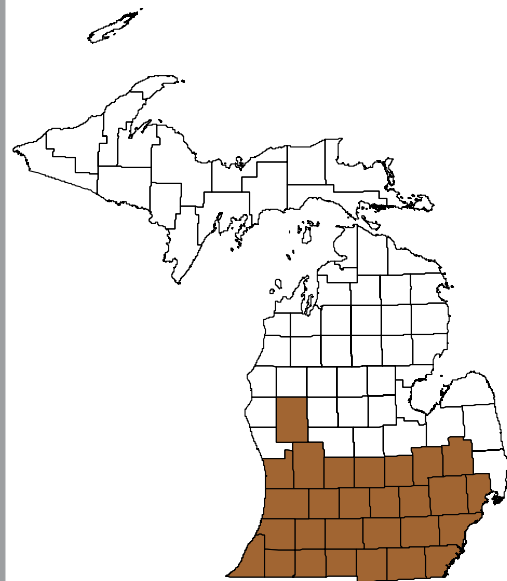




Photo by Joshua G. Cohen

Historical Distribution



Overview: Oak openings is a fire-dependent, savanna type dominated by oaks, having between 10 and 60% canopy, with or without a shrub layer. The predominantly graminoid ground layer is composed of species associated with both prairie and forest communities. Oak openings are found on dry-mesic loams and occur typically on level to rolling topography of outwash and coarse-textured end moraines. Oak openings have been nearly extirpated from Michigan; only one small example remains.

Global and State Rank: G1/S1

Range: Oak savanna¹ and prairie communities reached their maximum coverage in Michigan approximately 4,000-6,000 years ago, when post-glacial climatic conditions were comparatively warm and dry. During this time, xerothermic conditions allowed for the invasion of fire-dependent, xeric vegetation types into a large portion of the Lower Peninsula and into sections of the Upper Peninsula. With the subsequent shift of more mesic climatic conditions southward and the decimation of indigenous populations who maintained high levels of fire disturbance, there has been a recolonization of mesic vegetation throughout Michigan. The distribution of fire-dominated communities has been reduced to isolated patches, typically concentrated south of the climatic tension zone. In the 1800s, oak openings were located in the south-central Lower Peninsula of Michigan on sandy glacial outwash and coarse-textured moraines (Wing 1937, Comer et al. 1995, NatureServe 2004). Oak openings occurred within the range of bur oak plains and oak barrens, with oak openings dominating more on dry-mesic to mesic soils,

bur oak plains occupying more mesic, flat sites in the southwestern part of the Lower Peninsula, and oak barrens thriving on droughty sites. These similar oak savanna types often graded into each other. Oak openings were historically documented in the following counties: Allegan, Barry, Berrien, Branch, Calhoun, Cass, Clinton, Eaton, Genesee, Hillsdale, Ingham, Ionia, Jackson, Kalamazoo, Kent, Lapeer, Lenawee, Livingston, Macomb, Montcalm, Monroe, Newaygo, Oakland, Ottawa, Shiawassee, St. Joseph, Van Buren, Washtenaw, and Wayne (Chapman 1984, Comer et al. 1995). General Land Office surveyors' notes indicate that high concentrations of oak openings occurred in Calhoun County (20% or 75,570 ha), Jackson County (9% or 33,919 ha), Van Buren County (9% or 33,349 ha), Kalamazoo County (9% or 32,253 ha), Cass County (8% or 30,498 ha), and St. Joseph County (8% or 29,839 ha) (Comer et al. 1995). Presently only one known occurrence of oak openings has been documented in Michigan (Ionia County). Degraded remnants may exist within the original range. In addition to southern Michigan, oak openings occurred in upper midwestern United States and Canada, with its range including southern Ontario and western New York (NatureServe 2004).

Rank Justification: Circa 1800, oak savanna communities covered some 11-13 million ha (27-32 million ac) of the Midwest. Presently oak savanna remnants occur on just 0.02% of their circa 1800 extent (Nuzzo 1986). The notes of the original land surveyors of Michigan reveal that in the 1800s, oak openings covered approximately 375,359 ha (927,512 ac) or just under 2.5% of the state, distributed primarily in the south-central portion of the Lower Peninsula (Comer et al. 1995). Today only

¹Throughout this abstract *oak savanna* will be used as a general term referring to open-canopy oak communities.



five occurrences of this globally imperiled community remain, one of 1.2 ha (3 ac) in Ionia County, Michigan and four in New York, totaling 47 ha (115 ac) in Monroe and Erie Counties (NatureServe 2004). If degraded oak opening remnants do persist elsewhere in the former range, extensive rehabilitative management efforts would be required for restoration (Bronny 1989).

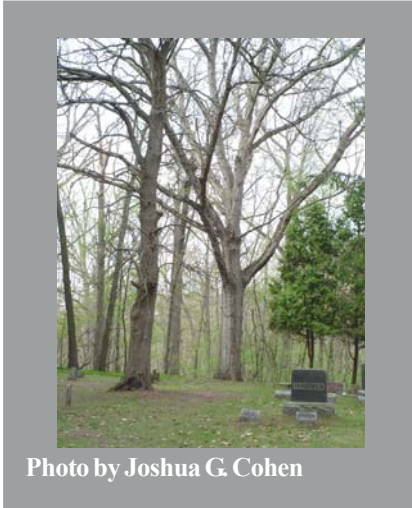


Photo by Joshua G. Cohen

Many cemeteries were established on former oak savanna. Michigan's sole oak opening occurs on the slope adjacent to this Ionia County cemetery.

Following European settlement of prairies, settlement and conversion to agriculture of oak openings and other savanna types rapidly followed (Veatch 1927, Kenoyer 1930). Many towns, college campuses, parks, and cemeteries of the Midwest were established on former oak savanna (Chapman 1984, Packard 1988, Bronny 1989, Hutchinson 1994). Early settlers of Michigan also utilized oak openings for pasture and exploited them for fuel and timber supplies (Stout 1946, Bronny 1989, Hutchinson 1994). Alteration of historic fire regimes has shifted most oak savannas into woodlands and forest (Cottam 1949, Curtis 1959, Faber-Langendoen 1993). The decrease in Native American populations across the Midwest in the 1700s-1800s likely resulted in a decrease in fire frequency. Wildfire suppression policies instituted in the 1920s in concert with road construction, expansion of towns, and increased agriculture caused a dramatic decrease in fire frequency and intensity (Abrams 1992). The reduction of fire in the landscape resulted in the succession of open oak savanna to closed-canopy forests with little advanced regeneration of oaks and a vanishing graminoid component (Chapman et al. 1995). With the absence of fire, oak savannas converted to closed canopy forest within decades (estimates range from 25 to 40 years) (Stout 1946, Curtis 1959) with more mesic savannas, such as bur oak plains, deteriorating more rapidly (Apfelbaum and Haney 1991, Abrams 1992, Packard 1993, McPherson 1997). The rapid conversion to oak forest occurred because of the prevalence in the understory of oak grubs, which are repeatedly

fire-suppressed oaks with huge root masses that allowed them to achieve canopy ascension following release from annual fires (Cottam 1949, Chapman 1984, Kline 1997a, Bowles and McBride 1998). Frequently these oak grubs were *Quercus velutina* (black oaks), which became canopy co-dominants with the advent of fire suppression.

Oak savanna remnants are often depauperate in floristic diversity as the result of fire suppression and subsequent woody encroachment, livestock grazing, and the invasion of exotic species. Sustained grazing introduced soil disturbance, prevented oak establishment, and caused decreases in native forbs and grasses with increases in weeds (native and exotic) (Bray 1960, McPherson 1997, Jones 2000). Due to their high edge-to-area ratio, savannas were susceptible to exotic species invasion by such aggressive shrubs as buckthorns and honeysuckles (Apfelbaum and Haney 1991), which create dense shade that depresses or eliminates graminoid species that provide fine fuels for ground fires (Anderson and Bowles 1999). Groundlayer vegetation of savanna remnants has been inhibited by low levels of light filtering through the dense overstories and impenetrable understories (often dominated by exotic shrubs) and by the thick litter layers that have accumulated from over a century of fire suppression (Bowles and McBride 1998, Abella et al. 2001).

Landscape and Abiotic Context: Oak openings occurred primarily on level to rolling topography of glacial outwash plains and coarse-textured end moraines. Oak openings were also found on steep slopes of ice-contact features (Chapman 1984, Albert 1995, NatureServe 2004, Kost et al. 2007). In general, oak savannas were most prevalent on the western side of major firebreaks such as rivers (Grimm 1984, Leitner et al. 1991). Soils of oak openings were well-drained, moderately fertile, sandy loams or loams with slightly acid to neutral pH (6.1-7.3) and low water retaining capacity (Chapman 1984, NatureServe 2004, Kost et al. 2007). Oak openings occurred adjacent to more mesic communities, such as bur oak plains, mesic prairie, and wet-mesic prairie (Brewer et al. 1984, Chapman 1984) and also likely graded into oak barrens, a drier savanna type, as well as dry-mesic southern forest and dry southern forest. Historically, oak openings occurred in a complex, shifting mosaic with these and other plant communities that depended on frequent fire.

Oak openings were distributed across Michigan's Region I, Southern Lower Michigan (Albert et al. 1986). This region has a warm, temperate, rainy-to-cool, snow-forest climate with hot summers and no dry season. The daily maximum temperature in July ranges from 29° to 32° C (85° to 90° F), and the daily minimum temperature in January ranges from -9° to -4° C (15° to 25° F). The number of freeze-free days is between 120 and 220, and the average number of days per year with snow cover of 2.5 cm or more is between 10 and 60. The mean annual total precipitation for Region I is 820 mm (Albert et al. 1986, Barnes 1991).



Natural Processes: Cottam (1949) and Curtis (1959) suggested that oak savannas originated when prairie fires spread into surrounding closed oak forest with enough intensity to create open canopy conditions (also see Anderson and Brown 1986, Anderson and Bowles 1999). Other researchers have proposed that savannas also originated following invasion of prairie by oaks during prolonged lulls in annual fire regimes (Grimm 1984, Anderson and Bowles 1999). Repeated low-intensity fires working in concert with drought and windthrow then maintained these savannas (Stout 1946, Curtis 1959, Faber-Langendoen and Tester 1993). Within dry-mesic savanna systems, such as oak openings, it is likely that annual or nearly annual fire disturbance was the primary abiotic factor influencing savanna structure and composition. Fires prevented canopy closure and the dominance of woody vegetation (Leitner et al. 1991). Presently, the prevalent catalyst of fires is lightning strike, but historically, Native Americans played an integral role in the fire regime, accidentally and/or intentionally setting fire to prairie and savanna ecosystems (Day 1953, Chapman 1984, Grimm 1984, Dorney and Dorney 1989, Bowles and McBride 1998, Anderson and Bowles 1999). Where large-scale herbivores (i.e., elk and bison) were abundant, grazing may have helped inhibit the succession of oak savanna to woodland (McClain et al. 1993, Ritchie et al. 1998).

The character of oak savannas can differ dramatically, primarily as the result of varying fire intensity and frequency, which are influenced by climatic conditions, soil texture, topography, size of physiographic and vegetative units, and landscape context (i.e., proximity to water bodies and fire-resistant and fire-conducting plant communities) (Grimm 1984, Bowles et al. 1994, Chapman et al. 1995, Anderson and Bowles 1999). Historically, fire regimes were also influenced by the number and distribution of indigenous peoples (Chapman 1984). Infrequent, high-intensity fires kill mature oaks and produce savannas covered by abundant scrubby oak sprouts. Park-like openings with widely spaced trees and an open graminoid/forb understory are maintained by frequent, low-intensity fires, which occur often enough to restrict maturation of oak seedlings and encroachment by other woody species (Chapman et al. 1995, Faber-Langendoen and Davis 1995, Peterson and Reich 2001).

Oak openings are thought to have fallen within the more open end of this physiognomic spectrum. Oak openings were found primarily on level to undulating topography, a landscape in which fires spread rapidly, evenly, and frequently (Grimm 1984). However, fires were probably less frequent in oak openings compared to bur oak plains, which occurred in more uniformly level landscape positions. In addition, the rich mesic soils of bur oak plains supported high coverage of grasses and forbs. Fertility affected the structure of these savanna types by influencing pyrogenicity of vegetation; vigorous growth of grasses resulted in heavy fuel loading (Anderson 1991b, Rebertus and Burns 1997, NatureServe 2004). As grass

coverage increased, so too did fire frequency. Compared to bur oak plains, oak openings dominated by white oak occurred on less fertile soils with less graminoid coverage and subsequently less fire disturbance. The frequent fire regimes of these systems explains the canopy dominance of bur oak and white oak, which are the most fire resistant of the oaks with their deep roots, capacity to resprout, and thick, insulating bark that prevents girdling by surface fires (Tester 1989, Faber-Langendoen and Davis 1995, Kline 1997a). Isolated canopy oaks within these savannas seldom burn because of low fuel loads beneath their crowns, which shade out light-demanding vegetation. In addition, winds sweep away oak leaves from beneath the crowns, and isolated trees may divert wind so that fires tend to move around the trees (Anderson and Brown 1983, 1986).

Oak savanna and prairie fires occur during the spring, late summer, and fall. Flammability peaks bimodally in the spring before grass and forb growth resumes and in the late summer and autumn after the above-ground biomass dies (Grimm 1984). Many savanna and prairie species are highly pyrogenic in that they produce more biomass than can be decomposed. Each year these perennials die back to enlarged subterranean organs, exposing only dead, desiccated material with their buds remaining protected beneath the soil. The excess herbage of slowly decomposing graminoids such as bluestems (*Andropogon gerardii* and *Schizachyrium scoparium*) annually provides fuels for frequent low-intensity fires (Anderson 1991a, Rebertus and Burns 1991, Homoya 1994, Pauly 1997). These fires increase nutrient and light availability and bolster forb and graminoid diversity by stimulating germination, flowering, growth, and seed production while deterring woody vegetation (Tester 1989, Botts et al. 1994, Packard and Mutel 1997). While spring burns damage living portions of woody plants, summer fires are typically more detrimental to shrubs and trees than dormant-season burns (White 1983, Anderson 1997). Growing-season fires are more damaging to woody species because they occur after energy and inorganic nutrient reserves have been invested into the leaves. In general, increased fire frequency results in decreased canopy cover, basal area, and density of woody stems (White 1983, Anderson and Brown 1986, Faber-Langendoen and Davis 1995, Pauly 1997). Because annual fires also limit oak establishment (Faber-Langendoen and Davis 1995), recruitment of oak seedlings to sapling and overstory classes requires a fire-free interval of several years (Apfelbaum and Haney 1991, Leach and Ross 1995, Pruka and Faber-Langendoen 1995). Oak seedlings establish in canopy gaps in which their survival has been found to be inversely related to grass or fuel cover (Rebertus and Burns 1997). The absence of fire in oak savannas causes increased litter layer and fuel loads, decreased herb layer diversity, increased canopy and subcanopy cover, invasion of fire-intolerant species (often non-native shrubs), and ultimately,



the formation of a closed-canopy oak community, often within 20–40 years (Curtis 1959, Chapman et al. 1995, Faber-Langendoen and Davis 1995, Tester 1996, Abella et al. 2001).

Numerous biotic factors influence the patterning of vegetation of oak savannas. In addition to widely distributed overstory trees, savannas are characterized by scattered ant mounds. Mound building ants play a crucial role in the soil development of prairies and savannas; ants mix and aerate the soil as they build tunnels and bring nutrients and clay particles to the topsoil from the subsoil (Kline 1997a). As mentioned earlier, herbivores can limit woody establishment and encroachment, and grasses and forbs help maintain the frequent fire regime with their flammable properties. Open canopy conditions are also preserved by the development of a dense herbaceous litter which suspends tree propagules and interferes with the ability of radicles to reach the soil surface (McPherson 1997). The unique structure of oak savannas with scattered canopy trees creates a shifting mosaic of light and shade that contributes to the complex patterning of diverse vegetation (Anderson and Bowles 1999). Savanna trees influence vegetative composition by affecting the distribution of nutrients, light, and moisture. Isolated savanna trees have been referred to as islands of fertility: soil and nutrients accumulate beneath their canopies. In addition, savanna oaks provide critical roosting sites and shade for numerous animal species (Belksy and Canham 1994, McPherson 1997, Will-Wolf and Stearns 1999). Ellsworth and McComb (2003) hypothesize that the extinct passenger pigeon (*Ectopistes migratorius*) played a crucial role in creating and maintaining oak savanna dominated by white oak and bur oak. Roosting in savanna oaks and oak forest trees in the thousands, flocks may have helped perpetuate frequent fires by contributing a significant source of fine fuel with branch and twig breakage. In addition, pigeon preference for acorns of the red-oak group may have provided a competitive advantage for the more fire-tolerant white-oak species (bur oak and white oak) in savannas and oak forests. Floral composition and diversity of savannas was also historically influenced by herds of elk and bison which established sites for a wide array of plant species with wallows and trampled areas (Kline 1997a, Steuter 1997).

Vegetation Description: Oak openings, like many other oak savanna types of the Midwest, only remain in small, degraded remnants. As a result, little is known about the composition and vegetative patterning of these systems (Leach and Givnish 1999); too much of the fabric has been gone for too long to be sure of the whole pattern (Chapman 1984). Since only one example of this community type is known from Michigan, information in this section is derived from limited information from that site, historical accounts, early plant collections, and extrapolation based on examples from neighboring states.

The oak openings were described by Michigan settlers as park-like savanna of widely spaced mature oaks with a wide range of shrub cover above the forb and graminoid ground

layer (Stout 1946, Cottam 1949, Peters 1970, Chapman 1984). The broad-crowned, scattered oaks were typically of the same age cohort typically 10 to 60 feet apart, with diameter at breast height ranging widely between 10 and 80 inches (Lanman 1871). The canopy layer generally varied from 10 to 60% cover (NatureServe 2004) and was dominated by *Quercus alba* (white oak) with co-dominants including *Quercus macrocarpa* (bur oak), and *Quercus muehlenbergii* (chinkapin oak) (Lanman 1871, Beal 1904, Cottam 1949, Chapman 1984, NatureServe 2004). As noted earlier, white oak and bur oak with their thick bark, deep roots, and resprouting abilities are the most fire resistant of the oaks. In addition, expansive root systems that can extend down several meters and branch extensively laterally allow these oaks to withstand extreme drought stress (Albertson and Weaver 1945, Abrams 1992, Faber-Langendoen and Tester 1993). Both species of oak are long-lived, often remaining as canopy dominants for 200–300 years (Cottam 1949).



Photo by Joshua G. Cohen

Bur oak (pictured) and white oak are extremely fire-resistant. Both have thick, corky, insulating bark, deep roots, and the capacity to resprout after fire.

Important canopy associates included *Carya glabra* (pignut hickory), *Carya ovata* (shagbark hickory), *Quercus rubra* (red oak), and *Quercus velutina* (black oak) (NatureServe 2004). Oaks, especially black oak, were dispersed in the understory as fire-suppressed grubs which reached just over a meter tall (Peters 1970, Brewer and Kitler 1989, Bowles and McBride 1998, Anderson and Bowles 1999). Shrubs occurred scattered or clumped in the understory, ranging widely in cover from 0 to 50% depending on fire frequency (Pruka and Faber-Langendoen 1995). The most common shrubs were fire-tolerant species such as *Corylus americana* (American hazelnut), *Ceanothus americanus* (New Jersey tea), and *Amorpha canescens* (lead-plant, state special concern) (Veatch 1927, Cottam 1949, Bader 2001, NatureServe



2004). Shrubs such as *Cornus foemina* (gray dogwood), *Prunus americana* (wild plum), and *Rhus glabra* (smooth sumac) occasionally formed thickets in fire-protected microsites (Kline 1997a, Bader 2001, NatureServe2004). Oak openings were characterized by a discontinuous layer of trees and shrubs and a continuous herbaceous layer (Skarpe 1992). Typically, oak openings graded into prairie or bur oak plains on one edge and drier savanna or dry-mesic forest/dry forest on the other. According to Bray (1958) and Curtis (1959), the flora of savannas were a mixture of prairie and forest species, with prairie forbs and grasses more abundant in high light areas and forest forbs and woody species in the areas of low light (NatureServe 2004). Packard (1988) suggests that many of the species of oak savanna were in fact savanna specialists that thrived in the mottled light conditions provided by the scattered oak canopy. The ground layer of these systems was dominated by a diverse array of graminoids and forbs. Plant species richness in oak savanna remnants in Wisconsin ranged between 16 and 30 species per square meter (Leach 1994, Leach and Givnish 1999). High floral diversity was the result of extensive microsite heterogeneity associated with complex gradients in light intensity (partial canopy coverage created a shifting mosaic of light and shade), fire disturbance, and soil properties (i.e., fertility, moisture, and texture) (Leach and Givnish 1999, Foster and Tillman 2003).

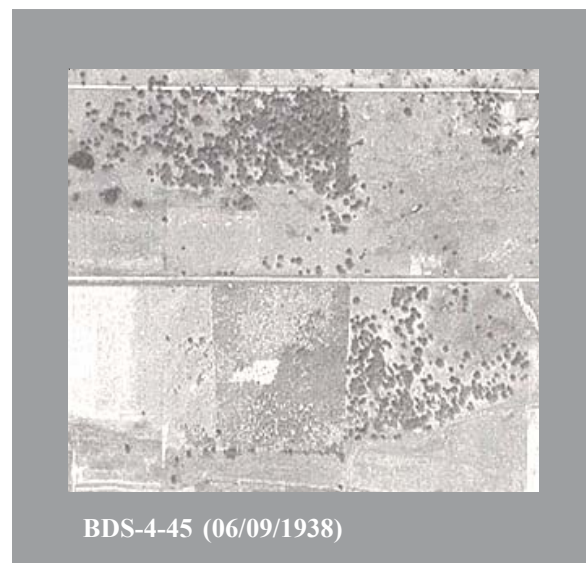
For a given oak savanna, the proportion of forbs to graminoids was likely a function of light availability and soil texture with graminoids increasing with sand and solar irradiance and forb coverage increasing with silt content and shade (Leach and Givnish 1999). Grasses, which provided the primary source of fine fuel for annual fires, reached heights of over a meter in areas of high light intensity (Anderson 1991a). Common grass species included *Andropogon gerardii* (big bluestem), *Schizachyrium scoparium* (little bluestem), and *Sorghastrum nutans* (Indian grass). Prevalent forbs included *Amphicarpaea bracteata* (hog peanut), *Anemone cylindrica* (thimbleweed), *Asclepias purpurascens* (purple milkweed, state special concern), *Asclepias tuberosa* (butterfly-weed), *Aster laevis* (smooth aster), *Aster pilosus* (frost aster), *Coreopsis palmata* (prairie coreopsis, state threatened), *Desmodium canadense* (showy tick-trefoil), *Eupatorium sessilifolium* (upland boneset, state threatened), *Erigeron strigosus* (daisy fleabane), *Euphorbia corollata* (flowering spurge), *Galium boreale* (northern bedstraw), *Gentiana flavida* (white gentian, state endangered), *Kuhnia eupatorioides* (false boneset, state special concern), *Lathyrus venosus* (veiny pea), *Lespedeza capitata* (bush-clover), *Lespedeza hirta* (bush-clover), *Monarda fistulosa* (wild-bergamot), *Pycnanthemum virginianum* (mountain mint), *Rudbeckia hirta* (black-eyed Susan), *Silene stellata* (starry campion, state threatened), *Solidago juncea* (early goldenrod), *Taenidia integerrima* (yellow pimpernel), *Triosteum perfoliatum* (horse-gentian, feverwort), *Veronicastrum virginicum* (Culver's root), and

Zizia aurea (golden alexanders). (List compiled from Curtis 1959, Bray 1960, Chapman 1984, Packard 1988, Leach and Ross 1995, Pruksa 1995, Bader 2001, NatureServe 2004.)

Vegetation of oak savannas has developed numerous adaptations for living in fire-prone, high-light, water-stressed environments. Such traits include heavy pubescence to deflect the sun and wind, leathery or waxy leaves to reduce water loss, and underground organs and ephemeral life cycles to survive frequent fire disturbance (Homoya 1994, Kline 1997a). The majority of herbaceous species found in oak savannas are perennials (Tester 1989): Leach and Givnish (1999) found 88% of ground cover savanna species to be of this fire-adapted (or tolerant) life form.

Following fire suppression much of the herbaceous diversity of savannas was lost as woody encroachment and eventual canopy closure created uniformly low-light conditions (Leach and Givnish 1999). Bowles and McBride (1998) found a positive association between light levels and species richness and a negative relationship between solar irradiance and alien species richness. Fire-suppressed savanna remnants, especially mesic systems, are often characterized by high levels of invasive exotics such as *Lonicera tatarica* (Tatarian honeysuckle), *Rhamnus cathartica* (common buckthorn), and *Alliaria petiolata* (garlic mustard) (Packard 1988, Apfelbaum and Haney 1991, Botts et al. 1994, Anderson and Bowles 1999).

Conservation and biodiversity management: As noted, oak openings have been nearly extirpated from Michigan,



Remnants of oak openings can be found by comparing the notes of original land surveyors and early aerial photographs. This photograph from Ionia County, taken in 1938, shows a promising site.



with only one remnant documented. The prime conservation priority for this globally imperiled community is to survey for restorable remnants.

Using the notes of the General Land Office surveyors and aerial photographs from the early twentieth century, researchers can locate areas with widely spaced, large-crowned oaks. Though more challenging to discern on site and today after decades of fire suppression, oak savanna remnants can often be recognized by the occurrence of scattered, large-diameter, open-grown oaks or “wolf trees,” which are now surrounded by a forest of younger trees (often black oaks of the same age cohort) with smaller crowns and diameters. Conservationists in search of oak openings remnants should be looking for scattered, 200-300-year-old, open-grown oaks greater than two feet in diameter. Because of the enhanced visibility through forested landscapes, leaf-off is the best time to search for the structural indicators of historical savanna. Once a suspected savanna remnant has been located, follow-up visits should occur through the course of the growing season to search for flora indicative of open light conditions. Plant species of oak savannas can persist through cycles of canopy closure and removal (Chapman et al. 1995). The occurrence of oak savanna indicator species in closed-canopy oak forests reveals the presence of a native seedbank and highlights that area as a potential target for restorative management. Numerous oak savanna researchers have compiled extensive lists of potential savanna indicator species from literature research and inventory of savanna remnants (Packard 1988, Pruka 1995, Packard and Ross 1997, Bader 2001).

As noted by Packard (1988), the existence of oak savanna depends on active restoration: this is especially true for oak openings. If remnants are located, the first management step will be the restoration of the oak savanna physiognomy. Where canopy closure has degraded the savanna character, one can selectively cut or girdle the majority of trees (White 1986), leaving between 10 and 60% canopy closure. Degraded savannas that have been long deprived of fire often contain a heavy overstory and understory component of shade-tolerant species that cannot initially be controlled by prescribed fire but can be removed by mechanical thinning (Abella et al. 2001, Peterson and Reich 2001). Many of the shade-tolerant shrubs in the understory of oak savanna remnants are invasive exotic species that require intensive management to eliminate. Where enough fine fuels remain, repeated understory burns can be employed to control the undesirable underbrush (Apfelbaum and Haney 1991). However, mechanical thinning or girdling in conjunction with application of specific herbicides may be necessary to eliminate such tenacious species as *Lonicera tatarica* (Tatarian honeysuckle) and *Rhamnus cathartica* (common buckthorn). To maximize the effectiveness of woody species removal, herbicide should be immediately applied directly to the cut stump or girdled bole, and efforts should be

concentrated during appropriate stages in plant growth cycles (i.e., when root metabolite levels are lowest late in the growing season or during the winter) (Reinartz 1997, Solecki 1997). The process of restoring the open canopy conditions and eliminating the understory should be conducted gradually, undertaken over the course of several years. As noted by Botts et al. (1994), too rapid a reduction in canopy can lead to severe encroachment of weedy species. The incremental opening of the canopy, especially when followed by the implementation of prescribed fires, can result in the germination of savanna species dormant in seedbanks during fire suppression.



Photo by Joshua G. Cohen

Suppression of fire in oak openings leads to woody species encroachment and eventually canopy closure.

Fire is the single most significant factor in preserving oak savanna landscapes. Once savanna conditions have been re-established, the reintroduction of annual fire is essential for the maintenance of open canopy conditions. In some instances prairie grasses may need to be seeded or planted to provide an adequate fuel matrix to support frequent burns (Botts et al. 1994, Packard 1997a, 1997b). Seed and plant donors should come from local sources and similar vegetative communities (Apfelbaum et al. 1997). In addition to maintaining open canopy conditions, prescribed fire promotes internal vegetative patchiness and high levels of grass and forb diversity, deters the encroachment of woody vegetation and invasive exotics, and limits the success of dominants (Bowles and McBride 1998, Leach and Givnish 1999, Abella et al. 2001). Numerous studies have indicated that fire intervals of 1-3 years bolster graminoid dominance, increase overall grass and forb diversity, and remove woody cover of saplings and shrubs (White 1983, Tester 1989, Abella et al. 2001). Burning at longer time intervals will allow for seedling establishment and the persistence of woody plants: Apfelbaum and Haney (1991) recommend gaps of five to ten years to allow for canopy cohort recruitment. Varying the burn interval from year to year and by season can increase the diversity of savanna remnants.



Repeat spring burns favor warm season grasses and late flowering species at the expense of cool season grasses and early flowering species; fall burning has the reverse effect (Kline 1997b). Influenced by high spring water tables, early spring burns often carry irregularly through savannas. Such patchy burns can be useful for establishing refugia for fire-sensitive species and may permit oak seedling establishment (Chapman et al. 1995). Patchy burns are often the result of frequent low-intensity fires, which carry sporadically through areas with low fuel loads. In contrast, infrequent fires are often more uniform in coverage, spreading evenly through areas of high fuel accumulation (Ladd 1991). While spring burns damage living portions of woody plants, summer fires, which simulate lightning season burns, are typically more detrimental to shrubs and trees than dormant-season burns (White 1983, Anderson 1997). Growing-season fires have a greater negative impact on woody species because they occur after energy and inorganic nutrient reserves have been invested into the leaves. Fall burns typically are slow moving, low-intensity fires due to high relative humidity and slow wind speed, while late spring and summer burns are often more intense due to higher wind speeds and lower relative humidity (King 2000). Pauly (1997) recommends that prescribed fires occur when relative humidity ranges between 25 and 60% (below 20% is hazardous and above 70% is difficult to burn) and wind speeds range between 3 and 15 miles per hour. To maximize damage to woody species, burns should be prescribed when relative humidity is near 30%. Winds over 15 miles per hour may be appropriate for oak savannas if heavier winds are needed to drive the fire through scattered trees and sparse fuels (Pauly 1997). As a general rule, half to two-thirds of an area should be burned during a given season (Packard 1997b).

Where rare invertebrates and herptiles are a management concern, burning strategies should allow for ample refugia to facilitate effective post-burn recolonization (Michigan Natural Features Inventory 1995, Siemann et al. 1997). Insects and herptiles, characterized by fluctuating population densities, poor dispersal ability, and patchy distribution, rely heavily on unburned sanctuaries from which they can reinvade burned areas (Panzer 1988). In areas where fire is undesirable or unfeasible, mowing or selective cutting can be utilized and should be conducted in late fall or winter to minimize detrimental impact to herbaceous species and rare animals (Chapman et al. 1995, Michigan Natural Features Inventory 1995, King 2000). Livestock grazing can also be employed to prevent the establishment of woody species (Bronny 1989, McClain et al. 1993).

Resource managers in southern Michigan face a complex management dilemma. Following decades of fire suppression, oak savanna communities have converted to closed-canopy oak systems. Many of these dry southern and dry-mesic southern forests provide critical habitat for forest-dwelling species, such as neotropical migrant birds. Conversion of

closed-canopy oak forests to oak savannas would likely favor species that are generalists and edge-dwellers. Robinson (1994) expressed concern that fire management and savanna restoration may exacerbate the formidable problems of forest fragmentation in the Midwest (i.e., cowbird parasitism and nest predation). In addition, the high proportion of edge-like habitat of savannas leaves them susceptible to invasion by aggressive exotic and native plants (Solecki 1997). Conversion of oak forest to oak savanna requires a long-term commitment to invasive species control and fire restoration (Peterson and Reich 2001). Conservationists must weigh the costs and benefits of each option and regionally prioritize where to manage for oak savanna systems. Savanna remnants selected for restoration should be large in size, with good landscape context (adjacent to high-quality natural communities), and have a high probability of success. Restoration of oak openings should be orchestrated in conjunction with the management of adjacent communities such as wet-mesic prairie, bur oak plains, oak barrens, dry southern forest, and dry-mesic southern forest. Due to the high levels of biodiversity within these landscapes and the rarity of many of the fire-dependent communities and species, sustained conservation efforts within oak savanna landscapes are likely to pay rich dividends (Leach and Givnish 1999).

Research needs: Considering that oak openings and many other savanna types of the Midwest were essentially gone before the inception of ecological management (Packard 1988), there is much to be learned about their composition and vegetative patterning (Leach and Givnish 1999). As noted by numerous scientists (Nuzzo 1986, Minc and Albert 1990, Faber-Langendoen 1993, Leach and Ross 1995, Pruka and Faber-Langendoen 1995, Bowles and McBride 1994), no single definition of *Midwest oak savanna* is universally accepted, and numerous distinct community types have been lumped under the term. Misunderstanding and misuse of the term can be alleviated by the continued refinement of regional classifications that correlate species composition, site productivity, ecological process, and landscape context. In states like Michigan, where oak openings are nearly extirpated, a primary research need is to inventory for restorable remnants.

Understanding spatial and temporal variability of oak openings is crucial for determining the direction of restoration management. Management of oak savanna remnants can be determined by site-specific research of site characteristics and circa 1800 composition and structure (Minc and Albert 1990, Bowles et al. 1994, Bowles and McBride 1998). Investigation into the frequency, periodicity (seasonality), and intensity of fires in oak openings is needed to guide restoration activities. In addition, because limitations imposed by safety concerns and landscape fragmentation can hamper the effectiveness of prescribed fire, maintaining the ecological integrity of oak savannas requires experimentation with different disturbance combinations (i.e., cutting, girdling, mowing, herbiciding, and/



or grazing) (Botts et al. 1994, Bowles and McBride 1998, King 2000, Abella et al. 2001). Numerous rare insects have host plants occurring on oak savannas. The impacts of fire and alternative management techniques on rare faunal populations and their host vegetation need to be studied (Chapman et al. 1995, Siemann et al. 1997). Effects of management need to be monitored to allow for assessment and refinement.

It is essential to determine what role seedbanks, vegetative reproduction, and external seed sources play in restoration of oak openings. When sowing or planting supplemental flora, managers must determine which species are the most appropriate to add and where they should be established. In addition, because of the daunting problem of exotic-species encroachment, research needs to examine management strategies that minimize invasive-species introduction and dominance.

For globally imperiled savannas such as oak openings, which only occur in scattered, small remnants, some of these research questions cannot be directly addressed. Conservationists will likely need to extrapolate from lessons learned from studies and management of more common and extensive savanna types such as oak barrens (Will-Wolf and Stearns 1999).

Michigan indicator species: *Amorpha canescens* (lead-plant, state special concern), *Amphicarpaea bracteata* (hog peanut), *Andropogon gerardii* (big bluestem), *Asclepias purpurascens* (purple milkweed, state special concern), *Baptisia lactea* (white or prairie false indigo, state special concern), *Camassia scilloides* (wild-hyacinth, state threatened), *Ceanothus americanus* (New Jersey tea), *Corydalis flavula* (yellow fumewort, state threatened), *Coreopsis palmata* (prairie coreopsis, state threatened), *Corylus americana* (American hazelnut), *Eryngium yuccifolium* (rattlesnake-master, state threatened), *Eupatorium sessilifolium* (upland boneset, state threatened), *Euphorbia corollata* (flowering spurge), *Gentiana flavida* (white gentian, state endangered), *Kuhnia eupatorioides* (false boneset, state special concern), *Lespedeza capitata* (bush-clover), *Panicum leibergii* (Leiberg's panic-grass, state threatened), *Quercus alba* (white oak), *Quercus macrocarpa* (bur oak), *Quercus velutina* (black oak), *Ranunculus rhomboideus* (prairie buttercup, state threatened), *Schizachyrium scoparium* (little bluestem), *Silene stellata* (starry campion, state threatened), *Sorghastrum nutans* (Indian grass), *Triosteum perfoliatum* (horse-gentian, feverwort), *Veronicastrum virginicum* (Culver's root), and *Zizia aurea* (golden alexanders). (List of potential oak openings indicators derived from Curtis 1959, Chapman 1984, Packard 1988, Leach and Ross 1995, Pruka 1995, Bader 2001, NatureServe 2004.)

Other noteworthy species: Rare plants that may have been associated with oak openings include: *Amorpha canescens* (lead-

plant, state special concern), *Asclepias purpurascens* (purple milkweed, state special concern), *Aster sericeus* (silky aster, state threatened), *Baptisia lactea* (white or prairie false indigo, state special concern), *Baptisia leucophaea* (cream wild indigo, state endangered), *Bouteloua curtipendula* (side-oats grama grass, state threatened), *Camassia scilloides* (wild-hyacinth, state threatened), *Corydalis flavula* (yellow fumewort, state threatened), *Eryngium yuccifolium* (rattlesnake-master, state threatened), *Eupatorium sessilifolium* (upland boneset, state threatened), *Euphorbia commutata* (tinted spurge, state threatened), *Gentiana flavida* (white gentian, state endangered), *Gentiana puberulenta* (downy gentian, state endangered), *Geum triflorum* (prairie-smoke, state threatened), *Helianthus mollis* (downy sunflower, state threatened), *Hieracium paniculatum* (panicled hawkweed, state special concern), *Kuhnia eupatorioides* (false boneset, state special concern), *Lechea minor* (least pinweed, state special concern), *Lechea stricta* (erect pinweed, state special concern), *Linum sulcatum* (furrowed flax, state special concern), *Panicum leibergii* (Leiberg's panic-grass, state threatened), *Polytaenia nuttallii* (prairie-parsley, state extirpated), *Ranunculus rhomboideus* (prairie buttercup, state threatened), *Ruellia humilis* (hairy ruellia, state threatened), *Scutellaria elliptica* (hairy skullcap, state special concern), *Silene stellata* (starry campion, state threatened), *Sisyrinchium strictum* (blue-eyed grass, state special concern), *Sporobolus clandestinus* (dropseed, state special concern), *Tomanthera auriculata* (eared false foxglove, state extirpated), and *Trichostema dichotomum* (blue curls, state threatened).

The oak savannas with surrounding prairie habitat share a rich diversity of invertebrates including numerous butterflies, skippers, grasshoppers, and locusts. However, the fragmented and degraded status of midwestern oak savannas and prairies has resulted in the drastic decline of numerous insect species associated with savanna habitats and prairie/savanna host plants (Chapman et al. 1995). Rare butterflies, skippers, and moths of savanna communities include: *Atrytonopsis hianna* (dusted skipper, state threatened), *Catocala amestris* (three-staff underwing, state endangered), *Erynnis p. persius* (persius duskywing, state threatened), *Hesperia ottoe* (ottoe skipper, state threatened), *Incisalia henrici* (Henry's elfin, state special concern), *Incisalia irus* (frosted elfin, state threatened), *Lycaeides melissa samuelis* (Karner blue butterfly, state threatened/federal endangered), *Papaipema beeriana* (Blazing star borer, state special concern), *Papaipema sciata* (Culver's root borer, state special concern), *Pygarcia spraguei* (Sprague's pygarcia, state special concern), *Pyrgus centaureae wyandot* (grizzled skipper, state special concern), *Schinia indiana* (phlox moth, state endangered), *Schinia lucens* (leadplant flower moth, state endangered), *Spartiniphaga inops* (Spartina moth, state special concern), and *Speyeria idalia* (regal fritillary, state endangered). Other rare invertebrates include *Lepyronia gibbosa* (Great Plains spittlebug, state threatened), *Neoconocephalus ensiger* (conehead grasshopper, state special concern), *Nicrophorus americanus* (American



burying beetle, state endangered), *Oecanthus pini* (Pinetree cricket, state special concern), *Orphulella p. pelidna* (barrens locust, state special concern), *Prosapia ignipectus* (red-legged spittlebug, state special concern), and *Scudderia fasciata* (pine katydid, state special concern). A diversity of mound building ants thrives in savannas and prairies.

Rare raptors that exploit oak savannas include *Accipiter cooperii* (Cooper's hawk, state special concern), *Circus cyaneus* (northern harrier, state special concern), and *Tyto alba* (barn owl, state endangered). Rare species of songbird include *Ammodramus henslowii* (Henslow's sparrow, state threatened), *Ammodramus savannarum* (grasshopper sparrow, state special concern), *Dendroica discolor* (prairie warbler, state endangered), and *Lanius ludovicianus migrans* (migrant loggerhead shrike, state endangered). *Tympanuchus phasianellus* (sharp-tailed grouse, state special concern) utilize oak savannas (Byre 1997, Kline 1997a). Typical songbirds include *Melospiza lincolnii* (Lincoln's sparrow), *Passerina cyanea* (indigo bunting), *Pooecetes gramineus* (vesper sparrow), *Sial sialis* (eastern bluebird), *Spizella passerina* (chipping sparrow), *Spizella pusilla* (field sparrow), *Toxostoma rufum* (brown thrasher), *Vermivora pinus* (blue-winged warbler), and *Vermivora ruficapilla* (Nashville warbler). Additional avian species that utilize this habitat include: *Accipiter striatus* (sharp-shinned hawk), *Bartamia longicauda* (upland sandpiper), *Bonasa umbellus* (ruffed grouse), *Buteo jamaicensis* (red-tailed hawk), *Carduelis tristis* (American goldfinch), *Charadrius vociferus* (killdeer), *Falco sparverius* (American kestrel), *Icterus galbula* (Baltimore oriole), *Melanerpes erythrocephalus* (red-headed woodpecker), *Meleagris gallopavo* (wild turkey), *Otus asio* (eastern screech-owl), *Tyrannus tyrannus* (eastern kingbird), and *Zenaida macroura* (mourning dove). Savanna restoration with prescribed fire in Minnesota resulted in an increased abundance of open country bird species, including many species that have been declining in central and eastern North America (Davis et al. 2000). The now extinct passenger pigeon (*Ectopistes migratorius*) was likely a keystone species in oak ecosystems, roosting in oaks by the thousands.

Cryptotis parva (least shrew, state threatened) and *Microtus ochrogaster* (prairie vole, state endangered) are rare mammals that may be found in oak savannas. It is possible that oak savannas provided habitat for *Myotis sodalis* (Indiana bat, state endangered) (Kline 1997a). Additional mammals commonly associated with the oak savanna communities include: *Canis latrans* (coyote), *Microtus pennsylvanicus* (meadow vole), *Odocoileus virginianus* (white-tailed deer), *Sciurus niger* (fox squirrel), *Spermophilus tridecemlineatus* (thirteen-lined ground squirrel), *Taxidea taxus* (badger), *Vulpes vulpes* (red fox), and *Zapus hudsonia* (jumping meadow mouse). Historically, bison and elk were important herbivores influencing oak savanna ecosystems, and *Canis lupus* (wolf, state threatened) was probably a keystone predator.

Several rare reptiles are known from oak savannas. They include *Clonophis kirtlandi* (Kirtland's snake, state endangered) (Packard 1993), *Elaphe o. obsoleta* (black rat snake, state special concern), *Sistrurus c. catenatus* (eastern massasauga, state special concern, federal candidate species), and *Terrapene c. carolina* (eastern box turtle, state special concern). Some of the more common amphibians and reptiles that frequent the oak savannas include: *Bufo a. americanus* (eastern American toad), *Bufo fowleri* (Fowler's toad), *Heterodon platirhinos* (eastern hog-nosed snake), and *Opheodrys vernalis* (smooth green snake).

Similar communities: Bur oak plains, lakeplain oak openings, mesic prairie, oak barrens, oak-pine barrens, and dry-mesic prairie.

Other Classifications:

Michigan Natural Features Inventory Presettlement Vegetation (MNFI): Mixed Oak Savanna

Michigan Department of Natural Resources (MDNR): Grass and 00(zero)-oak with <100 trees per acre.

Michigan Resource Information Systems (MIRIS): 33 (Oak or Pine Opening), 412 (Central Hardwood), 4122 (White Oak), 4123 (Black Oak), 4129 (Other Oak).

The Nature Conservancy National Classification:

CODE; ALLIANCE; ASSOCIATION; COMMON NAME

V.A.6.N.c.2; *Quercus macrocarpa* – (*Quercus alba*)
Wooded Herbaceous Alliance; *Quercus alba* – *Quercus macrocarpa* / *Andropogon gerardii* Wooded Herbaceous Vegetation; White Oak – Bur Oak Openings

V.A.6.N.c; *Quercus macrocarpa* – (*Quercus alba*)
Wooded Herbaceous Alliance; *Quercus macrocarpa* – (*Quercus alba*, *Quercus velutina*) / *Andropogon gerardii* Wooded Herbaceous Vegetation; North-Central Bur Oak Openings

Related Abstracts: Blazing star borer, Bur oak plains, Cooper's hawk, Culver's root borer, dry-mesic prairie, eastern box turtle, eastern massasauga, Henslow's sparrow, Karner blue butterfly, lakeplain oak openings, mesic prairie, migrant loggerhead shrike, northern harrier, oak barrens, oak-pine barrens, oak openings, ottoe skipper, prairie-smoke, prairie warbler, purple milkweed, and red-legged spittlebug.



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