 6,000 to 8,000 ybp (years before present) which is widely credited with allowing prairie vegetation to become established in Michigan.

Descriptions of Quaternary vegetation change published in the last 20 years (listed in Grimm and Jacobson 2004) tend to disregard the idea advanced by Gleason (1922a; see also Benninghof 1964 and Stuckey 1981) that the beginnings of the Prairie Peninsula are traceable to the early postglacial of 10,000 to 13,000 ybp (King 1981). Perhaps this neglect stems from an over-emphasis on highly obvious fossil pollen changes of the mid-postglacial that are interpreted as a period when global mean temperature was about 1 C higher than today. At that time prairie vegetation expanded at the expense of forest. Radiocarbon dat-

TABLE 4. Comparison of prairie and savanna classifications in southern Lower Michigan.

Presettlement Vegetation Mapping (Comer et al. 1995)	Ordination of Prairies and Savannas (Chapman 1984)	Michigan Natural Features Inventory Plant Community Classification (Kost et al. 2007)
	Palustrine Prairie & Fen	
Wet prairie	Wet meadow	Southern wet meadow
	Fen	Prairie fen
	Lakeplain wet prairie	Lakeplain wet prairie, lakeplain wet-mesic prairie
	Wet prairie	Wet prairie, wet-mesic prairie, wet-mesic sand prairie
	Terrestrial Prairie	
Upland prairie	Mesic prairie	Mesic prairie
	Mesic sand prairie	Mesic sand prairie
	Oak openings (hillsides)	Hillside prairie
	Oak openings	Dry-mesic prairie
	Dry sand prairie/oak barrens	Dry sand prairie
	Terrestrial Savanna	
Mixed oak savanna	Bur oak plains	Bur oak plains
	Oak openings	Oak openings, lakeplain oak openings
Black oak barrens	Dry sand prairie/oak barrens	Oak barrens
	Not included	Oak-pine barrens, pine barrens

ing has placed the beginning of this prairie expansion at about 7,000 or 8,000 ybp in southeast Minnesota (Wright 1968) and northern and central Illinois (King 1981) and 6,000 ybp in southwest Michigan (Manny et al. 1978).

The palynological signal interpreted as prairie expansion consists of an increase in *Quercus* pollen, a decline in *Fagus* pollen, and an increase in forb and grass pollen. However, because most prairie and savanna forbs and also shrubs are insect pollinated, the fossil pollen record which depends to such a large extent on wind-pollinated species provides only a broad indication of the existence of prairie vegetation and no specificity as to type of prairie.

Curtis (1959) suggested that a portion of the dry prairie flora arrived at a different time than wet prairie, most likely from the southwest, whereas the wet prairie flora was thought to originate in the southeast. It seems possible to us that some form of dry sand prairie that included one or both species of *Ambrosia* (Appendix 1) may have been the earliest of Michigan's prairie communities, developing as soon as one or a few thousand years after the glaciers receded and persisting on highly drought-prone landscapes prior to the expansion of prairie in the mid-postglacial hypsithermal period.

The classification of prairie and savanna in our study is coarser than that of the Michigan Natural Features Inventory (MNFI)(Kost et al. 2007; Table 4) but finer than the presettlement vegetation types available digitally (Comer et al. 1995; Table 4). The greatest difference between our study and the MNFI classification is MNFI's recognition of a wet-mesic prairie community distinct from wet prairie (discussed above). Our study also combined prairie and savanna vegetation structure into a single prairie-savanna type for the dry-mesic oak openings type and the dry sand prairie/oak barrens type, whereas the MNFI classification separated these into a prairie and savanna segment on a vegetation continuum influenced by tree canopy shading. The ordination of our study did not include enough savanna stands (due to their rarity and poor quality) to separate prairie from savanna in the analysis. Yet historical data argue that prairie and savanna existed as distinct plant communities. It is the rarity of these types today which prevented a full analysis by ordination techniques.

Dry Sand Prairie/Oak Barrens

As mentioned, these historically distinct types were not separated in the ordination and are discussed together here. At a landscape scale, patches of dry sand prairie often intermingle with extensive oak barrens, although a century of fire suppression has resulted in much oak barrens succeeding to oak forest. The groundlayer and shrubs of dry sand prairie are largely indistinguishable from those of oak barrens, a savanna type supporting an open canopy of black oak (*Quercus velutina*), sometimes with scarlet oak (*Quercus coccinea*, including northern pin oak, *Q. ellipsoidalis*). Little and big bluestem (*Schizachyrium scoparium, Andropogon gerardii*) and Pennsylvania sedge (*Carex pensylvanica*) are dominant groundlayer plants. A close association of dry sand prairie and oak barrens occurs in the oak openings of northwestern Ohio (Anderson 1971).

Dry sand prairie/oak barrens is the most distinctive and cohesive of Michigan's extant prairie/savanna communities (Table 3). Stands share many species and the community has many indicators (Figure 6, Figure 7; Appendix 2). Thompson (1975) also noted that a greater proportion of dry sand prairie/oak barrens species were restricted to the type compared to other prairie/savanna communities.

Dry sand prairie/oak barrens resembles pine barrens (e.g., Houseman and Anderson 2002) and oak-pine barrens (Kost et al. 2007), all of which occur on extremely well-drained soils and possess vegetation that readily catches fire during drought. Dry sand prairie/oak barrens occurs primarily in southern Lower Michigan, while oak-pine barrens and pine barrens tend to occur farther north. Being farther north, the number of prairie species decreases and the abundance of Ericaceae, *Pinus*, and dry-site species such as *Comptonia peregrina* increases in oak-pine barrens and pine barrens.

The most intact dry sand prairie/oak barrens in Michigan are in Newaygo County (Figure 8; Hauser 1953; Chapman & Crispin 1984). Others were documented primarily in southwestern Michigan (Pokora 1970; Scharrer 1972; Schaddelee 1975; Thompson 1983; Chapman 1984). MNFI classifies some of these stands as oak-pine barrens.

The distinct nature and persistence of dry sand prairie and oak barrens may be due to soils and surficial geology. They usually occupy level sites and slopes of glacial outwash plains, sandy glacial lakebeds, and sand deposits in ice stagnation fields and coarse-textured end moraines. Good drainage and low site fertility together with the open architecture of the oak canopy prevent the development of deep shade. However, if fire or other disturbances are prevented, the tree canopy of oak barrens closes, though enough light may reach the ground flora

FIGURE 6. Hairy puccoon (*Lithospermum caroliniensis*) and lupine (*Lupinus perennis*) blooming around May 31 in the oak barrens of Allegan County. These plants often bloom with *Phlox pilosa* and *Asclepias tuberosa*, creating scenes spotted with yellow, blue, pink, and orange flowers. (Photo by Kim Chapman.)

FIGURE 7. Prairie smoke (*Geum triflorum*) is among the early blooming wildflowers in dry sand prairies. (Photo by Kim Chapman.)

FIGURE 8. Oak barrens in Newaygo County. The large trees are scarlet oak (*Quercus coccinea*, which includes northern pin oak) which resprouts from grubs if killed by fire or cutting. Oak brush is visible in the groundlayer. (Photo by Kim Chapman.)

for it to survive in a suppressed condition. The poor site conditions also exclude most Eurasian weeds that compete with native plant species in prairies and savannas. However, knapweed (*Centaurea maculosa*), sheep sorrel (*Rumex acetosella*), and hawkweeds (e.g., *Hieraceum aurantiacum*) can become abundant if soil is disturbed. If trees are removed or thinned by fire or cutting, the ground flora usually recovers quickly (Figure 9; Chapman et al. 1995). This makes dry sand prairie and oak barrens the most easily restored of Michigan's prairie and savanna types (Chapman et al. 1995).

Mesic Sand Prairie

Found typically on glacial outwash, sandy glacial lakeplains, and low sand dunes, the water table that supports mesic sand prairie's distinctive flora is near the soil surface in spring and late fall (Figure 10). Moist soil conditions in the spring and a drying period in mid- to late summer create a unique soil environment which allows dry sand prairie species (e.g., *Danthonia spicata, Helianthemum canadense*) to grow beside wet prairie species (e.g., *Equisetum arvense, Liatris spicata, Pycnanthemum virginianum*). Davis (1908) noted this juxtaposition of species from different soil moisture regimes in his description of mesic sand prairie and savanna on the sand ridges of Saginaw Bay. In northwestern Ohio's oak openings region, Anderson (1971) and Tryon and Easterly (1975) described a similar mesic sand prairie on the lakeplain. In Michigan this plant community is dominated most often by *Schizachyrium scoparium*, sedges (e.g., *Carex pensylvanica*), and *Andropogon gerardii*. When the soil is disturbed

FIGURE 9. Oak barrens in Allegan State Game Area, Allegan Co. A profuse bloom of *Lupinus perennis* in May, 1978, was stimulated by a prescribed burn in April. American columbo also emerged in large numbers after this fire. The fire killed the lower branches of the oaks, increasing the light reaching grasses and forbs beneath the oaks. (Photo by Kim Chapman.)

Agrostis gigantea and *Poa compressa* increase. Shrubs, especially members of Ericaceae, can form dense patches.

Curtis (1959) did not recognize a distinct mesic prairie on sand. Umbanhowar (1992) re-analyzed Curtis' data and found that several of the Wisconsin mesic prairie stands on sandy soils were, in fact, floristically distinct from mesic prairie on heavier soils. Likewise Faber-Langendoen and Maycock (1987) reported the existence of a mesic prairie type on sandy lakeplain soils in southern Ontario. White and Madany (1981) documented mesic sand prairie in Illinois, citing *Scleria triglomerata* and *Aletris farinosa* as indicators. Clearly mesic sand prairie is a distinct and recognizable midwestern plant community containing an assemblage of species found only on sandy soils with a seasonally high water table.

Oak Openings (Hillsides)

Hillsides create distinct microclimates. Steep westerly aspects above lakes and broad valleys afford groundlayer herbs more sunlight at mid-afternoon—the hottest part of the day—than they could receive on level ground. The direct afternoon sun raises ambient air temperature and increases evaporation rates. Curtis (1959) points out that such sites are free of snow earlier in the spring than elsewhere, extending the growing season for early-blooming forbs (e.g., *Hepatica americana, Houstonia longifolia, Besseya bullii*). The soils of Michigan's oak openings on hillsides are always sandy and underlain by glacial outwash, which promotes good soil drainage. Winds from the south and west blow directly at the

FIGURE 10. Mesic sand prairie in Petersburg State Game Area, Monroe County. The sandy soils and seasonally high water table enable plants of wet sites (*Liatris spicata, Solidago riddellii*) to grow with plants of dry sites (*Rudbeckia hirta, Schizachyrium scoparium*). (Photo by Kim Chapman.)

slopes unimpeded by topographic barriers, increasing plant transpiration. These factors intensify soil moisture loss in drought years (e.g., in 1936 and 1989), reducing the growth rates of woody plants. It is this combination of factors that enables plants normally growing in sunny, dry locations (e.g., *Bouteloua curtipendula, Penstemon hirsutus, Phlox pilosa, Solidago nemoralis, Stipa spartea*) to persist surrounded by closed-canopy forests. This unique setting of hillside prairies was recognized by Cole (1901) in the Grand Rapids region.

Oak openings on hillsides are more similar to oak openings on level ground than to other communities, but the surrounding forest strongly influences the flora. Over a dozen species of trees and shrubs frequently occur, and six of the indicators are trees, shrubs, and vines. Herbs of prairie settings persist under gaps in the tree canopy. *Andropogon gerardii, Schizachyrium scoparium, Stipa spartea*, and *Poa compressa* are prominent. *Bouteloua curtipendula* grows in low abundance but is an indicator. Soil erosion on the steep slopes may reduce competition in the understory and allow short-statured herbs to persist (*Houstonia longifolia, Hepatica americana, Phlox* spp., *Campanula rotundifolia*, *Besseya bullii*).

Oak openings on hillsides are small and isolated from each other. Island biogeography theory (MacArthur and Wilson 1967) suggests that small patches of plant communities far from other similar patches should experience high rates of species extinction and low rates of colonization. Indeed, patches of oak openings on hillsides have the lowest mean number of species per stand (49). This level of richness is the same as in the small hill prairies of Illinois (Evers 1955). Alternatively, the low number of species in Michigan and Illinois hill prairies may be due to the small size of vegetation patches, simply an expression of the species-area phenomenon (Gleason 1922b).

In 1980 the canopy of most stands of oak openings on hillsides was nearly closed, and a layer of understory woody plants grew under the oak trees. Lacking recent grazing, fire, or timber harvest, trees and shrubs cast a dense shade and reduced the cover by shade-intolerant dominant grasses. With the dominant grasses suppressed and competition for surface soil moisture reduced, tree seedling survival increases, setting the stage for further shade suppression. The persistence of grasses and dry-site prairie forbs may have always depended on human intervention. The rough topography and forested setting made it unlikely that, historically, fire could spread to the hillsides from the annually burned prairies and savannas on level ground. Considering their commanding views and exposure to cooling winds, some hilltops were probably Potawatomi campsites and lookouts and may have been burned to maintain open conditions. Today these locations are still preferred home sites. Some stands studied in 1980 have since been damaged or encroached on by home construction.

Oak Openings

More stands exist of oak openings than of any other prairie or savanna community. The oak openings stands that lack trees are now called prairies, but they were derived from the groundlayer of savanna, not treeless prairie. The term oak openings is used here, even for treeless stands, because the plant community probably resembles that of the historical oak openings, except that the shade-tolerant plants that once mingled with shade-intolerant plants in the original oak openings now are largely absent. Though these oak opening remnants are steadily declining, dozens are dotted across the 200-mile breadth of Michigan's Lower Peninsula. The 1830s oak openings formed a continuous belt of vegetation which became the cropland, developments, and closed-canopy forests that characterize southern Lower Michigan.

Three lines of evidence (floristics, soils, community characteristics) support the idea that present-day oak openings originated with the original oak openings vegetation.

Floristics. We envision white settlement in the 1830s setting in motion a successional process that divided the flora of the oak openings into two parts: shade-tolerant species of closed-canopy forests, and shade-intolerant species confined to treeless "prairies." These prairies have persisted at forest edges, in field corners, in cemeteries, on abandoned cropland, and in rights-of-way. The growth of underbrush and shading, which caused the floristic separation, took place in 20 years as noted by writers in Michigan at the time (e.g., Cooper 1848) and documented by Curtis (1959) in historical accounts from Wisconsin.

Daniels (1904) understood that the oak openings flora had become divided into shaded and sunny environments. His list of oak openings plants included species of closed-canopy oak forest (e.g., *Agrimonia gryposepala, Agrostis perennans, Amphicarpa bracteata, Anemonella thalictroides, Bromus pubescens,* *Desmodium glutinosum, Galium pilosum, Elymus hystrix, Sanguinaria canadensis, Scrophularia marilandica, Solidago flexicaulis, Trillium grandiflorum*) and of prairies and savannas (*Aster oolentangiensis, Comandra umbellata, Coreopsis tripteris, Elymus canadensis, Galium boreale, Hypoxis hirsuta, Lactuca canadensis, Monarda fistulosa, Phlox pilosa, Rosa carolina, Veronicastrum virginicum*). Some of Daniel's oak openings plants grow in both shaded and sunny locations (e.g., *Geranium maculatum, Hepatica americana, Podophyllum peltatum, Thalictrum dioicum*).

In Ohio's oak openings region Anderson (1971) also documented the presence of herbs that grew in both woods and prairies. Where Anderson (1971) worked, the woods were burned, the woody understory was kept in check, light levels were relatively high inside the woods, and consequently several species grew in both prairies and woods (*Baptisia tinctoria, Coreopsis tripteris, Lupinus perennis, Monarda fistulosa, Sisyrinchium albidum*). Winn and Kapp (1986) observed similar patterns of plant distribution in dry sand prairie and adjacent oak woodlands of west-central Michigan.

Curtis (1959) also documented the differential response of prairie species across a light gradient; some species (e.g., *Amphicarpa bracteata, Aster laevis, Cornus racemosa, Corylus americana, Helianthus strumosus*) were most frequent under the oak crowns where mid-day light levels were below 1,000 foot-candles; some (e.g., *Amorpha canescens, Andropogon gerardii, Helianthus laetiflorus, Schizachyrium scoparium, Stipa spartea*) most frequent between oak crowns or where a tree had died (10,000 foot-candles), and some (e.g., *Coreopsis palmata, Euphorbia corollata, Monarda fistulosa, Solidago ulmifolia*) most frequent in intermediate shade conditions.

Until the cessation of annual burning in the mid-1800s, both shade-tolerant and shade-intolerant plants of Michigan's oak openings grew within meters of each other under varying light conditions caused by different tree densities in the historical oak openings. After burning ceased, light grazing enabled the shade-intolerant plants to persist in woodlands, but when livestock were removed forest succession resumed. As forest succession converted the majority of the oak openings to forest, shade-intolerant plants tended to coalesce into what today are called prairies. There they survived as long as tree cutting, plowing, scraping, burning, or grazing continued at less than destructive intensities.

Soils. While soils of oak openings are generally dry-mesic, the soils are not like those of dry-mesic prairies elsewhere in the tallgrass prairie region. Wisconsin's dry-mesic prairies are on udic mollisols, true prairie soils (Curtis 1959), while Michigan's oak openings occur on udic alfisols, or forest soils. Alfisols have less organic matter in the A horizon, have accumulated irons and other metals in the B horizon due to leaching, and have lower pH than mollisols of typical dry-mesic prairie. These soil characteristics are indicative of long-term forest occupancy, not treeless prairie.

Community Characteristics. Oak openings was the least homogeneous plant community studied, had a single indicator, and shared the most species with other communities. The lack of homogeneity may be related to the large geographic range of this community compared to other prairie communities; however, oak barrens spans an equally large range, but is more homogeneous. An alternative explanation is that oak openings comprised the extensive matrix in which the other prairie types with their specialized requirements were embedded. The common species of oak openings were those having a wide geographical distribution, broad ecological amplitude, and good dispersal abilities (vagility). Daniels had observed early in the 20th century the spread of oak openings plant species into the unused portions of the landscape: fencelines, hedgerows, pastures, forest edges, and roadsides.

> The flora of the oak openings is gradually becoming general to the whole upland region. Groves have been planted or encouraged to grow even in the prairie district, and the hardy autumn vegetation springs up in fence corners, and survives in some fashion the frequent pasturings (Daniels 1904).

Many oak openings species also grow in other prairie/savanna communities, colonize disturbed ground, and persist despite continuing disturbance (e.g., *Achillea millefolia, Anemone cylindrica, Asclepias tuberosa, Aster laevis, Aster oolentangiensis, Aster pilosus, Erigeron strigosus, Euphorbia corollata, Lespedeza capitata, Rudbeckia hirta, Solidago nemoralis, Solidago speciosa*). The total effect is a lack of distinctness in the oak openings community.

The large number of trees and shrubs in the oak openings of this study (Appendix 1) also supports the idea that modern oak openings is derived from historical oak openings. Davis (1904) listed thirty-five species of trees, shrubs, and vines as characteristic of oak openings and Curtis (1959) noted the large number of shrubs in his oak openings type compared to prairies.

Oak openings of this study had fewer graminoid species compared to other communities, but this may be due to the loss of shade-tolerant grasses from oak openings stands. The groundlayer of current oak openings is dominated by *Andropogon gerardii, Schizachyrium scoparium*, forbs, and in some stands *Poa pratensis*. By contrast Daniels (1904) said that the groundcover of oak openings included several sedge species and woodland grasses (*Agrostis perennans, Bromus ciliatus, B. latiglumis, B. pubescens, Elymus canadensis, E. striatus, E. virginicus, Festuca nutans, Hystrix patula, Muhlenbergia schreberi, M. sylvatica, M. tenuifolia, Panicum latifolium*).

Vegetation Change. Our imperfect understanding of oak openings has prevented scientists and conservationists from fully understanding how to restore and manage it. The central question of restoration and management hinges on how changes in canopy closure influence changes in the shrub and groundlayer, and vice versa.

All evidence suggests that oak openings were diverse structurally and hence floristically. Soil moisture and texture played a role in the distribution of oak openings plants, but we believe that more significant variation in flora depended on the amount of tree canopy as demonstrated in a study of the grassland-savanna-forest gradient in central Minnesota (Chapman and Reich 2007). Where it was sparse, oak openings probably looked like prairie and where it was dense it resembled modern dry oak woodland. Different herbs and the height and extent of the shrub layer waxed and waned depending on the time since the last fire, the severity of the fire, cycles of wet and dry weather, and herbivory.

Curtis used 50% tree canopy cover to separate forest from savanna, but this dividing line was admittedly arbitrary (Curtis 1959: 92). Early writers described Michigan oak openings as varying from scattered trees to nearly closed canopies (Chapman 1984). Estimates of tree density in vegetation identified as oak openings ranged from 10 to 120 trees/ha (4.4 to 49 trees/ac) (Beal 1904; Wing 1937; Gordon and May 1959). Using GLO data from Kalamazoo Co., Brewer and Kitler (1989) concluded that bur oak savannas had tree densities mostly in the range from about 2 to 24 trees/ha (about 1 to 10 trees/ac); mean density was 7.2/ha (just under 3/ac). What canopy cover these densities yield depends strongly on crown sizes. Crown size ("maximum crown area") is tightly correlated with trunk diameter at breast height (dbh) in open-grown oaks and hickories, according to Law et al. (1994). Based on this relationship, 50% canopy cover for trees of 61cm (24in) dbh is provided by 33–34 trees/ha (12–13 trees/ac). Fifty percent canopy cover for trees of 30.5 cm (12in) dbh—more more closely representative of white and bur oaks in the Original Land Survey data for Kalamazoo County—requires about 111 trees/ha (45 trees/ac). In sum, we can conclude little more than that presettlement oak savannas showed broad, interrelated variations in tree density, tree diameter, and canopy cover.

The dynamics of canopy closure and re-opening revolve around a central question. In a fire-maintained system how do grasses and trees co-exist? Over thousands of years the trees should be killed and fail to perpetuate themselves because frequent fire prevents tree seedling establishment.

To answer this question for South African savannas, Higgins et al. (2000) created a model based on tree life history traits—especially resprouting capacity and stem growth rates—and empirical data on fuel loading and seedling establishment. Adult trees died at a low, constant rate; establishment episodes to offset this loss occurred infrequently. Drought during the growing season was the main limitation for seedling establishment. The simulations highlighted the role of what the authors (following Bond and van Wilgen 1996) called "gullivers" and Americans call "grubs." Storage of reproduction as grubs in the African study proved to be essential to the persistence of trees in savannas. When the storage term was omitted from the model, the population growth rate of trees was zero or negative. The last factor in the model is fuel loading. On dry sites, dead grasses and other plants that provide fuel accumulate slowly and fires are less frequent. Here grubs can escape fire and enter the canopy more often, but fires are catastrophic when they occur, killing many trees. On moist sites, fuel loading is high, and fires can be ignited annually, consuming all woody material over time except trees with fire-resistant bark. (The lack of downed woody material in Michigan's oak openings and bur oak plains was often noted in early accounts.) If grubs are present in moist savanna, they resprout but reach the canopy only in rare periods of higher rainfall or continuous grazing when fire is excluded. The African model showed fluctuations in both grub and tree densities over time in all moisture regimes, but the fluctuations were mild in moister savannas and large and erratic in dry savannas.

Michigan's savannas correspond well to this model. Moist savanna (i.e., bur

FIGURE 11. Bur oak owes its fire tolerance in part to corky wings on the branches, as well as a thick bark on the trunk. (Photo by Richard Brewer.)

oak plains) involved a long-lived, slow-growing, thick-barked tree that survived the intense annual fires caused by rapid accumulation of fuel (Figure 11); tree seedling establishment occurred in wet climatic episodes or perhaps when dense herds of grazers reduced fuel loading. Bur oak plains may also have contained black and white oak brush at the time of settlement (Brewer and Kitler 1989). Dry savannas (i.e., oak barrens) consisted of shorter-lived, faster-growing, thinner-barked trees (e.g., black oak, northern pin oak, scarlet oak) that were top-killed by less frequent but catastrophic fires occurring during drought; these red-oak group trees have excellent resprouting capacity and rapidly grew to large trees between catastrophic fires. (Life history traits of oaks are summarized in Fowells 1965.) Oak openings, dry-mesic in soil moisture, were dominated by white oak which is intermediate in fire susceptibility between bur oak and the red oak group (Curtis 1959). Here, intermediate fuel loading allowed the possibility of annual but less intense fires than in bur oak plains, sufficient to top-kill saplings of the red oak group that were present.

Fuel loading and fire intensity were affected by setting: dry savannas tended to occur on infertile, dry, sandy, level sites such as outwash plains and channels, and sandy lakes plains. Moist savannas occupied level, moist, rich sites, such as the edges of Prairie Ronde. Oak openings were found on rolling and steep topography with better drainage than bur oak plains and more fertile soils than oak barrens.

A good store of grubs is essential to perpetuating the canopy in the African model. As we have seen, oak grubs were widely reported as present in Michigan's oak openings and other savannas. White settlers remembered for the rest of their lives the effort required to dig the huge root masses out of their fields (Chapman 1984). Glidden (1892) implied that oak grubs grew at a density of 395/ha (160/ac).

Historical accounts widely reported that frequent burning of savannas kept oak grubs in a constant state of resprouting. When the frequent fires ceased, the oak grubs rapidly grew to saplings and eventually trees within 20 years of fire cessation (e.g., Cooper 1848; Curtis 1959). Locations where all trees were top-killed by catastrophic fire were called "brush prairie" or "brush savanna" (Curtis 1959). In Michigan these are represented by level, dry sites such as the Oxford Plains in Oakland County (Drake 1872) and portions of the Allegan and Newaygo Sand Plains, and also by level, moist sites where the city of Kalamazoo was founded (Turner 1911).

> There is quite an idea that this village site [Kalamazoo] was a grassy plain with scattering bur oaks; but it was a plain covered with a thick and tall hazel brush, so thick that I have seen a wolf jump up so as to see what caused the row he heard; and the burr oaks were very small, little more than grubs (Turner 1911).

In most savanna situations, fire is an essential element in perpetuating the tree-herbaceous mixture (Higgins et al. 2000; Daly et al. 2000). As we have seen, storage (in the sense of Warner and Chesson [1985]) of tree layer species as grubs is crucial for the continuing survival of the tree component. The other side of the savanna paradox is how, after a period in which the absence of fire has produced continuous shade, grasses and forbs manage to return when fire again becomes prevalent. We suggest that storage is also a major element in this process.

The appearance or reappearance of long-unnoticed prairie/savanna forbs and grasses following fire or tree thinning in forested sites has been frequently reported by restorationists. Although the soil seed bank is one obvious possible source, studies that have evaluated the seed bank suggest that its potential contribution is low (Kline and McClintock 1994; Rosburg et al. 1994). Still, the findings of Stritch (1990) and Rosburg et al. (1994) show that a few prairie and, especially, savanna species may have at least limited representation in the soil seed bank. For most species, however, storage is evidently in the form of underground plant parts. Close inspection of the forest floor in former prairie or savanna sites reveals various species represented by small, often flowerless above-ground plants which retain sizable roots or underground stems (McCarty and Hassien 1986). After the reintroduction of fire, these may be transformed into large, vigorously flowering specimens (Stritch 1990). Probably some individual plants are completely cryptic, with no above-ground parts.

Even in the absence of fire, the death of individual oak trees or branches can contribute to the persistence of shade-intolerant species by opening gaps where these species may expand or possibly colonize. Such holes in the canopy result from ice storms, windthrow, tornados, fungal disease, and in the past passenger pigeon nesting and roosting.

The distribution and abundance of shade-tolerant and shade-intolerant species likely varied at the same location over time. Herbs and shrubs varied in vigor when light levels changed due to disturbance or lack of it, but may have per-

FIGURE 12. Basal rosettes of American columbo, *Frasera caroliniensis*, a long-lived perennial that blooms once when conditions are favorable, then dies. This life history trait and others adapt it well to the temporally and spatially varying tree canopy cover of the oak savanna ecosystem. (Photo by Richard Brewer.)

sisted at some locations for centuries (Figure 12). Shade-tolerant species are favored on north-facing slopes which receive no direct sun and are less likely to burn due to cool, moist conditions and light fuel loads. Conversely, shade-intolerant species are likely to be present on the sunnier slopes where more sunlight reaches the ground, creating warm, dry conditions and making such sites more liable to carry fire.

Different disturbances in different physiographic settings probably created a great variety of vegetational structure in the oak openings setting. Included were areas of widely spaced oak trees, sometimes with crowns nearly touching, but allowing much light to reach the ground due to openness of oak branches; prairie islands and oak groves of many sizes spotted through the savanna matrix; and brush savannas of resprouting oaks, shrubs, and grasses. Herbaceous plants would be distributed based on their light requirements. But the pattern of the landscape would also vary in time, based on types, severity, and recentness of disturbance. Today the small size of oak openings does not allow scientists to understand fully the structural and floristic dynamics of the original oak openings as created by landscape-scale fires.

Mesic Prairie

In the 1830s Michigan's upland prairie was nearly all mesic prairie which is today the rarest prairie type (Figure 13). Several mesic prairies documented by

FIGURE 13. Thompson Road Prairie, Howard Twp., Cass Co., in 1970 before right-of-way maintenance switched from burning to bulldozing and herbiciding. In the 1970s this site supported the richest collection of mesic prairie species in Michigan, and may still do so since the remnant persists. (Photo by Richard Brewer.)

Scharrer (1971) were destroyed when Amtrak and ConRail upgraded their lines in the 1970s and 1980s (Kohring 1981).

Mesic prairie is a distinctive type, with 25 indicator plants (Figure 13). *Andropogon gerardii*, *Schizachyrium scoparium*, and a variety of forbs dominated mesic prairies and *Spartina pectinata* may be abundant in depressions of these otherwise level sites. Michigan's mesic prairies were intermediate in soil conditions among prairie types, and possess nearly the same pH and water retaining capacity as Wisconsin mesic prairie (Curtis 1959). The neutral and moist soil conditions allowed species that grow in wet or dry locations to co-occur. Species frequent in wet prairies (*Silphium terebinthinaceum, Solidago altissima, Spartina pectinata, Thalictrum dasycarpum, Veronicastrum virginicum, Zizia aurea*) grew with species of drier sites (*Helianthus occidentalis, Lithospermum canescens, Solidago rigida*).

One feature involved in determining the set of species that constitutes mesic prairie was discussed by Brewer (Figure 14; 1985). The height of plants in flower increases progressively through the year. Plants flowering in the April 5–June 14 period averaged 0.75m in height; in June 15–July 31 they averaged 2.3m; and August 1–October 20 they averaged 3.7m in height. The species that fit this height-flowering season pattern are the characteristic members of the mesic prairie flora. Consider a species that flowers at short stature in mid-summer. If insect pollinated, it would be unsuccessful because its flowers are less noticeable to insects. If wind-pollinated, pollen exchange would be limited because the flowers are submerged in the calm air within taller foliage.

FIGURE 14. Spring 1963 view of Oshtemo Fruit Belt Prairie, Kalamazoo County, studied by R. Brewer. Articles (1984, 1985) in *The Michigan Botanist* refer to the roadbed (center of photo), the slope (left side of photo), and ridgetop (the flat strip not visible left of slope). This site supported mesic and dry-mesic prairie plant communities. (Photo by Richard Brewer.)

Origins. In forested regions such as Michigan, drought, wildfire, and location contributed to the origin and persistence of prairie. The existence of historical and extant mesic prairies (and the now vanished bur oak plains) has been attributed to their occurrence on level outwash plains (Robinson 1969). Documented historical wildfires are associated with drought conditions (Curtis 1959; Pyne 1982). After the Wisconsinan glaciers retreated from southern Michigan beginning 13,500 years ago, several warmer periods interspersed with cooler periods occurred in Michigan and adjacent states around 10,000 ybp, 7,000 ybp, 4,500 ybp, and 900 ybp (King 1981; Smith and O'Shea 2002). In these warmer periods the dominant vegetation shifted from fire-intolerant species (e.g., spruce, fir, hardwood forest) to fire-tolerant species (e.g., pine, oak, grasses). Beginning around 10,000 ybp American Indians facilitated this conversion by their use of fire, a practice that continued until European settlement. During warming periods, drought-induced catastrophic wildfire, assisted by Indian-set fires, is likely to have destroyed forests and created grasslands and savannas.

The well-drained gravel and sand deposits of outwash plains experience soil moisture loss during drought to a greater degree than glacial till regions in southern Michigan (Robinson 1969). The level surface of outwash plains and lack of natural fire breaks would also allow fires to spread over the entire surface and reach surrounding forests. Thus outwash plains, drought, and fire together may be responsible for the creation and persistence of prairie in Michigan despite the present-day moist climate that favors forest over prairie (Robinson 1969).

Why did some outwash plains become treeless prairie and some bur oak plains? Both historical prairie locations and bur oak plains today support hardwood forests containing maple and other mesophytic species. One possibility proposed by Curtis (1959) is that treeless prairies were created by catastrophic wildfire where mesophytic forest species dominated and oaks were absent. Conversely, where bur oak was present in mesophytic forests, catastrophic wildfire resulted in a savanna containing bur oaks. Dry-site oaks (*Q. velutina, Q. coccinea*) were probably absent from the mesophytic forests while others (*Q. alba, Q. rubra*) could not survive the subsequent high intensity fires occurring on these level sites.

Following this concept, Prairie Ronde, Michigan's largest prairie, originated when mesic forest was destroyed by catastrophic fire. Indeed, the west side of Prairie Ronde is adjacent to a large area of beech-maple forest (Hodler et al. 1981; Brewer et al. 1984). By contrast, the east side of Prairie Ronde is adjacent to an oak savanna region (Hodler et al. 1981; Brewer et al. 1984), with bur oak savanna located closest to the prairie. In this scenario, catastrophic wildfire at the east side of Prairie Ronde affected forests containing oaks, resulting in oak savanna rather than treeless prairie. Catastrophic wildfire in another, westward section of the mesic forest (the future Prairie Ronde) led to treeless prairie. Later wildfires within Prairie Ronde, ignited annually by Indians and facilitated by the level surface of the outwash plain, contributed to the persistence of the treeless prairie, the bur oak plains, and probably also the oak openings to the east. These later fires, propelled by westerly winds, would have eaten into the beech-maple forest west of Prairie Ronde only slowly or not at all.

Jones (2000) documented savanna creation from forest on Manitoulin Island, Ontario. Bur oak savanna was created following a catastrophic 1865 wildfire in a maple-basswood-red oak-ironwood forest. That fire was exacerbated by extensive blow-downs of the shade-tolerant hardwood trees due to their shallow rooting on thin soils over bedrock. It seems possible that some combination of blowdown and fire could have been important in conversion of mesic forest to bur oak plain or mesic prairie in southern Michigan. Windthrow is a frequent occurrence on flat till areas of heavy soil (Brewer and Merritt 1978) as well as thin outwash overlying till.

Historical Versus Extant Mesic Prairie. Some of Michigan's historical mesic prairies occurred on udic mollisols, true grassland soils with a deep, dark, organic-rich upper horizon formed under grass (U.S. Soil Survey 1960). Veatch (1927) recognized that Michigan's historical prairie soils resembled those found in the prairie regions of Illinois. Prairies on udic mollisols disappeared because they were excellent agricultural land. However, Michigan's extant mesic prairies are on udic alfisols, forest soils with a brown upper soil horizon that formed under forest cover (U.S. Soil Survey 1960).

We believe that Michigan's extant mesic prairies studied here derived from the shade-intolerant segment of the bur oak plains flora. This may explain why Michigan's extant mesic prairies share few indicator species with Wisconsin's mesic prairies (Curtis 1959; Chapman 1984). Instead, Michigan's extant mesic prairies are most like Wisconsin's oak openings plant community. However, they are distinct from Michigan's oak openings community, which occurs on dry-mesic, coarse-textured soils and rolling topography, and was usually dominated by white oak, not bur oak. Michigan's extant mesic prairies also contain a large number of woody plant species and herbs (e.g., *Cacalia atriplicifolia, Frasera caroliniensis*) that are strongly associated with woodland and oak forests (Voss 1996).

Today's mesic prairies were probably created when railroads were built in bur oak plains between 1838 and 1850 and before grazing and farming destroyed the groundlayer of the adjacent bur oak openings. Trees were cleared from the rights-of-way during railroad construction, and afterwards fires were ignited by locomotive sparks and (as recently as the 1950s) by maintenance crews, killing woody plants. These disturbances enabled groundlayer herbs, grasses and sedges to colonize from the increasingly shaded adjacent bur oak plains communities, and over decades the frequent fires preserved the shade-intolerant groundlayer herbs, grasses and sedges in the rights-of-way. Meanwhile forest succession eliminated the shade-intolerant flora from bur oak openings, and agriculture destroyed all vestiges of nearby prairie vegetation. Only in cemeteries from the early settlement period (e.g., Harrison Cemetery near Schoolcraft in Prairie Ronde, Figure 2) can the original mesic prairies of Michigan be found today.

Wet Prairie

Michigan's wet prairies represent a segment in a complex environmental-floristic gradient that includes wet meadows and fens. The indicator species of Michigan's wet prairie, and importance of *Calamagrostis canadensis* and sedges, suggest it is more like Wisconsin sedge-dominated wet meadows than grass-dominated wet prairies (Curtis 1959; Brewer 1965). Wet prairie in Michigan is found on mineral soil and has indicator species that are absent or uncommon in sedge-dominated wet meadows (Figure 15). Michigan's wet prairies support prairie grasses (*Spartina pectinata, Sorghastrum nutans, Andropogon gerardii, Schizachyrium scoparium*) which vary in abundance depending on elevation above flood level. *Calamagrostis* and sedges (*Carex bebbii, C. stricta*) are important in wet prairie, but not to the exclusion of other grasses.

Indians reported that beaver created extensive wet prairies on the flat glacial lakebeds of southeastern Michigan (Hubbard 1838), suggesting that flooding was important in wet prairie creation and persistence. Curtis (1959) also noted that wet prairies were frequently flooded. Today wet prairie is found chiefly along streams, rivers, and lakeshores, which are difficult to drain and use, and less commonly in upland depressions of outwash plains, which are easier to modify for agricultural use.

Relation to Wet Meadow and Fen. Past researchers (Pepoon 1907; Gleason 1917; Kron 1982) did not agree on definitions of wet prairie, wet meadow (or sedge meadow), and fen (or prairie fen) in southern Lower Michigan. Kost et al. (2007) provide technical guidance for distinguishing these three distinctive plant communities.

Wet meadows in southern Lower Michigan have neutral water chemistry like wet prairie, but unlike wet prairie they occur on organic soil as fens do. Wet meadows are dominated by *Calamagrostis* and sedges and lack the prairie

FIGURE 15. *Anemone canadensis* is one of the first wildflowers to bloom in Michigan's wet prairies. (Photo by Kim Chapman.)

grasses found in wet prairies. Fens in southern Lower Michigan, Illinois, and southern Wisconsin occur on muck soils saturated by alkaline groundwater and are dominated by prairie grasses, other grasses, and sedges in varying proportions (Curtis 1959; White & Madany 1981; Chapman 1984).

Curtis (1959) proposed that a large portion of the wet prairie flora originated in the southeastern United States and arrived in our region at a different time than the dry prairie flora. In this scenario, Michigan's wet prairies should be more similar to wet meadows of New York state than wet prairies of Wisconsin, which they appear to be.

Gleason (1917) studied a fen six miles north of Ann Arbor that he called wet prairie for its similarity to northern Illinois wet prairie. The fen was level, had few shrubs, was dominated by grasses, and supported species Gleason learned while studying at the University of Illinois (e.g., *Andropogon gerardii, Helianthus grosseserratus, Lilium philadephicum, Oxypolis rigidior, Phlox pilosa, Silphium terebinthinaceum, Sorghastrum nutans, Sporobolus heterolepis*). However, the Ann Arbor site was on Houghton muck, a typical fen soil, while wet prairie in Michigan and elsewhere is on mineral soil. Illinois and Wisconsin wet prairies are more alkaline than Michigan's wet prairies, and support calciphiles restricted to fens in southern Lower Michigan (e.g., *Cypripedium candidum, Gentiana procera, Muhlenbergia mexicana, Solidago ohioensis*). Other species in Gleason's prairie are restricted to fens and bogs in southern Michigan (*Parnassia glauca, Potentilla fruticosa, Sarracenia purpurea, Tofieldia glutinosa*).

Curtis noted that fen appeared to be a hybrid of plant communities, and Gleason's "wet prairie" exemplifies this. Besides the calciphiles and fen/bog plants mentioned above, species of southern Michigan bogs (*Betula pumila, Rhamnus alnifolia, Sarracenia purpurea, Solidago uliginosa, Toxicodendron vernix*) and alkaline moist Great Lakes shorelines (*Cladium mariscoides, Carex sterilis, Lobelia kalmii, Muhlenbergia glomerata, Parnassia glauca, Rhynchospora capillacea, Solidago ohioensis, Viola cucullata, Zigadenus glauca*) regularly occur in southern Michigan's fens (Chapman 1984). Some fen plants (*Cirsium muticum, Liatris spicata*) also grow in lakeplain wet prairies.

Vegetation Conversion to Reed Canary Grass. When annual burning ceased, Michigan's wet prairies persisted longer than upland prairies. They were cut for hay, which minimally affected original species abundance and diversity while discouraging invasion by trees and shrubs.

Agricultural practices are known to alter wet prairie (Curtis 1959). The main alteration was due to invasion and replacement of wet prairie plants by reed canary grass (*Phalaris arundinacea*). Although it is considered a native plant, Eurasian strains introduced for agriculture may exist in Michigan (Voss 1972); they were bred to improve early- and late-season forage production, which may increase invasive qualities and ability to displace native plants (Apfelbaum & Sams 1987; Merigliano & Lesica 1998). Grazing facilitated this conversion: Curtis (1959) observed replacement of wet prairie by reed canary grass, Kentucky bluegrass (*Poa pratensis*), and redtop (*Agrostis gigantea*) within three years after the introduction of grazing.

Farmers also dug ditches and installed drain tiles in wet prairies to lower the water table. Such drainage allowed earlier mowing for hay and minimized the risk of farm equipment becoming mired. Kercher et al. (2004) concluded that reed canary grass invasion of wet meadows is accelerated by disruption of hydrology. Michigan's wet prairies also experience increased flooding and drying in agricultural regions. Upland cropland produces surface runoff which floods wet prairies more frequently than before cultivation, but between storms the soil of wet prairies becomes drier due to drainage and diminished groundwater recharge in surrounding cropland. Drainage also stimulates the growth of woody plants (Curtis 1959). When wet prairies of Michigan and nearby states were drained, they were rapidly colonized by willows, aspen, and other woody plants (Davis 1908; Rogers 1966; Anderson 1971).

Lastly, runoff from cropland and urban areas carries sediment (to which phosphorus is attached) and nitrogen (from fertilizers and manure spread on fields). Inputs of sediment, phophorus, and nitrogen encourage the growth of reed canary grass (Perry et al. 2004).

As long as haying occurred, shrubs and trees did not invade these water-starved wet prairies of southern Michigan. After 1950, however, haying largely ceased and forest succession progressed rapidly. Where grazing was practiced, forest succession was delayed, but eventually prairie grasses and forbs were eliminated by reed canary grass invasion.

Lakeplain Wet Prairie

This prairie type has a limited continental range but is easily recognized by its unique combination of species and setting on glacial lake plains, often with mesic sand prairie (Hayes 1964; White and Madany 1981; Chapman 1984). A large area of Michigan's lakeplain wet prairie remained intact in 1900 in Bay and Tuscola Counties, 70 years after the upland prairies were first broken (Figure 16). These last large wet prairies were nearly destroyed in 1880–1910 by immense steam dredges deployed to create farmland out of marshes and wet prairies near Saginaw Bay.

> Among the great enterprises originating in Bay county, is one not known anywhere else in the whole State, of the same kind, known as the Miller and Daglish reclamation of the Saginaw marshes, located partly in Bay and Saginaw counties. This is one of Judge Albert Miller's pets, and consists in the drainage by dredging with a steam dredge around some 1,000 acres of marsh, much of which was under water, making the land fully susceptible of raising grain or grass, and all this was done at much less cost than to clear any timber land, leaving the land completely cleared without stumps. The land is kept clear of water by a small steam engine run at occasional times, at very small cost (Partridge 1881).

The prairies of Saginaw Bay and their destruction were documented by Davis (1898, 1908). Other lakeplain wet prairies were studied by Anderson (1971) and Tryon and Easterly (1975) in Ohio, or noted by settlers and surveyors in southeastern Michigan (Anderson 1819; Hubbard 1838; Farmer 1848; Farmer 1890; Everett 1959). Foerste (1882) found several species of lakeplain wet prairie on the banks of Belle Isle in the Detroit River, including *Platanthera leucophaea*, a federally-endangered orchid (Figure 17). At the time, excursionists gathered the orchids for wildflower bouquets.

FIGURE 16. *Solidago ohiensis* in a lakeplain wet-mesic prairie, Huron County. This plant grows in Great Lakes interdunal wetlands, prairie fens, and prairies where soil pH is also alkaline; several other lakeplain prairie species have a similar distribution in Michigan. Michigan's lakeplain prairies preserve the expansive vistas once seen in upland prairies such as Prairie Ronde in Kalamazoo County. (Photo by Kim Chapman.)

FIGURE 17. *Platanthera leucophaea*, the state and federal endangered prairie white fringed orchid, is an indicator of lakeplain wet-mesic prairie, growing here with *Iris virginica* in Bay County. (Photo by Kim Chapman.)

The dominant plants of lakeplain wet prairie are *Calamagrostis canadensis, Carex aquatilis, C. lanuginosa*, along with lesser amounts of *Andropogon gerardii, Schizachyrium scoparium, Panicum virgatum, Sorghastrum nutans*, and *Spartina pectinata*. Faber-Langendoen and Maycock (1987) described a similar community on Walpole Island, Canada. Their prairie classification at this location also included wet-mesic prairie. Wet-mesic prairie probably exists on Michigan's lakeplains at the lower slopes of sand ridges and on broad flats between wet and mesic sites. Faber-Langendoen and Maycock's wet-mesic prairie contains indicators (Appendix 2) of both mesic sand prairie (e.g., *Quercus palustris, Lobelia spicata, Equisetum arvense, Muhlenbergia mexicana, Krigia biflora*) and of lakeplain wet prairie (e.g., *Liatris spicata, Aster dumosus, Prenanthes racemosa, Asclepias incarnata, Stachys tenuifolia, Potentilla anserina*).

Dolomitic limestone, limestone bedrock, and gravel derived from these materials dominate much of the Great Lake's shoreline of Lower Michigan or are present in submerged reefs. Over the past 10,000 years this material has been ground to sand by waves and ice and this sand forms much of the shore and dune sand of Lakes Michigan, Huron, and Erie where lakeplain wet prairie is found. The high calcium and magnesium carbonate content of this lake sand elevates the soil pH along coasts and on lakeplains (Voss 1972). Calcareous soils are not present on sand ridges of the lakeplain (where mesic sand prairie occurs) because precipitation has leached the carbonates from the organic-poor sands of the ridges. The alkaline soil and proximity to the shoreline also facilitates colonization of lakeplain wet prairie by species of interdunal wetlands and calcareous fens (e.g., *Carex buxbaumii, Solidago ohioensis, Hypericum kalmii, Potentilla fruticosa*).

CONSERVATION APPLICATIONS

Michigan's prairies and savannas are a diverse, distinctive, and unique element in the continental expanse of tallgrass prairie and savanna. Given the loss of 99.9% of approximately 930,000 ha (2.23 million ac) of Michigan prairie and savanna, every remnant should be preserved and expanded.

The rarity of oak savanna is remarkable because it once defined the character of much of southern Lower Michigan. It is endangered not just in Michigan but throughout eastern North America (Nuzzo 1986; Noss 1995). It should be the priority of every natural resource professional, public land manager, and environmental policy-maker to identify large expanses of potential savanna and begin restoring an open oak canopy and understory. Chances for success will be highest in the historical oak savanna regions where prairie and savanna indicator plants are seen at edges of oak forests. Oak savanna restoration would benefit not just plants, but several declining bird species that preferentially use brushland and open woodland (e.g., Yellow-shafted Flicker, Golden-winged Warbler, Brown Thrasher, Yellow-breasted Chat, Red-headed Woodpecker, Eastern Kingbird, and perhaps Black-billed Cuckoo) (Chapman and Reich 2007). Other wildlife would benefit, including the majority of southern Michigan's butterfly species which need abundant flowering plants and partial shade in the growing season, a condition to be found in high quality oak savanna.

Our understanding of Michigan's prairies and savannas leads us to conclude that landscape scale restoration is needed. Savanna was the landscape matrix in which prairie and other southern Michigan communities were embedded. The dynamics of canopy closure and re-opening depended in large part on landscape scale fire interacting with site factors and long climatic trends, especially drought. Out of this dynamic emerged local variation in plant and animal species distribution and abundance as modified by microsite factors of soil, water table, slope, and aspect. Catastrophic disturbance created both prairie and savanna, and frequent disturbance maintained them in a region where climate favored forest over grassland and savanna. We also must remember that large continuous forests penetrated and surrounded Michigan's savanna landscapes, and still do. These forests were also cleared for agriculture, grazed, and now experience fragmentation due to development. Southern Lower Michigan's large forest remnants support animal species which decline as forests are reduced in size and isolated from one another. Clearly important forest locations must be considered when selecting sites for savanna restoration.

Oak savanna restoration must begin with larger management units than are customary in southern Michigan: 40–160 acres and larger should be the starting size. The approach and outcomes described by Stritch (1990) and Chapman et al. (1995) provide technical guidance. Reducing woody plant dominance is the most important goal in savanna restoration, and fire is the most cost-effective and ecologically appropriate tool to achieve this goal.

There is much resistance to using fire in Michigan's forests. It is considered unnatural, harmful to forest development, and problematic due to technical difficulties and a lack of experience. Our research provides ample evidence that, in fact, removing fire from Michigan's landscape has altered in a brief period the landscape that persisted over southern Lower Michigan for thousands of years and varied only at local scales of distribution and abundance in response to climate and disturbance. Ironically a preservationist mentality in Michigan's conservation community has perpetuated the negative impact of European settlement on savanna and prairie. If Michigan's conservation community wishes to have prairies and savannas, it should be open to the destruction of certain forest canopies, aware of the role that oak resprouts play in Michigan's ecology, and dedicated to frequent burning of fire-adapted communities—every year initially, then perhaps every other year once tree canopy cover falls below 50%. Eventually large savanna landscapes will be created which would, we believe, resist invasion by light-seeded early-successional trees (e.g., green ash, box-elder, elm) and non-native invasive shrubs (e.g., Tatarian honeysuckle) due to their widespread suppression by fire, and contain a range of tree canopy cover and light conditions which could support the potential species diversity of Michigan's savanna regions. There is considerable evidence that disturbance, rather than lack of disturbance, tends to maintain ecological stability and diversity over time (Pickett and White 1985). This is especially true of fire-adapted communities like prairie and savanna.

Reintroducing fire over large areas in southern Michigan will have unknown outcomes at a detailed level but at a broad level outcomes are generally known. Fire across large areas will result in greater heterogeneity of vegetation patches and a greater variety of plant and animal life compared to that found in small savanna and prairie remnants. The long time scale of savanna vegetation dynamics is encouraging: 170 years of fire suppression may not be too long to recover many features and ecological processes of savanna in southern Lower Michigan. The best candidates for restoration are large public lands to which can be added large private conservation lands in former oak openings and prairie regions. Marginal cropland on poor soils and abandoned hay meadows and pastures in savanna regions sometimes are colonized by prairie and savanna plants. These are good candidates for restoration if also adjacent to oak forest which was formerly savanna.

We support recent state and federal efforts toward restoring warm-season grasses and savanna in Michigan. Wherever possible, however, we encourage a gradual aproach that draws upon available biodiversity stores, such as existing patches containing appropriate prairie/savanna herbs, as well as seed banks and other cryptic stores that may be brought to light by fire. More drastic efforts, such as plowing and planting, should not be pursued until a thorough biological inventory has demonstrated an absence of existing appropriate flora. Adaptive management principles are clearly needed: goals for outcomes are checked against actual outcomes measured in restoration areas, and changes in management practices are implemented if the goals are not being achieved (e.g., Nyberg 1999).

An alternative to restoring savanna with fire on public forestland is to plant prairie on cropland, then plant oak seedlings in the established prairie. Since most cropland is privately owned, it would need to be purchased. Non-tiled, non-irrigated cropland in southern Lower Michigan is priced at $2000–$4000 per acre (Wittenberg and Harsh 2006). A one-time prairie planting would cost $1500–$5000 per acre, followed by 2–3 years of weed management (mowing and herbiciding) at $1500–$3500 /acre/year. Thereafter prescribed burning could be employed at a cost of $500–$1000/acre/year. Planting is best done on poorer soils because of the large number of aggressive agricultural weeds adapted to heavy soils. By contrast, restoration on public forestland would entail one-time costs of preparing a site for a prescribed burn (e.g., installing fire breaks) and carrying out the burning ($500–$1000/acre/year). Once established, oak seedlings could be planted at a cost of $300–$1000/acre depending on seedling size. A significant challenge in this approach is how to protect the oak seedlings while managing the prairie with fire or other means. In short, the public forestland restoration choice is cheaper and would give faster results than planting cropland with prairie and oak seedlings.

Michigan's distinct combination of extensive savanna with embedded upland and wet prairies differs from the prairie-savanna conditions of states farther west. Large-scale conservation of Michigan's prairies and savannas will preserve a unique ecological landscape and re-create an interesting and beautiful setting for scientific study and the enjoyment of Michigan's citizenry.

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APPENDIX 1. Presence (%) of species in Michigan prairie and savanna plant communities. Species with >50% presence or high indicator ranking are reported. For a full species list see Chapman (1984).

	DSPB[1]	MSP	OOH	OO	MP	WP	LWP
Species							
Achillea millefolium var. occidentalis		100		69	75		60
Agrostis hyemalis		50					
Aletris farinosa		67					
Allium canadense						83	60
Ambrosia artemisiifolia	67						
Ambrosia psilostachya	50						
Amorpha canescens				<50			
Amphicarpa bracteata						50	
Andropogon gerardii	83	83	67	92	100	50	100
Anemone canadensis						50	60
Anemone cylindrica	67	67	83	92	75		
Anemone virginiana						83	
Angelica atropurpurea						50	
Antennaria parlinii	83	50	67	69	50		
Apios americana						100	
Apocynum androsaemifolium	67	83			75	67	
Apocynum cannabinum	50					50	100
Arabis glabra	50						
Arabis lyrata	50						
Aristida purpurascens	50						
Artemisia campestris	83						
Asclepias amplexicaulis	50						
Asclepias incarnata							60
Asclepias sullivantii							60
Asclepias syriaca	67			54	50	67	60
Asclepias tuberosa	83	83	50	100	75		
Asclepias verticillata	67						
Aster dumosus							80
Aster ericoides		50					100
Aster laevis		50		85	75	50	
Aster lanceolatus						67	
Aster novae-angliae						100	80
Aster oolentangiensis	83	50	50	69	50		
Aster pilosus				69			
Baptisia lactea					<50		
Baptisia tinctoria		50					
Besseya bullii			50				
Blephilia ciliata	50						
Bouteloua curtipendula			<50				
Bromus ciliatus						50	
Cacalia atriplicifolia					50		
Calamagrostis canadensis						83	100
Calystegia sepium						50	80
Campanula rotundifolia			67				
Carex bebbii						67	
Carex bicknellii					50		
Carex buxbaumii							60
Carex pensylvanica	100	50	50	54			
Carex stricta						50	
Carya glabra			67				

APPENDIX 1. Continued.

	DSPB[1]	MSP	OOH	OO	MP	WP	LWP
Ceanothus americanus	100		67	69	100		
Cicuta maculata						83	60
Cirsium discolor							60
Cirsium muticum							60
Comandra richardsiana	67	50	83	77	75	50	100
Coreopsis palmata					75		
Coreopsis tripteris	50	100	50		100	50	
Cornus florida			50				
Cyperus filiculmis	100						
Dalea purpureum					<50		
Danthonia spicata	83	67					
Desmodium canadense		83		54		83	80
Desmodium canescens					<50		
Desmodium illinoense				54	50		
Desmodium marilandicum	50			62			
Desmodium sessilifolium				<50	<50		
Dioscorea villosa					75		
Echinacea purpurea					<50		
Eleocharis elliptica							100
Equisetum arvense		67				67	60
Equisetum hyemale							
Equisetum laevigatum		67			50		
Erigeron annuus					50		
Erigeron philadelphicus							80
Erigeron strigosus	67	67		85	50		
Eryngium yuccifolium					50		
Eupatorium maculatum						67	
Euphorbia corollata	100	67	67	92	75		
Euthamia graminifolia		83			75	100	60
Fragaria virginiana	100	100		85	75	83	100
Frasera caroliniensis					50		
Galium boreale			67		100	83	
Galium pilosum	50				50		
Galium trifidum							80
Gentiana alba					50		
Gentiana andrewsii						100	60
Geranium maculatum					75	50	
Gnaphalium obtusifolium	67						
Hedeoma pulegioides				<50	<50		
Helianthemum canadense	83	50			50		
Helianthus divaricatus	50		67		50		
Helianthus giganteus						83	
Helianthus occidentalis	67			69	75		
Helianthus pauciflorus					<50		
Helianthus strumosus					75		
Heliopsis helianthoides					<50		
Hepatica americana			<50				
Heuchera americana var. hirsuticaulis		50			75		
Hieraceum gronovii	67						
Hieraceum longipilum	100			54			
Houstonia longifolia			<50				
Hypoxis hirsuta						50	
Iris virginica						67	60
Juncus balticus							100
Juncus tenuis		67					

APPENDIX 1. Continued.

	DSPB[1]	MSP	OOH	OO	MP	WP	LWP
Juniperus virginiana			67				
Krigia biflora		50					
Krigia virginica	67						
Kuhnia eupatorioides					50		
Lactuca canadensis	100	50		77	100		
Lathyrus palustris						50	80
Lechea villosa		50					
Leersia oryzoides							
Lespedeza capitata	67	83	50	77	75		
Lespedeza hirta	50		50		75		
Liatris aspera	83						
Liatris cylindracea	50						
Liatris spicata		67					100
Linaria canadensis	50						
Lithospermum canescens				54	75		
Lithospermum caroliniense	67						
Lobelia spicata		50					
Lupinus perennis	83						
Luzula multiflora		50			75		
Lycopus americanus						50	80
Lysimachia ciliata						50	
Lysimachia quadriflora							100
Lythrum alatum							60
Monarda fistulosa	67	83	50	77	75	83	80
Monarda punctata	67						
Muhlenbergia mexicana						50	
Oenothera clelandii	50						
Onoclea sensibilis						50	
Oxypolis rigidior						100	
Panicum commonsianum	50						
Panicum depauperatum	50						
Panicum leibergii					<50		
Panicum oligosanthes	83				75		
Panicum virgatum							100
Penstemon hirsutus	50		67				
Phlox bifida			<50				
Phlox pilosa	50	50	67		75		
Phlox subulata			<50				
Pinus strobus			50				
Platanthera leucophaea							60
Polygala polygama	67						
Polygala sanguinea		83					
Polygonatum biflorum	50						
Polygonatum pubescens	50						
Populus grandidentata			50				
Potentilla anserina							60
Potentilla arguta				<50	<50		
Potentilla simplex		67		54	50		
Prenanthes racemosa							80
Prunus serotina			50				
Prunus virginiana	50						
Pteridium aquilinum		67	67		50		
Pycnanthemum virginianum		83				83	80
Quercus alba			83				
Quercus rubra			50				

APPENDIX 1. Continued.

	DSPB[1]	MSP	OOH	OO	MP	WP	LWP
Quercus velutina			100				
Ranunculus fascicularis	50				75		
Ratibida pinnata				69	75	83	
Rhus copallina	<50						
Rhus typhina			50				
Rosa carolina	50		50	77	100		
Rosa palustris							60
Rudbeckia hirta	83	83	67	85	75	50	60
Ruellia humilus					<50		
Salix humilis		67		62	100		
Sassafras albidum			50				
Schizachyrium scoparius	100	100	67	85	100		80
Scirpus validus							60
Scleria triglomerata		50					
Senecio plattensis	50						
Silphium integrifolium					50		
Silphium laciniatum					<50		
Silphium terebinthinaceum					50	67	
Smilacina racemosa			67	54	75		
Smilacina stellata						50	
Solidago altissima					50	83	100
Solidago gigantea						50	
Solidago juncea	83	67		69			
Solidago nemoralis	100	67	67	85	50		80
Solidago ohioensis							100
Solidago riddellii						67	
Solidago rigida		50		54	100	50	
Solidago speciosa	67			62	50		
Sorghastrum nutans	50	67		54	100	67	100
Spartina pectinata					50	83	100
Specularia perfoliata	67						
Spiraea alba		67					
Sporobolus heterolepis					<50		
Stachys tenuifolia							100
Stipa avenacea	<50						
Stipa spartea			67				
Taenidia integerrima					75		
Tephrosia virginiana	50						
Thalictrum dasycarpum					100	100	
Thelypteris palustris						100	
Tradescantia ohiensis	83		67	77	100		
Trichostema dichotomum	<50						
Verbena stricta					75		
Vernonia missurica							80
Veronicastrum virginicum		50			100	83	60
Vicia americana					50		
Viola pedata	50		50				
Viola pedatifida					<50		
Viola sagittata		67					
Viola sororia					50		
Vitis aestivalis			83				
Ziza aurea					75	67	60

[1]DSPB = Dry sand prairie/barrens; MSP = Mesic sand prairie; OOH = Oak openings on hillsides; OO = Oak openings; MP = Mesic prairie; WP = Wet prairie; LWP = Lakeplain wet prairie

APPENDIX 2. Predictive levels of indicator species in Michigan prairie and savanna plant communities (see Methods, p. 9).

High	Medium-High	Medium	Medium-Low	Low
DRY SAND PRAIRIE & OAK BARRENS				
Artemisia caudata	Ambrosia psilostachya	Polytrichum piliferum	Cyperus filiculmis	Ambrosia artemisiifolia
	Arabis glabra	Rhus copallina	Liatris aspera	Asclepias amplexicaulis
	Arabis lyrata	Stipa avenacea	Lupinus perennis	Hieraceum gronovii
	Asclepias verticillata	Trichostema dichotomum		Liatris cylindracea
	Blephilia ciliata			Lithospermum caroliniensis
	Cladonia spp.			Monarda punctata
	Gnaphalium obtusifolium			Panicum depauperatum
	Krigia virginica			Polygala polygama
	Linaria canadensis			Polygonatum biflorum
	Oenothera rhombipetala			Prunus virginiana
	Panicum commonsianum			Senecio plattensis
	Polygonatum pubescens			Tephrosia virginiana
	Specularia perfoliata			
MESIC SAND PRAIRIE				
	Baptisia tinctoria	Polytrichum juniperinum	Agrostis hyemalis	Acer rubrum
	Juncus tenuis	Solidago rugosa	Aster ericoides	Aletris farinosa
	Lechea villosa		Krigia biflora	Equisetum arvense
	Polygala sanguinea		Lobelia spicata	Liatris spicata
	Spriraea alba		Populus tremuloides	Quercus palustris
			Pycnanthemum virginianum	Scleria triglomerata
				Viola sagittata
OAK OPENINGS (HILLSIDES)[1]				
Vitis aestivalis	Besseya bullii	Amelanchier arborea	Quercus rubra	
	Campanula rotundifolia	Bouteloua curtipendula		
	Cornus florida	Hepatica americana		
	Pinus strobus	Houstonia longifolia		
	Populus grandidentata	Phlox bifida		
	Stipa spartea	Phlox subulata		
OAK OPENINGS[2]				
	Aster pilosus			
MESIC PRAIRIE				
Helianthus strumosus	Gentiana flavida	Viola pedatifida	Coreopsis palmata	Cacalia atriplicifolia
	Frasera caroliniensis		Dioscorea villosa	Erigeron annuus
	Vicia americana		Geranium maculatum	Eryngium yuccifolium

MESIC PRAIRIE (continued)				
	Viola sororia		Poa pratensis	Kuhnia eupatorioides
			Rhus glabra	Quercus macrocarpa
			Taenidia integerrima	Rubus hispidus
			Thalictrum dasycarpum	Silphium integrifolium
			Verbena stricta	Silphium terebinthinaceum
			Zizia aurea	Solidago altissima
				Spartina pectinata
WET PRAIRIE				
Apios americana	Amphicarpa bracteata		Anemone virginiana	Eupatorium maculatum
Oxypolis rigidior	Angelica atropurpurea		Galium boreale	Onoclea sensibilis
Saxifraga pensylvanica	Aster simplex		Helianthus giganteus	
Thelypteris palustris	Bromus ciliatus		Ratibida pinnata	
	Carex bebbii		Thalictrum dasycarpum	
	Hypoxis hirsuta			
	Lysimachia ciliata			
	Muhlenbergia mexicana			
	Phalaris arundinacea			
	Salix interior			
	Smilacina stellata			
	Solidago gigantea			
	Solidago riddellii			
LAKEPLAIN WET PRAIRIE				
Aster dumosus	Asclepias incarnata		Andropogon scoparius	
Eleocharis elliptica	Asclepias sullivantii		Aster ericoides	
Galium trifidum	Carex buxbaumii		Erigeron philadelphicus	
Lysimachia quadriflora	Cirsium muticum		Liatris spicata	
Populus deltoides	Fraxinus pensylvanica		Panicum virgatum	
Prenanthes racemosa	Lythrum alatum		Poa compressa	
Solidago ohioensis	Platanthera leucophaea		Solidago nemoralis	
Stachys tenuifolia	Potentilla anserina			
Vernonia missurica	Rosa palustris			
	Scirpus validus			

"[1]Comandra richardsiana, Penstemon hirsutus, and Quercus alba reached maximum presence in Oak Openings (Hillsides) but occurred in <50% of stands of this plant community."

"[2]Amorpha canescens, Anemone cylindrica, Asclepias tuberosa, Aster laevis, and Erigeron strigosus reached maximum presence in Oak Openings but occurred in <50% of stands of this plant community."