9 Deep-Soil Savannas and Barrens of the Midwestern United States

ROGER C. ANDERSON AND MARLIN L. BOWLES

Introduction

Eastern Prairie–Forest Transition

Midwestern savannas occupied a transitional area between eastern deciduous forest and tallgrass prairie. These savannas were part of the eastern prairie–forest transition (Curtis 1959; Anderson 1983; Nuzzo 1986) that extended as a broad arc along the eastern edge of the northern mixed and tallgrass prairies from the Canadian provinces of Alberta, Saskatchewan, and Manitoba southward into Texas (Figure 9.1). We discuss deep-soil savannas (also called black soil, mesic, and tallgrass savannas and barrens) that occurred in the glaciated landscapes of Minnesota, southern Michigan and Wisconsin, Ohio, Indiana, and Illinois. These deep-soil savannas occurred on sites with fine-textured soils, where growth of trees was not severely limited by edaphic factors. Savannas with shallow soil profiles over bedrock, and those with sandy soil with low fertility and water-holding capacity, are considered in other chapters (see Chapters 8 and 21). Essentially all of the original Midwest, mesic, deep-soil savanna vegetation was lost to fire protection and agricultural activities, including overgrazing (Curtis 1959; Nuzzo 1986). These savannas are among the rarest natural vegetation types in the world.

Savannas of the Midwest occupied the eastern edge of a large, triangular-shaped grassland that extended from the Rocky Mountains into the Midwest (Risser et al. 1981; Anderson 1990). The grassland nar-rowed eastward, producing the well-known prairie peninsula (Transeau 1935). Across the long west–east axis of this grassland, the climate becomes progressively less suitable for growth of grass and more favorable for trees, as periods of periodic drought and low humidity during summer decrease and annual precipitation and its reliability increase (Borchert 1950; Risser et al. 1981). During major drought years, moisture stress can be pronounced in the eastern part of this peninsula (Borchert 1950). Low winter precipitation can result in incomplete recharge of subsoil moisture, which is used by deep-rooted trees in soils without drainage restriction. Grasses generally have shallower roots than trees and do not rely on this source of moisture. Thus, summer droughts preceded by winters without deep-soil moisture recharge are more detrimental to trees than to grasses. For example, during the drought of 1933–34, the region of incomplete recharge of deep-soil moisture in the Midwest generally corresponded to the prairie peninsula (Britton and Messenger 1969).

Consequently, at its eastern end, the grassland became increasingly fragmented and interspersed with forest and savanna, forming a broad transition zone to the deciduous forest of the east and the conifer forest in the north. Interaction of climate, topography, and fire produced a mosaic of vegetation types, including prairie, forest, and savanna, that varied depending upon the relative importance of these interacting factors (Anderson 1991; Robertson, Anderson and Schwartz 1997).
Figure 9.1. The distribution of the eastern prairie-forest transition (adapted from Anderson 1982 and Nuzzo 1986).

**Defining the Savanna Community**

As a result of varied tree canopy structure and density, the savanna vegetation matrix is transitional to forest and prairie (Curtis 1959; Anderson 1990; Leach 1996; Taft 1997). Fire regimes structure the savanna canopy (Faber-Langendoen and Davis 1995), which in turn creates a solar irradiance gradient and a corresponding distribution of ground-layer species (Gilbert and Curtis 1953; Bray 1958; Curtis 1959; Leach 1994; Pruka 1994a, b; Leach 1996; Bowles and McBride 1998). Shaded areas in savanna experience a shifting mosaic of light and shade to which the shade-tolerant species apparently are adapted. Areas beneath tree crowns receive high levels of solar irradiance before leaves develop on the tree canopy. This irradiance allows spring-flowering species, such as shooting star (*Dodecatheon meadia*) and wild hyacinth (*Camassia scilloides*), which are also found in prairies, to complete their relatively short aboveground growth cycles before a marked reduction in solar irradiance occurs (Gustafson and Anderson 1994; Gustafson 1996). Variation in soil depth and moisture, temporal change in fire regime and canopy structure, plant competition, and plant–animal interactions occur across the light gradient. The individualistic ecological responses of plant species across these multiple gradients produce a complex continuum of savanna vegetation (Bray 1958; Skarpe 1992; Belsky and Canham 1994; Leach 1994, 1996; Pruka 1994a; Packard and Mutel 1997).

The transitional vegetation types containing elements of prairies and forests have been called a variety of names, but most often, perhaps, they have been referred to as barrens, oak openings, or savannas. Heikens and Robertson (1994) note that the term *barrens* has generated considerable confusion in the botanical literature. *Barrens* has been used
syonymously with prairie, savanna, oak
opening, glade, scrub prairie, brush prairie,
grassland, and others. Similarly, the term
savanna has been defined differently by vari-
sous investigators, and use of it has changed
historically. J. White (1994) indicated that in
Illinois in the 1700s and 1800s, the word
savanna referred to grassland with few or no
trees and was used as a substitute for prairie
by emigrants from Great Britain or New
England.

Elsewhere, savanna has been defined as a
vegetation type having a tree canopy cover of
10%–50% in Missouri (Nelson 1985), to
complete canopy closure in Ohio (Nuzzo
1986) (see Figure 1.1, Introduction, this vol-
ume). These varied definitions likely result
from dynamic relationships occurring among
forest, savanna, and prairie, and reflect the
difficulty of separating a vegetation contin-
um into discrete classification units. There is
also regional variation in vernacular usage of
terms that describe vegetation. Use of these
different definitions of savanna creates diffi-
culties when comparisons are being made
between studies.

We adopt Curtis’s (1959) conceptual defi-
nition of savanna (i.e., as being part of a vege-
tation continuum between forest and prairie, Figure 9.2) as well as his classifica-
tion for savannas. He arbitrarily defined
savanna as a vegetation type having more
than one mature tree per acre (2.5 trees ha
⁻¹), but less than 50% tree canopy cover.
Curtis divided the savanna into oak openings
and barrens. Oak openings were character-
ized by scattered open-grown, broad crown
oaks (usually bur oak [Quercus macrocarpa])

Figure 9.2. Artist’s conception of the prairie-
savanna–woodland/forest continuum that charac-
terized portions of the Midwestern U.S.A. prior to
settlement by Europeans. (From Packard and
Mutel 1997.)
with a mixed understory of prairie species and species adapted to shady woodland habitats. Barrens included brush prairies, sand barrens (similar to sand prairies in terms of herbaceous species composition), and the hill’s oak (*Quercus ellipsoidalis*) and jack pine (*Pinus banksiana*) barrens that occupied sandy soil in the central and northern portions of Wisconsin. Barrens on deep, fine-textured soils tended to have more shrubs and coppices of trees, which were maintained by reoccurring fires, than did oak openings. Nomenclature follows Mohlenbrock (1986).

**Origin of Midwest Savanna**

Several workers described changes in vegetation during the Holocene based on analysis of fossil pollen deposits (King 1981; Winkler, Swain and Kutzbach 1986; Baker et al. 1992; Griffin 1994). Pollen deposits indicate that mesic forests occupied much of the Midwest following Wisconsinan glaciation (9,000–10,000 yr BP). Many species of oaks probably were restricted to sites with low availability of soil nutrients and water and that were not occupied by mesophytic species.

Midwest savannas originated during the relatively warm and dry postglacial period that peaked about 5,500–8,000 yr BP (McAndrews 1966; King 1981; Winkler, Swain and Kutzbach 1986; Baker et al. 1992; Griffin 1994). However, there was regional variation within the Midwest regarding when oak savannas became established during the Holocene (King 1981; Baker et al. 1996; Winkler 1997). In Illinois, the drying trend during the Holocene began about 8,700–7,900 yr BP, and prairie began to replace deciduous forest in southern Illinois. Prairie influx into central Illinois occurred a few hundred years later (about 8,300 yr BP) and oak forests began to displace mesic forests in northern Illinois at the same time. During the hottest and driest part of the Holocene in Illinois (8,000–6,000 yr BP), prairies occupied most of the state (King 1981). Oak openings appeared in northern Illinois and southern Wisconsin and Minnesota about 5,500 yr BP (McAndrews 1966; Griffin 1994). In Illinois, the climate became cool and moist about 5,000–3,500 yr BP, and the area of prairie decreased (Delcourt and Delcourt 1981; King 1981).

More recently, however, Baker et al. (1996) reported that in northeastern Iowa, forest dominated from about 8,000 to 5,100 yr BP. After 5,100 yr BP, forest was replaced by prairie, probably resulting from an increased flow of arid Pacific air and from fire, which these authors do not attribute to aboriginal burning. Oak savanna appeared about 3,000 yr BP in northeast Iowa, perhaps indicating the climate was becoming cooler and more moist, and less favorable for prairie than it had been previously. Similarly, Winkler (1997) found that in southcentral Wisconsin a Holocene peak in charcoal in lake and bog sediments (6,500–3,500 yr BP)
indicated that the highest frequency of regional fires occurred during that portion of the Holocene. The peak of charcoal in sediments was associated with a fire-adapted oak savanna landscape (Winkler 1994, 1997). After 3,500 yr BP, the vegetation in southcentral Wisconsin was dominated by closed oak forest. This change in vegetation is suggested by a decrease in charcoal found in sediments and a decline in charcoal stable carbon isotope data (δ¹³C below -26 per mil), indicating domination by C3 plants, which is typical of arboREAL landscapes (Winkler 1997).

Despite some regional variation in the timing of vegetation change during the Holocene, maintenance of vegetation patterns immediately prior to European settlement is attributed to aboriginal burning of the landscape under a climatic regime that could support forest, prairie, or savanna (Curtis 1959; Grimm 1984; Anderson 1990). Occurrence of the three vegetation types on the landscape was a function of fire frequency, which was largely controlled by topography. Level to gently rolling landscapes had frequent fires and supported tallgrass prairies. In dissected landscapes, spread of fire was reduced, permitting establishment of trees. Closed forests were associated with areas sheltered from fires, such as ravines or along waterways that served as firebreaks. These sheltered locations supported shade-tolerant, fire-sensitive, mesophytic forests of sugar maple (Acer saccharum), basswood (Tilia americana), and, in the eastern portion of the prairie-forest transition, beech (Fagus grandifolia). Woodlands and savannas dominated by fire-tolerant oaks occurred in areas where fires occurred less frequently than in prairies, but with shorter return time than in closed mesophytic forests (Figure 9.3) (Gleason 1922; Curtis 1959; Anderson and Anderson 1975; Rodgers and Anderson 1979; Grimm 1984; Anderson 1990, 1991; Abrams 1992). Curtis (1959) proposed that during the Holocene, sites supporting mesic forest species were converted to prairie because the combination of drought and fires eliminated these species from all but the most sheltered sites. However, fires did not eliminate oaks because of the fire-resistant bark in some species, such as bur oak, and the ability to resprout after being top-killed, an adaptive feature in all oaks (Stearns 1991; Abrams 1992). Mesic forests experienced occasional fires with fire return times as long as centuries. In these forests, the shade-intolerant red oak was a pioneer species. Even with long fire intervals (centuries), the intolerant red oak apparently persisted on mesic sites, because of its long life span. However, shade-tolerant mesophytes could dominate smaller-tree size classes on mesic sites for most of the time between fires (Curtis 1959; Adams and Anderson 1980; Abrams 1992; Will-Wolf and Roberts 1993).

Rodgers and Anderson (1979) reported that in central Illinois, prairies were associated positively with Mollisols, but that forests and savannas tended to be negatively associated with these soils. Generally, savanna and forest tended to have the same associations with soils, and both were positively associated with Alfisols. These results suggest that savannas developed as a result of forest degradation. Nevertheless, in the Big Woods area of southeastern Minnesota, some pre-settlement savannas may have originated by trees invading prairie (Grimm 1984). Occurrence of aspen (Populus tremuloides and some P. grandidentata) and, to some extent, bur oak on prairie soils resulted from trees of these species invading prairie around the periphery of forested areas and forming savannas (Grimm 1984).

**Types of Deep-Soil Savannas:**

**Oak Openings and Barrens**

**Oak Openings**

Oak openings occurred on fine-textured soil and, as described by European settlers in the 1800s, had an orchardlike appearance with scattered broad crown white and bur
oaks with an understory of prairie species (Curtis 1959; J. White 1994). Soils of oak openings were considered to be fertile and suitable for the growth of crops (J. White 1994). Latrobe (1835) described the oak opening of Michigan and Illinois as having rich vegetable soils. Similarly, Little (1861) described the soil of the oak opening in Illinois as being "better adapted to production of fruit than our prairie soils." Shepherd (1850) described soils of the oak openings as being the best wheat lands.

In contrast to dominance by coppices of shrubs and oak grubs in barrens, as we describe later, Curtis (1959) indicated that the thick bark of bur oak helped it to withstand prairie fires and to colonize prairie. This allowed development of classic savanna structure associated with oak openings on mesic sites: scattered, large, open-grown trees with a prairie understory (i.e., with an orchard- or parklike appearance). Nearly annual fires that were set by native Americans and by occasional lightning strikes (Curtis 1959; Vogl 1977) maintained this savanna, which more closely resembled a grassland with trees than barrens. Drought-driven summer fires also may have been important in structuring this vegetation (Anderson 1982).

Oak openings had fewer shrubs than barrens, or in some cases oak openings appeared to lack woody understory, enhancing their parklike appearance. Nevertheless, there was a rapid woody succession of oak openings to closed oak forests following fire protection associated with European settlement (Cottam 1949; McCune and Cottam 1985; Bowles and McBride 1994; J. White 1994). Thus few, if any, intact savannas survive on deep silt loam soil in the Midwest (Curtis 1959; Medany 1981; Apfelbaum and Haney 1991; Packard 1991; Bowles and McBride 1996). Because this vegetation type disappeared soon after settlement, the original species composition and structure of savannas are poorly described. Burning often is presumed to have maintained a graminoid fuel matrix in savanna (Curtis 1959; Apfelbaum and Haney 1991; Packard 1991, 1993). However, oak sprouts and shrubs such as American hazel (Corylus americana) were frequent in oak openings, demonstrating a strong similarity to brush prairie (Cottam 1949; McAndrews 1966; Bowles, Hutchison and McBride 1994).

In Wisconsin, Bray (1960) found mostly grazed mesic savannas, formerly the most widespread savanna type. However, Bray sampled 103 species across 59 stands and established the distribution of herbaceous species and trees across a moisture gradient. The 103 species were distributed almost equally in their occurrence in prairie and forest, demonstrating that oak openings were floristically intermediate between the two vegetation types.

Bray (1958) also identified a strong relationship between variation in species composition and canopy gaps that was controlled by irradiance (Table 9.1). With a 10%-50% canopy cover definition of savanna, prairie herbaceous species are an important component of the savanna vegetation matrix, with an admixture of shade-tolerant savanna species found in woodlands with intermediate irradiance levels (Bray 1958). The eight silt loam savannas studied by Betz (1992) also reflect a strong floristic affinity to tallgrass prairies (Table 9.2), and he considered them to be most closely allied to oak openings. The transitional soils on these eight sites had A horizons shallower than in prairie soils. Betz (1992) suggests that the sites may have originated as the result of trees invading prairie, although transitional soils could result from prairie invading forest that was degraded by repeated fires.

**Deep Soil Barren/Brush Prairies**

In the prairie-dominated, glaciated landscapes of central and northern Illinois, early settlers and surveyors used the term *barrens* to describe habitats perceived as being unproductive because they lacked canopy trees and their vegetation was intermediate between
Deep-Soil Savannas and Barrens of the Midwestern United States

Table 9.1. Relation of selected common oak opening species to illuminance (after Bray 1955) from Curtis (1959). Values are average quadrat frequency in quadrats occurring within the indicated range of illuminance in lux.

<table>
<thead>
<tr>
<th>Light species</th>
<th>0–10.760 lux.</th>
<th>10.760–100.760 lux</th>
<th>100.760+ lux</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amorpha canescens</td>
<td>28</td>
<td>61</td>
<td>77</td>
</tr>
<tr>
<td>Helianthus lactiflorus</td>
<td>24</td>
<td>38</td>
<td>77</td>
</tr>
<tr>
<td>Sisymbrium arvense</td>
<td>21</td>
<td>37</td>
<td>63</td>
</tr>
<tr>
<td>Andropogon gerardii</td>
<td>21</td>
<td>35</td>
<td>61</td>
</tr>
<tr>
<td>Schizachyrium scoparium</td>
<td>8</td>
<td>13</td>
<td>56</td>
</tr>
<tr>
<td>Panicum leonardii</td>
<td>16</td>
<td>33</td>
<td>55</td>
</tr>
<tr>
<td>Aster sericeus</td>
<td>2</td>
<td>20</td>
<td>47</td>
</tr>
<tr>
<td>Bouteloua curtipendula</td>
<td>9</td>
<td>18</td>
<td>47</td>
</tr>
<tr>
<td>Petalostemon purpureum</td>
<td>3</td>
<td>5</td>
<td>38</td>
</tr>
<tr>
<td>Aster ericoides</td>
<td>19</td>
<td>22</td>
<td>29</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Intermediate species</th>
<th>0–10.760 lux.</th>
<th>10.760–100.760 lux</th>
<th>100.760+ lux</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euphorbia corollata</td>
<td>37</td>
<td>60</td>
<td>49</td>
</tr>
<tr>
<td>Galium boreale</td>
<td>43</td>
<td>55</td>
<td>23</td>
</tr>
<tr>
<td>Monarda fistulosa</td>
<td>37</td>
<td>49</td>
<td>22</td>
</tr>
<tr>
<td>Coreopsis palmata</td>
<td>37</td>
<td>47</td>
<td>45</td>
</tr>
<tr>
<td>Solidago ulmilifolia</td>
<td>40</td>
<td>43</td>
<td>7</td>
</tr>
<tr>
<td>Aster azures</td>
<td>37</td>
<td>41</td>
<td>4</td>
</tr>
<tr>
<td>Comarata richardsiana</td>
<td>17</td>
<td>41</td>
<td>34</td>
</tr>
<tr>
<td>Anemone cylindrica</td>
<td>28</td>
<td>31</td>
<td>7</td>
</tr>
<tr>
<td>Rosa sp.</td>
<td>27</td>
<td>30</td>
<td>23</td>
</tr>
<tr>
<td>Smilacina stellata</td>
<td>21</td>
<td>25</td>
<td>17</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Shade species</th>
<th>0–10.760 lux.</th>
<th>10.760–100.760 lux</th>
<th>100.760+ lux</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphicarpa bracteata</td>
<td>61</td>
<td>50</td>
<td>15</td>
</tr>
<tr>
<td>Cornus racemosa</td>
<td>59</td>
<td>38</td>
<td>7</td>
</tr>
<tr>
<td>Helianthus strumosus</td>
<td>53</td>
<td>47</td>
<td>22</td>
</tr>
<tr>
<td>Aster laevis</td>
<td>40</td>
<td>29</td>
<td>0</td>
</tr>
<tr>
<td>Corylus americana</td>
<td>41</td>
<td>26</td>
<td>38</td>
</tr>
<tr>
<td>Aralia nudicaulis</td>
<td>36</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Carex pensylvanica</td>
<td>33</td>
<td>30</td>
<td>5</td>
</tr>
<tr>
<td>Ratibida pinnata</td>
<td>29</td>
<td>24</td>
<td>4</td>
</tr>
<tr>
<td>Geranium maculatum</td>
<td>23</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Amsynum androsaefolium</td>
<td>19</td>
<td>14</td>
<td>7</td>
</tr>
</tbody>
</table>

Grassland and forest (Bowles and McBride 1994). According to J. White (1994), the single unifying characteristic of barrens was the presence of fire-maintained brush and tree sprouts. Barrens often had tallgrass, but were characterized by underwood or brushwood of fire-resistant shrubs or oak grubs, rather than the open-grown trees of the oak openings (Bowles and McBride 1994; J. White 1994).

Gleason (1922) indicated that barrens in Illinois represented a late stage of fire-caused forest degradation. They were characterized by 1.2–1.5-m-high sprouts of scrub oak, apparently shingle oak (Quercus imbricata).
black oak (Q. velutina), and Hill's oak, and American hazel and wild plum (Prunus americana). Similar vegetation in Wisconsin was called “brush prairie” by Curtis (1959). Grimm (1984) also indicated that part of the savanna habitat he studied in eastern Minnesota “was scrub, a dense thicket of fire-stunted oak and brush.” According to Curtis, from a distance, brush prairies were indistinguishable from tallgrass prairies because nearly annual fires reduced trees to “brush” or “grubs.” Oak grubs formed when nearly annual prairie fires killed the tops of young oaks but shoots would sprout from the persistent root system the next year. Over a period of years, possibly as long as centuries, a massive root system developed, often with a large, surface root plate 0.6–0.9 m in diameter. The term *grub* is from the German *gruben*, to dig, in reference to the method used by European settlers to laboriously remove these massive root systems from their agricultural fields (Curtis 1959). The shrub New Jersey tea or red root (Ceanothus americanus) also produced a large underground root burl as a result of repeated top-killing and sprouting.

The vegetation structure and ecological features of former barrens are poorly known. Barrens were most common on uneven or rolling topography or along stream drainages (e.g., Peck 1834), which reduced fire effects. They also developed on the west sides of forests penetrated by eastward-moving prairie fires driven by prevailing westerly winds (Gleason 1913). In addition to landscape fire effects, the thin bark of black, shingle, and Hill's oak probably facilitated top-killing by fire and respouting, which contributed to formation of barrens. Because barrens lacked canopy trees, their spatial vegetational patterns may not have been related to a light gradient. However, the clonal structure of shrubs such as hazel may have resulted in a mosaic of low, woody vegetation with few grasses, and openings dominated by grasses.
and prairie forbs. Without fire, these communities were unstable. They probably disappeared more rapidly than oak openings, but left no old open-grown trees as markers of their former presence. According to Gleason (1922), large areas of barrens were converted into forest "as by magic" when the anthropogenic fires that maintained them were stopped and the oak sprouts became trees. As a result, even-aged forest stands with hazel understories may have been derived from barrens. Forests of this kind, however, often have trees with multiple stems that originated from basal root plates.

The floristic composition of former barrens can be reconstructed, to some extent, from historic descriptions. Bowles and McBride (1994) indicate that more than 30 shrub species may have characterized barrens, including hazel, New Jersey tea, dogwoods (Drummonds dogwood [Cornus drummondii], pale dogwood [C. obliqua], gray dogwood [C. racemosa], and red osier dogwood [C. stolonifera]), wild crab (Malus coronaria and M. ioensis), wild plum, sumac (Rhus spp.), rose (Rosa spp.), prairie willow (Salix humilis), and prickly ash (Zanthoxylum americanum). Barrens that formed along the western flanks of forests were dominated by hazel, with black oak and shingle oak forming the interior of the forest margin (Gleason 1913).

Bowles and McBride (1994) prepared a composite barrens flora using four historic annotated species lists compiled by Mead (1846), Higley and Raddin (1891), Brendel (1887), and Hus (1908) from areas that included barrens vegetation at the time of the Government Land Surveys. The list of 247 taxa includes 41 woody, 191 herbaceous, and 15 graminoid species thought to occur in deep-soil barrens. The most remarkable of the annotated lists included 108 "barrens" species published by S. B. Mead, a medical doctor, as part of a larger annotated list of Illinois plants from Augusta (Hancock County), Illinois (Mead 1846). Although Packard (1988) suggested that the species list represents tallgrass savanna, it has little similarity to extant silt loam savannas. For example, only 18 (23%) of the 77 nonwoody species on Mead's 1846 list occur in the silt loam cemetery savannas (Betz 1992).

There is no way of knowing exactly the kinds of habitats from which historic species listed for barrens were derived. However, the historic barrens flora lists contain a mixture of herbs, grasses, shrubs, and trees from habitats other than barrens (Curtis 1959; Steyermark 1963; Mohlenbrock 1986; Swink and Wilhelm 1994). The diversity of species and the variety of extant habitats that these species currently occupy suggest that barrens occurred across a wide range of landscape and moisture conditions. It is likely that barrens, brush prairies, and oak openings were part of a vegetation continuum on the pre-settlement landscape.

Extant savannas, although degraded, provide some insight into the nature of this vegetation continuum. For example, in a savanna restoration site in McLean County, central Illinois, three of the four species of Carex (C. blanda, C. cephalophora, and C. jame-sii) on the composite barrens list prepared by Bowles and McBride (1994) occur on the restoration site. Government Land Office (GLO) survey records indicate that this restoration site was likely an oak opening at the time of the survey (1836) (Anderson et al. 1994). The site has been prescribed burned in February or March each year since 1989. No plants were introduced during the restoration. Carex is the dominant ground cover. Currently, there are no C4 prairie grasses on the site, owing to a past history of cattle grazing and the development of a woody understory canopy after cattle were removed from the site in 1967. Grasses on the site are C3 species associated with open woodlands or forest edges (e.g., bottlebrush grass [Elymus hystrix], Bromus pubescens,
Table 9.3. Frequency (>15%) in 25-m² quadrats of herbaceous species sampled on two dates in 1994 at the ParkLands Foundation Savanna Restoration site (McLean County, Illinois).

<table>
<thead>
<tr>
<th>Species</th>
<th>May 12 (%) freq.</th>
<th>June 22 (%) freq.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Grasses</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dicranum alpinum</td>
<td>72</td>
<td>92</td>
</tr>
<tr>
<td>Poa pratensis</td>
<td>68</td>
<td>88</td>
</tr>
<tr>
<td>Bromus pubescens</td>
<td>52</td>
<td>60</td>
</tr>
<tr>
<td>Dactylis glomerata</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td>Elymus villosus</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td>Festuca obtusa</td>
<td>28</td>
<td>20</td>
</tr>
<tr>
<td><strong>Sedges</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carex blanda</td>
<td>72</td>
<td>36</td>
</tr>
<tr>
<td>Carex hirsutella</td>
<td>0</td>
<td>80</td>
</tr>
<tr>
<td>Carex pensylvanica</td>
<td>64</td>
<td>16</td>
</tr>
<tr>
<td>Carex cephalophora</td>
<td>20</td>
<td>48</td>
</tr>
<tr>
<td>Carex sparganoides</td>
<td>0</td>
<td>28</td>
</tr>
<tr>
<td><strong>Forbs</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geum canadense</td>
<td>80</td>
<td>88</td>
</tr>
<tr>
<td>Tradescantia virginiana</td>
<td>80</td>
<td>0</td>
</tr>
<tr>
<td>Taenidia integerrima</td>
<td>76</td>
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<tr>
<td>Dodecatheon meadii</td>
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<tr>
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<tr>
<td>Viola sororia</td>
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<td>Sanicula gregaria</td>
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<td>Erigeron strictus</td>
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<td>Phlox divaricata</td>
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<td>Claytonia virginica</td>
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<td>Potentilla simplex</td>
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<td>Ranunculus fceculus</td>
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<tr>
<td>Melilotus alba</td>
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<tr>
<td>Sisyrinchium albidum</td>
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<tr>
<td>Viola spp.</td>
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<td>20</td>
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<tr>
<td>Erythronium albidum</td>
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<td>0</td>
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<tr>
<td>Oxalis sp.</td>
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<tr>
<td>Plantago rugelii</td>
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<td>Taraxacum officinale</td>
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<td>Rudbeckia hirta</td>
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<td>Antennaria plantaginifolia</td>
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<td>Oxalis violacea</td>
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Festuca obtusa, and Dianthus acuminata) (Table 9.3).

In spring, the restored savanna supports a number of species that distinguish it from the adjacent woodland, either because the species are somewhat ephemeral (e.g., the shooting star, wild hyacinth, and spiderwort [Tradescantia virginiana]) or because they flower in spring (e.g., yellow pimpernell [Taenidia integerrima] and early buttercup [Ranunculus fascicularis]). The frequency of several species differed markedly between May and June (Table 9.3). These differences reflect the ephemeral nature of some species, the progressive development of the vegetation from spring into summer, sample variation, and the difficulty in identifying some Carex spp. in a vegetative condition.

**Current Status**

**Rare, Threatened, and Endangered Species**

Apparently because of the transitional nature of savanna and the occurrence of woodland and prairie species in savanna, no rare, threatened, or endangered species are restricted to this habitat. For example, at least 20 tallgrass prairie species attributed to savanna have been listed as threatened or endangered at the state level because of concern for their conservation. However, most of these species are at their eastern geographic range limits, where prairie habitat is fragmented, rare, and intergrades with savanna. Because prairie is part of the savanna matrix, many of these regionally rare prairie plants also are present in savanna habitat. In contrast, only a few non-prairie species recorded for deep-soil savanna habitat have been listed at the state level. Some of these species may have strong savanna affinities because of their tolerance of intermediate light levels. For example, Liatris scariosa var. nieuweiandii, an Illinois threatened species, appears to be primarily a savanna species in Illinois (Bowles, Wilhelm and Packard 1988), but not elsewhere (e.g., Voss 1996).

**Preservation**

Because deep-soil savannas were maintained only with recurrent fires (Curtis 1959; Anderson and Brown 1983; Cole and Taylor 1995; Bowles and McBride 1998), few examples survived intact into the 20th century. Fire cessation resulted in rapid conversion of many deep-soil savannas to forest, as oak sprouts and grubs quickly grew into closed oak forests (Cottam 1949; Curtis 1959). Overgrazing following European settlement altered savanna composition by reducing the abundance of, or eliminating, grazing-intolerant species. Agriculture and land development fragmented and destroyed remnants. As a result, Bray (1960) examined only a few examples of mesic (deep-soil) savanna in Wisconsin that were not subjected to grazing (Curtis 1959). In a survey for remnant natural areas in Illinois in the 1970s, only two high-quality deep-soil savanna remnants were located, both occurring in small pioneer cemeteries (J. White 1978; Madany 1981). In a 1985 survey of savannas known in the midwestern states, no additional high-quality deep-soil savanna remnants were found (Nuzzo 1986). Shrub, or brush prairies, on deep soils apparently are even more imperiled. Curtis (1959) did not provide data on this vegetation type in Wisconsin, and none was identified by recent statewide surveys. In a reassessment of the status of northern Illinois savannas, two barrens remnants and two additional oak openings, totaling less than 50 hectares, were found (Bowles and McBride 1996). In the absence of fire on sites where edaphic features limit tree growth, conversion of savannas to forest occurs more slowly than on deep-soil savannas. Consequently, in Illinois and surrounding midwestern states, almost all savanna remnants occur on drouthy sand and gravel deposits, and no high-quality deep-soil
savanna remnants are known (Leach and Ross 1995).

**Restoration and Management**

As a result of their open structure and dependence on fire, savanna remnants are susceptible to rapid successional conversion to woodlands and invasion by exotic species. Most remnants are small, thus it often is difficult to restore landscape level fire. The small scale of the fires may reduce their effectiveness in suppressing woody vegetation (A. S. White 1983; Anderson and Brown 1986; Tester 1989; Kline and McClintock 1994). Invasive shrubs such as buckthorns and honeysuckles resprout and thus might not be killed by fire. Furthermore, fire intensity often is low where exotic shrub cover is high because shade depresses or eliminates graminoid species that provide finely divided fuels (Heidorn 1991). Thus, exotic woody species often need to be controlled by artificial cutting and treatment with herbicides (Lukin and Mattimore 1991). However, management efforts to reduce the abundance of native shrubs, such as gray dogwood, should be tempered to (1) ensure maintenance of nesting habitat for understory birds (Whelan and Dilger 1992) and (2) restore pre-European woody understory structure (Bowles, Hutchison and McBride 1994; Bowles and Spravka 1994).

In savanna remnants, many late-successional savanna species are poorly represented as mature plants and in seed banks (Johnson and Anderson 1986). Thus, management to restore deep-soil savannas must consider introduction of seed or plants of species that may have been lost to grazing, fire protection, and canopy closure. Determining which species to introduce is confounded by a lack of baseline data on species composition from intact savannas. This information has been supplemented to some extent by historic lists and original land survey notes (Bowles and McBride 1994), knowledge of the ecology of the species (Pruka 1995), and data from remnants that retain some original species (Anderson et al. 1994; Pruca 1994a, b; Leach 1996; Bowles and McBride 1998).

**Summary**

Deep-soil savannas of the Midwest occupied a transitional area between eastern deciduous forest and tallgrass prairie. These savannas included oak openings and barrens/brush prairie that tended to merge floristically and structurally with each other and with forest and prairie communities. Oak openings tended to have an open, parklike appearance with widely scattered trees and an understory of high floristic similarity to tallgrass prairies. Barrens/brush prairies apparently were derived from forested areas and had a woody undergrowth of trees and shrubs that was maintained in scrubby condition by repeated burning. Because of the transitional nature of barrens, brush prairie, and oak openings, there are relatively few species of plants that characterize these vegetation types. Maintenance of these savannas was strongly dependent upon periodic fire. In the later part of the 19th century, barrens and oak openings were rapidly converted to closed forest following cessation of fires associated with European settlement. Agricultural activities, including overgrazing, degraded most of the remaining savannas, and consequently there are few extant examples of this vegetation type.

**References**


Deep-Soil Savannas and Barrens of the Midwestern United States

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