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Vegetation Composition, Structure, and Chronological Change in a Decadent Midwestern North American Savanna Remnant

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ABSTRACT: Fire-maintained oak savannas on silt-loam soils essentially disappeared from midwestern North America soon after European settlement because of fire suppression and agriculture. As a result, there are no precise models for restoring this vegetation, and its management and recovery needs are uncertain. The Wolf Road Prairie Nature Preserve, Cook County, Illinois, contains a 2-ha savanna remnant that persisted on mesic silt-loam soils because grazing was excluded and because it was frequently burned until about 1965. We used tree increment cores to document temporal change in this savanna's tree density and canopy structure. The savanna has an open overstory canopy of mature *Quercus macrocarpa* (bur oak) and a dense 30-year-old subcanopy of *Q. macrocarpa* and *Q. ellipsoidalis* (northern pin oak) that matured from oak grub sprouts after cessation of annual wildfires. Herb-layer sample plots were classified into four species groups corresponding to a measured light intensity gradient that correlated with canopy tree density. The ground layer was dominated by shade-tolerant species that presumably have spread into former savanna openings, while shade-intolerant species, such as prairie plants, were restricted to the few remaining light gaps. Plot species richness and number of prairie species were highest at highest light levels, while alien species richness was highest under canopy shade. Forbs were the most important species group (78.6 Importance Value); woody species were much less important (18.8 IV), and graminoid vegetation was only a minor component that was restricted to light gaps. *Camassia scilloides* was the most important forb and was distributed bimodally across the light gradient. *Rubus allegheniensis* was the most important woody species, and *Carex pensylvanica* was the most important graminoid species. The site retains important components of savanna vegetation and could be restored to former savanna composition and structure, helping provide elements of a savanna restoration model. Restoration would require a return to high fire frequencies and reduction of the subcanopy to its former grub layer, which should increase abundance of light- and fire-adapted species and reduce alien species. However, restoring former structure may be difficult, partly because of the fire resistance of maturing subcanopy oaks and because the absence of graminoid fuel species will reduce the effectiveness of fire. In addition, landscape-scale fire processes, which might be most effective, will be difficult to implement in this small fragmented natural area. As a result, experimental cutting or girdling of oaks should be used to supplement fire in opening canopy gaps.

Index terms: silt-loam savanna, savanna light gradient, savanna species, successional change, savanna management

INTRODUCTION

Former Status and Decline of Savanna

At the time of European settlement, the northern border of the North American prairie peninsula (Transeau 1935) was a broad mosaic of prairie and oak-dominated savanna and woodland (Curtis 1959, Davis 1971, Anderson 1983). This vegetation was spatially patterned by fire regime and shifted temporally with climatic change; trees persisted in greatest densities where topographic relief reduced fire intensities, or where landscape firebreaks such as watercourses provided protection

against prairie fires driven by prevailing westerly winds (Gleason 1913; McAndrews 1966; Moran 1978, 1980; Grimm 1983, 1984; Anderson 1991; Leitner et al. 1991; Bowles et al. 1994). Curtis (1959) estimated that presettlement southern Wisconsin was 75% savanna, which occurred across a soil moisture continuum. He described mesic savanna as 10%–50% canopy cover of fire-resistant bur oak (*Quercus macrocarpa*) with a prairie ground layer. Black oak (*Q. velutina*) and white oak (*Q. alba*) characterized dry-mesic savannas and, along with bur oak, occurred as fire-sprouting grubs in brush prairie (Curtis

1959). Although data are lacking, historic descriptions suggest that frequent, if not annual Indian- and lightning-set fires maintained savanna, especially in mesic habitats (Curtis 1959, Vogl 1977). (Nomenclature follows Swink and Wilhelm 1994).

Few, if any, intact savannas survive on deep silt-loam soils in the Midwest (Curtis 1959, Madany 1981, Nuzzo 1986, Apfelbaum and Haney 1991, Packard 1991, Leach and Ross 1995). After European settlement, these savannas rapidly degraded as woody succession followed fire protection (Cottam 1949, McCune and Cottam 1985, White 1994, Bowles and McBride 1994). Subsequent overgrazing further degraded savanna vegetation, while agriculture and land development fragmented and destroyed remnants. Dry or dry-mesic savannas, especially on sand, have survived to a greater extent (Madany 1981) due to their poor agricultural potential and drought-sensitive soils that promote tree mortality and recurring fire (Faber-Langendoen and Tester 1993). Burning also can stabilize sand savanna (Anderson and Brown 1983), while rapid woody plant succession can occur with fire protection (Cole and Taylor 1995).

Restoration Needs: Understanding Species Composition, Light Gradient, and Fire Regime

Reference systems are necessary for guiding community restoration efforts (Aronson et al. 1995). Although restoration of silt-loam savannas has a high priority, guidelines are vague or conflicting because there is little quantitative information about the former composition, structure, and fire dynamics of this vegetation (Burger et al. 1991, Fralish et al. 1994, Leach and Ross 1995). For example, although burning is often presumed to have maintained a grass and sedge fuel matrix in savanna (Curtis 1959; Apfelbaum and Haney 1991; Packard 1991, 1993), postfire-sprouting oak grubs and shrubs such as hazel (*Corylus americana*) were frequent (Cottam 1949, McAndrews 1966, Bowles et al. 1994). Curtis (1959) indicated that the savanna flora was transitional with few modal species. This conclusion was based on the work of Bray (1960), who quantified a

strong prairie component in savanna, with few nonprairie species reaching their greatest abundance in this community. Bray (1958) found partial shade-tolerant savanna plants to occur primarily between about 750–1,250 and 10,000 foot candles (FC), with closed forest species most frequent at lower light intensities and prairie species more frequent at higher intensities. With a 10%–50% canopy cover definition of savanna, prairie species become an important component of the savanna vegetation matrix, while other savanna species also occur in woodlands that support intermediate light levels (Bray 1960). However, Packard (1988a, 1991) argued for recognizing a more specific savanna flora, citing the “barrens” vegetation of Mead (1846). Workers continue to reconsider Bray’s data (Packard 1993), and to examine modern savanna remnants and construct savanna species lists (e.g., Betz 1992, Pruka 1995).

Fire regime strongly influences structure and composition of savanna, with increasing fire frequency causing a decrease in canopy cover and limiting oak recruitment (Faber-Langendoen and Davis 1995); this in turn controls the canopy light gradient and corresponding distribution of ground-layer species (Gilbert and Curtis 1953; Curtis 1959; Bray 1960; Leach 1994; Pruka 1994a, 1994b). In a Minnesota sand savanna, greater richness of prairie plant species occurred after 13 annual burns in comparison to unburned savanna (White 1983). At the same site, Tester (1989) found that alternating 2-year burn and 2-year no-burn cycles maximized species richness and favored prairie species. Kline and McClintock (1994) also found that ground-layer species richness increased after burning of a southern Wisconsin oak forest. In a southern Illinois barrens, species richness was maximized by irregular temporal burning that allowed persistence of forest and prairie species (Anderson and Schwegman 1991). Additional factors, such as soil depth and moisture, plant competition, and plant-animal interactions also influence savanna composition (Bray 1958, Skarpe 1992, Belsky and Canham 1994, Leach 1994, Pruka 1994a).

Study Objectives

An understanding of historic and modern processes affecting the composition and structure of savanna remnants is vital for the successful restoration and management of these remnants, and for developing guidelines that can be applied to other savanna restorations. In this study, we used dendrochronological and historic data to suggest that a stable open savanna canopy existed from the early nineteenth to the mid-twentieth century at Wolf Road Prairie, an ungrazed midwestern North American silt-loam prairie and savanna remnant. We then used age structure of multiple-stemmed tree cohorts to describe a recent temporal change in canopy structure that correlates with reduced fire frequency—a process that occurred 150 years earlier in most savannas. By analyzing the spatial pattern of vegetation across the light and tree density gradient in this remnant, we sought to provide information about the process of savanna degradation and the potential for reversing this process for restoration. We also asked whether canopy structure affected patterns of species richness and the distribution of alien species, and if this information can be used to develop guidelines for canopy management that will help restore savanna vegetation.

STUDY AREA

Wolf Road Prairie (WRP), in Cook County, Illinois, persisted after European settlement because of recurring fires and protection from overgrazing; the site contains one of the few extant remnants of midwestern prairie and savanna vegetation (McFall and Karnes 1995). This 32-ha prairie is in the village of Westchester (41° 50′ N latitude, 87° 54′ W longitude), about 24 km west of Lake Michigan in suburban Chicago. The site occurs on the northern border of the prairie peninsula (Transeau 1935). The climate is continental, with hot humid summers and very cold winters. Annual average precipitation is 84 cm, with about 67% occurring during the growing season, but with great variation due to periodic summer drought. The site is level and moderately well drained. The silt-loam soils are developed in thin loess over the

Tinley ground moraine and belong to the Morley-Markham-Ashkum association, which includes transitional (light-colored) soils in savanna, and mollisols (dark-colored soils) in adjacent prairie (Mapes 1979).

Wolf Road Prairie lies 0.8 km north of the east-west oriented Salt Creek, adjacent to the north and east of the band of timber that bordered this natural firebreak. In 1821 the U.S. Government Public Land Survey (PLS) mapped the forest-prairie transition along the south border of WRP near the line between sections 30 and 31, T30N, R12E (Figure 1). Although such data are often biased, PLS witness tree distances from section lines can be used to reconstruct stand densities using the point-center-quarter method (Bourdo 1956, Cottam and Curtis 1956). At Wolf Road, the PLS recorded two white oak witness trees at each of two points along the line between Sections 30 and 31. The mean distance of these trees corresponds to 3.5 trees ha⁻¹, which suggests open savanna conditions. Bur oak is now the dominant tree in this area and was apparently misidentified as

white oak by the surveyors, because an old-growth bur oak occurs at the witness tree location southwest of the southeast corner of Section 30 (M.L. Bowles, pers. obs.).

In 1924, WRP was purchased for residential development and subdivided into lots with roads and sidewalks; when the stock market crashed in 1929 the project was abandoned (Hanson 1975, Packard 1980). The land remained vacant due to fragmented ownership, lack of utilities, and new zoning ordinances requiring larger lot size, and was not further disturbed, except for use of some lots as "victory gardens" during World War II (LaForce 1988). Later human impacts included repeated burning, which helped maintain prairie and savanna vegetation. The Save the Prairie Society initiated preservation of WRP in 1974; by 1994, most of the area had been acquired by the Illinois Department of Natural Resources and Cook County Forest Preserve District and dedicated as an Illinois Nature Preserve. Municipal burning restrictions have prevented effective fire management of the preserve, and cutting, herbicide application, and mowing of invading gray dogwood (*Cornus racemosa*) and the alien buckthorns *Rhamnus cathartica* and *R. frangula* are now required to maintain the prairie (M.L. Bowles, pers. obs.).

A 1955 aerial photo (Figure 2) indicates about 2 ha of open savanna in the same location as mapped by the Public Land Survey. Adjacent prairie and savanna vegetation are distinct on the photo, and fewer than 10 trees are visible in the savanna, indicating a density of less than 5 trees ha⁻¹. Lower limbs are apparently absent from these trees, presumably a result of frequent intense fires. The same trees and vegetation pattern appear on a lower resolution 1938 aerial (not shown). The composition of the historic WRP savanna ground layer is unknown, and earlier surveys that focused on the prairie (e.g., White 1978) did not recognize the significance of its savanna. Oak savanna still occupies about 2 ha at WRP and forms a distinct prairie border at approximately the same position as in the 1955 aerial photo. However, an oak subcanopy now shades the

savanna ground layer, and a matrix of prairie vegetation occurs only in larger canopy gaps.

METHODS

Data Collection

Data were collected during the 1995 growing season from plots located along eight stratified random north-south transect lines across the savanna (Figure 3). Diameters were measured (at 1.4 m) for all live and dead trees in 71 circular 25-m² (0.0025 ha) plots centered along the transects at 10-m intervals. Trees at plot edges were included if their centers were within the plot radius. Multiple stem sprouts were measured and recorded individually as well as by number of multiple-stemmed trees. As in a Wisconsin study (Kline and McClintock 1994), some trees identified as *Q. ellipsoidalis* also had taxonomic features of *Q. velutina*; hybridization between these taxa may have occurred at the site. Increment cores were taken from borings made (at 1.4 m) to the centers of 11 trees randomly selected among the transects. Regression of annual growth ring counts and respective tree diameters provided the equation, Tree Age = 14.4 + 1.4 x diameter in cm ($r = 0.69$, $p = 0.02$), which was used to estimate ages of tree cohorts.

We recorded presence of all herb, shrub, woody vine, and tree species less than 1 m high in 142 rectangular 0.5-m² plots at 5-m intervals along the eight transects ($n = 12-20$ plots per transect). Within each plot, we also estimated cover by recording the number of 0.01-m² (1-dm²) cells within which each plant was rooted. Dividing the number of cells occupied by total number of cells (50) estimates plot cover at 2% intervals. Because of the presence of sterile plants and seedlings of *Allium cernuum*, *A. canadense*, *Geum laciniatum* var. *trichocarpum*, and *G. canadense*, and unidentifiable sterile plants or seedlings of *Bidens* spp., *Carex* sp. (excluding *C. pennsylvanica*), *Cirsium* sp., *Crataegus* sp., *Melilotus* sp., *Poa* sp., *Viola* sp., *Ulmus* sp., and *Prunus* sp., these taxa were treated at the genus level as species data from 0.5-m² plots. Solar radiation penetrating the

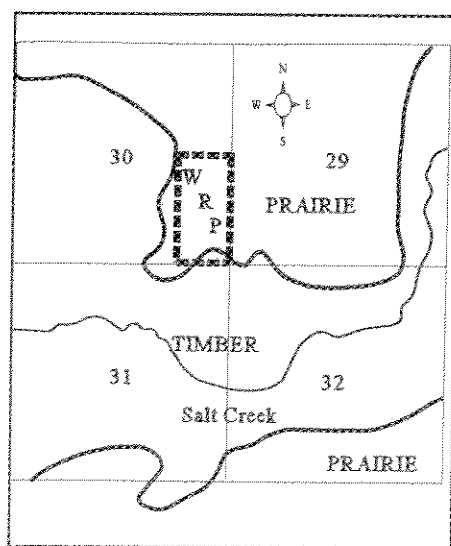


Figure 1. Distribution of timber and prairie (separated by heavy lines) at Wolf Road Prairie (WRP) in 1821. Map copied from original prepared from the U.S. Government Public Land Survey. Located in Township 30 North, Range 12 East, (41° 50' N latitude, 87° 54' W longitude). Wolf Road forms the east boundary of Section 30, and 31st Street forms its south boundary. Each Section is 1.6 km².

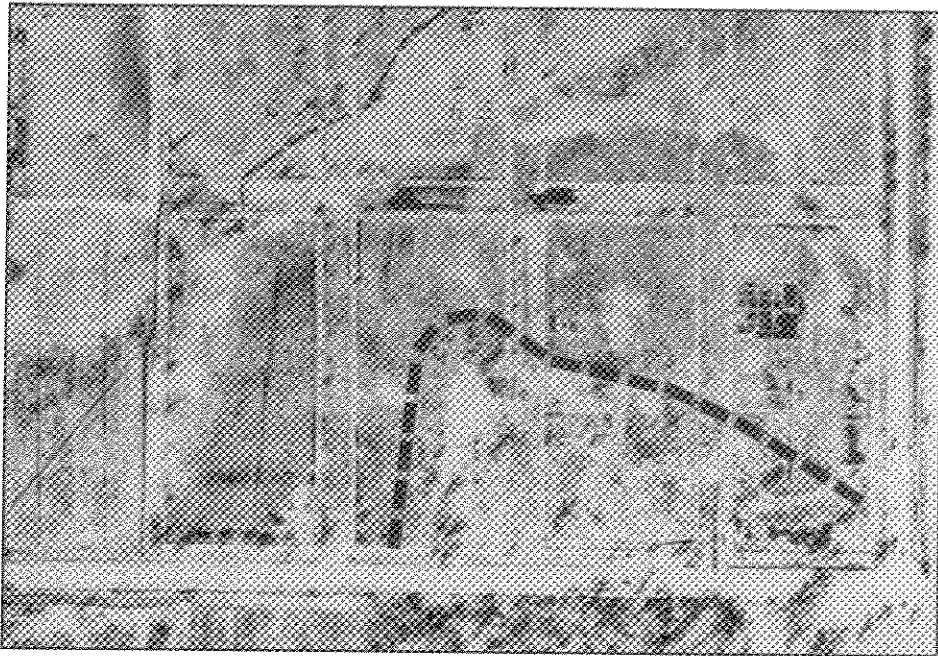


Figure 2. Aerial photo of savanna (south of dashed line) at Wolf Road Prairie on March 29, 1955. Location is based on tonal differences that correspond to historic (Figure 1) and modern (Figure 3) savanna and prairie location. Note absence of lower limbs on canopy trees. Human disturbances include ca. 1920s sidewalks (parallel white lines) and garden plots (dark squares). Top of photo is north. See Figure 3 for scale.

canopy was measured over each 0.5-m² plot under a clear sky between 11:00 am and 1:00 pm on September 2 and 3, 1995. These light levels were quantified by instantaneous measurements of lux (1 lumen per m²) at 1 m above each plot with

an Extech Instruments BF-232 digital light meter. Although instantaneous readings cannot characterize full growing season conditions, nor can lux measure photosynthetically active radiation (Anderson 1964), they allow identification of a canopy light

gradient and comparison with historic savanna light gradients measured in foot-candles (1FC = 10.76 lux) by Bray (1958). For comparisons to photosynthetically active radiation (PAR), we also approximated instantaneous PAR by the following formula: lux \times 0.018 = mol m⁻² s⁻¹ (Biggs 1984).

Data Analysis

Mean percent cover and frequency of ground-layer species in 0.5-m² plots were calculated by averaging these values across the eight sampling transects, and these species were then ranked by their Importance Values [IV = (relative frequency + relative cover) \div 2]. Tree species sampled from 25-m² plots were also ranked by their importance values [IV = (relative frequency + relative density + relative basal area) \div 3]. As indicated, tree cohort ages were estimated by the regression equation Tree Age = 14.4 + 1.4 \times diameter in cm, and per hectare stand densities of these cohorts were estimated from their sample plot densities. Historic (1955–1984) fire frequencies at WRP (presumably set by humans) were estimated by the number of fire alarm calls to the site, which were provided by the Westchester, Illinois, Fire Department. Such data cannot estimate fire intensity or coverage but can suggest mean annual fire rates. Ages of tree cohorts were then compared with these fire rates.

Herb-layer plots were separated into four groups by two-way indicator species analysis (TWINSPAN) of species cover using default options on PCORD software (McCune 1993). TWINSPAN uses reciprocal averaging to provide a polythetic divisive classification that separates species and plots across strong environmental gradients (Gauch 1982). We thus expected this procedure to classify herb-layer species groups in relation to light level and tree density gradients. For comparison, we also correlated light intensities with tree densities in the 0.0025-ha plots. We used one-way analysis of variance (Zar 1974) to test hypotheses of no significant differences in mean light values, tree densities, species richness, and alien species richness among the four TWINSPAN plot groups. Species with IVs $>$ 1.0 were then placed in light

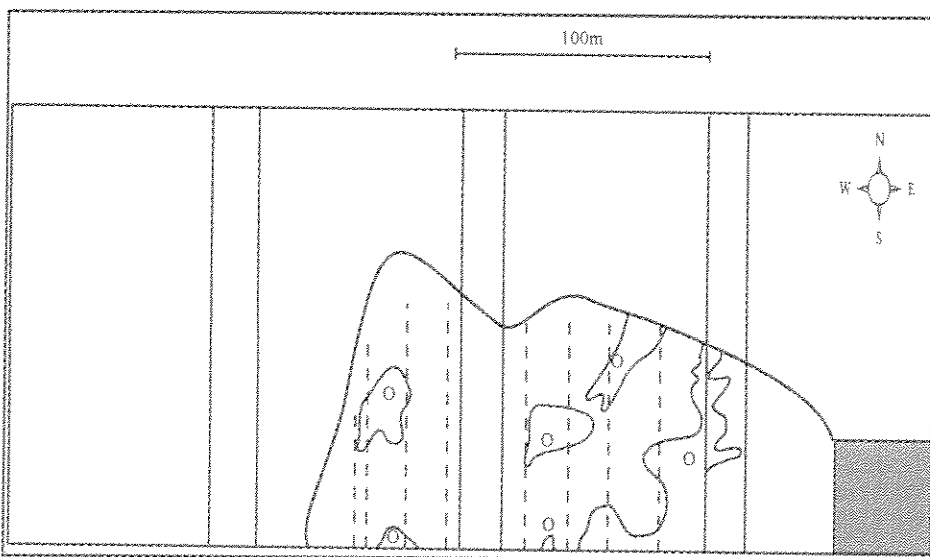


Figure 3. Modern location and canopy cover of savanna at Wolf Road Prairie. O = large canopy openings, parallel solid lines are sidewalks from ca. 1920s (see Figure 2). Dashed lines indicate sampling transect locations. Cross-hatched area is commercially developed.

preference categories following Bray (Table 18 in Curtis 1959), based on their distributions among the four TWINSPAN groups. We used Chi Square analysis (Zar 1974) to determine the probability that the proportion of plots occupied by each species did not differ among the four plot groups. Species were placed in a "low" light level category if their frequencies were greatest at lower light levels, or in a "high" light level category if their frequencies were greatest at higher light levels. Species were placed in an "intermediate" category if their frequencies were higher at intermediate light levels, or if their distributions did not differ across the light gradient.

RESULTS

Composition, Structure, and Chronological Change of Canopy and Subcanopy Trees

Six tree species representing 101 individual trees and 143 live and dead stems were sampled in the 71 25-m² plots, providing an estimate of 841 stems ha⁻¹ (Table 1). *Quercus macrocarpa* and *Q. ellipsoidalis* accounted for 91.4% of all tree species' IVs, and *Q. macrocarpa* was twice as important as *Q. ellipsoidalis*, reaching 43.7% frequency, 570.6 stems ha⁻¹, and 14.2 m² ha⁻¹ basal area (Table 1). Nearly 20% (19.6%) of all stems were dead, probably due to heavy subcanopy shade, with *Q. macrocarpa* accounting for 71.4% of this mortality. *Ulmus americana*, *Prunus serotina*, *Crataegus* sp., and *Acer negundo* com-

prised a minor component of the savanna.

The size class distribution of all trees was highly skewed, with only 11.2% of all stems greater than 0.25 m in diameter (Figure 4). Two *Q. macrocarpa* and one *Q. ellipsoidalis* greater than 60 cm in diameter were sampled; their estimated ages, which ranged from 90 to 150 years, indicate they originated between 1845 and 1905. The density estimate of trees from this cohort is 17.6 trees ha⁻¹, which would have favored savanna conditions during this time period. Thirteen oaks between 25 and 40 cm in diameter were sampled; their estimated ages (44–73 years) indicate that they originated between 1920 and 1951. These younger trees give a density estimate of 73.3 trees ha⁻¹, indicating a gain in tree density and canopy shade during this period. However, these trees are not apparent on the 1938 or 1955 aerial photos.

Eighty-eight percent of the 143 stems sampled were less than 25 cm in diameter and averaged 28 (\pm 1.36 SE) years in age, indicating that most trees originated in about 1967. This corresponds to a time period in which fire calls to WRP dropped from more than one to less than one annually (Figure 5). Many of the oaks were apparently maintained as postfire-sprouting grubs by frequent fires: 58% of all stems occurred in 41 multiple-stemmed trees (40.6% of all trees) with large rootstocks at the soil surface, suggesting at least 231 grubs ha⁻¹ in 1965. Trees were absent from 22 of the 71 25-m² plots, indicating that at least 31% of the area was

originally free of grubs. If trees with single stems originated from seed, a larger area was originally without grubs.

Composition of Herb-Layer Vegetation

The savanna ground layer at WRP is forb dominated (IV = 76.8), with a minor component of shrubs (IV = 18.8) and even less graminoid vegetation (IV = 4.4). Among the 96 species sampled, 11 species accounted for more than 50% of importance. *Camassia scilloides* was the most important species, with decreasing importance for *Circaea lutetiana*, *Geum* spp., the shrub *Cornus racemosa*, *Smilacina stellata*, *Eupatorium rugosum*, the shrub *Rubus allegheniensis*, *Allium* spp., *Solidago altissima*, *Polygonum virginianum*, and the invasive alien species garlic mustard *Alliaria petiolata* (Table 2). *Camassia scilloides* achieved its high IV because its 14% cover was almost three times that of *C. lutetiana*, the species with second highest mean cover. In contrast, mean plot frequencies were similar for these 11 species, ranging from 32.3% to 40.5% (Table 2). An additional 14 species had IVs >1.0, increasing the cumulative IV to more than 75 (Table 2). These species included a single graminoid species, the woodland sedge *Carex pensylvanica*, four species of open prairie-like habitats (*Fragaria virginiana*, *Potentilla simplex*, *Rosa carolina*, and *Solidago graminifolia*), the alien shrub *Rhamnus frangula*, and seven species that usually occur in forest or woodland habitats (Table 2).

Table 1. Composition and structure of canopy and subcanopy live trees at Wolf Road Prairie, Cook County, Illinois, based on 71 0.0025-ha plots. Density is per hectare, and basal area is square meters per hectare.

	% Frequency	Relative Frequency	Stem Density	Relative Density	Basal Area	Relative B.A.	Importance value
<i>Acer negundo</i>	1.41	1.85	5.88	0.70	0.09	0.34	0.96
<i>Crataegus</i> spp.	1.41	1.85	5.88	0.70	0.10	0.39	0.98
<i>Prunus serotina</i>	4.23	5.56	41.18	4.90	0.69	2.71	4.39
<i>Quercus ellipsoidalis</i>	22.54	29.63	205.88	24.48	9.79	38.70	30.94
<i>Quercus macrocarpa</i>	43.66	57.41	570.59	67.83	14.22	56.19	60.48
<i>Ulmus americana</i>	2.82	3.70	11.76	1.40	0.42	1.66	2.25
Total	76.07	100	841.17	100	25.31	100	100

Effects of Light Levels and Tree Density on Vegetation Pattern

Tree density and light intensity were significantly negatively correlated ($r = 0.29$, $P = 0.01$). TWINSpan classified four species plot groups corresponding to significant light and tree density gradients (Figure 6a) extending from 7,950 (± 594) lux under highest tree density (3.1 ± 0.58 trees 25 m^{-2}) to 45,920 (± 594) lux under lowest tree density (0.56 ± 0.29 trees 25 m^{-2}). This range of light corresponds to 738.8–4267.7 FC, and approximate instantaneous PAR readings ranging from ~ 143 –827 $\text{mol m}^{-2} \text{ s}^{-1}$ (see Table 3 for comparison of mean Lux, FC, and PAR). We refer to the highest light category as a canopy-gap because mean tree density was less than one stem per plot, and tree sampling plots were greater than 5 m across (Brokaw 1982). Ground-layer plots were most abundant in the two TWINSpan categories with lower light levels, which accounted for 65% of all plots. Mean ground-layer species richness was significantly higher under higher light levels, with more than 12 species per plot in canopy gaps and fewer than 10 under greater canopy shade (Figure 6b). Alien species richness, primarily *Alliaria petiolata* and *Solanum dulcamara*, was significantly higher under lower light levels, with more than one alien species per plot in canopy shade and less than one in canopy gaps. Spatial vegetation structure also responded to the light gradient, with graminoid species essentially restricted to canopy gaps (Figure 6c).

The 25 most abundant species (i.e., species with $IV > 1.0$ and total $IV > 75$), were almost equally distributed among the three light levels, with significantly different frequency distributions for species in the highest and lowest light level categories (Figure 7). Species that were most abundant at lower light levels had greater importance (total $IV = 36.34$) than species in the intermediate ($IV = 21.78$) or high ($IV = 18.21$) light level categories. Among the eight species most important at lower light levels, the alien mustard *Alliaria petiolata*, *Anemone thalictroides*, *Circaea lutetiana*, *Geum* spp., and *Smilacina stellata* were unimodally distributed. However, *Polygonum virginianum*, *Camassia scil-*

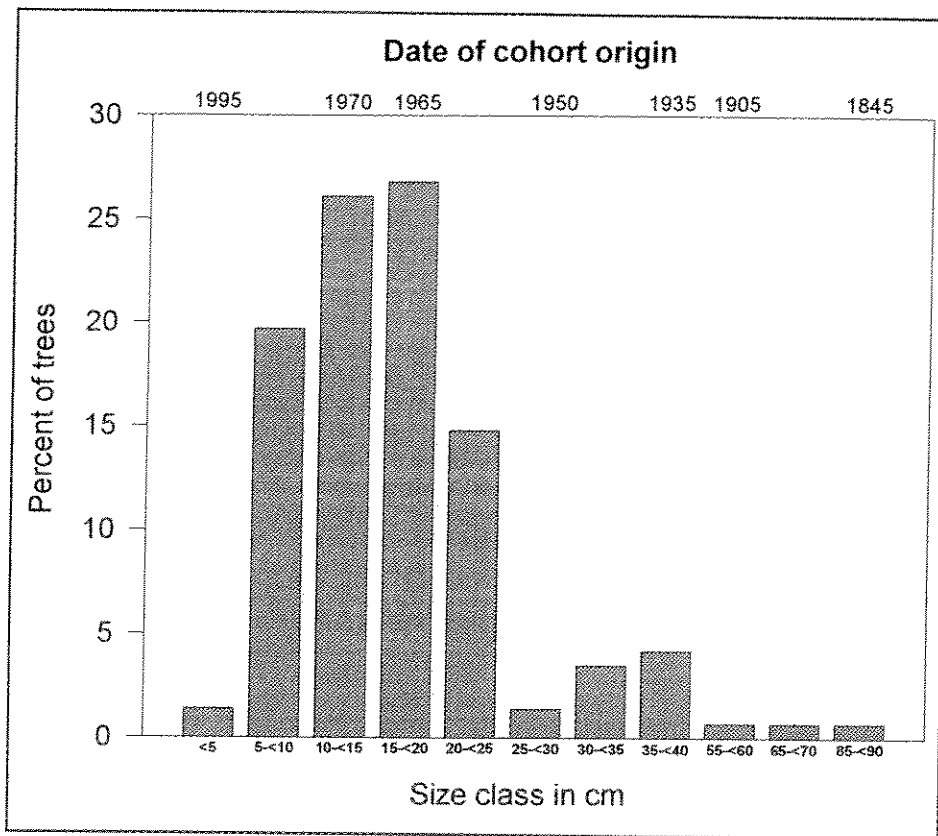


Figure 4. Estimates of percent tree distribution by 0.05-m diameter size class and chronology of tree cohort origin in savanna at Wolf Road Prairie. Based on 115 live trees sampled in 25 m^2 plots, and the regression equation: Tree Age = $14.4 + 1.4 \times \text{diameter in cm}$ ($r = 0.69$, $p = 0.02$).

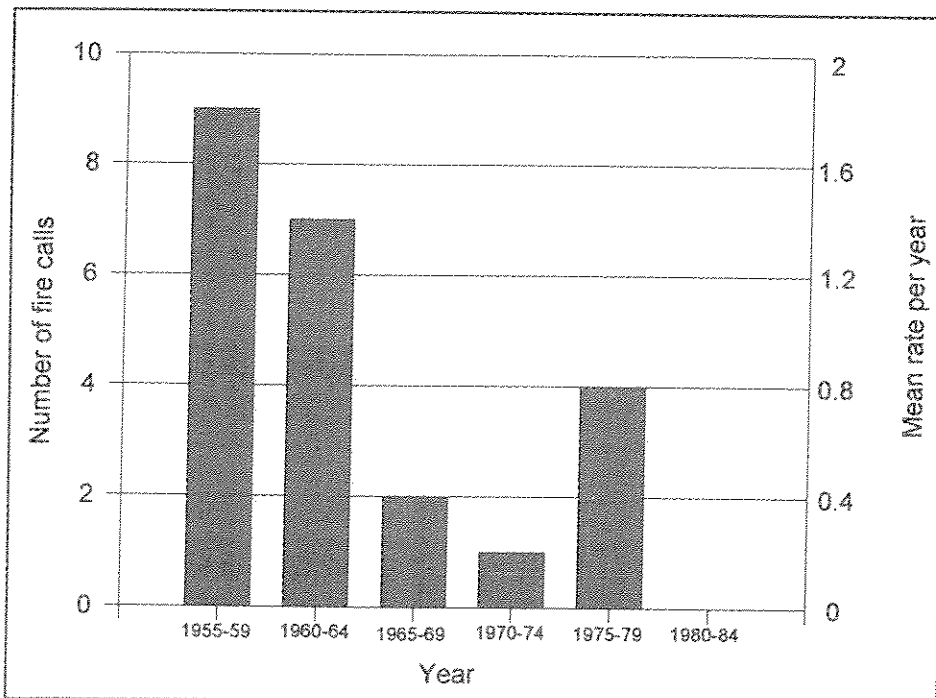


Figure 5. Five-year fire call frequency and mean annual number of fires calls by the Westchester, Illinois, Fire Department to Wolf Road Prairie between 1955 and 1984.

Table 2. Mean (\pm SE) percent plot cover and frequency, and importance values (IV) of ground layer vegetation with IV >1.0 in savanna at Wolf Road Prairie. Plot cover and frequency are averaged among eight sampling transects. IVs are based on relative cover and frequency among all 142 0.5-m²plots.

Species	Mean (\pm se) % Cover	Mean (\pm se) % Frequency	Importance Value
<i>Camassia scilloides</i>	14.0 \pm 0.4	40.5 \pm 9.1	8.1
<i>Circaea lutetiana</i>	5.5 \pm 0.1	49.5 \pm 12.6	6.7
<i>Geum</i> spp.	4.0 \pm 0.2	43.7 \pm 10.4	5.0
<i>Cornus racemosa</i>	2.75 \pm 0.1	51.6 \pm 7.1	4.8
<i>Smilacina stellata</i>	3.9 \pm 0.1	46.0 \pm 7.4	4.8
<i>Eupatorium rugosum</i>	3.5 \pm 0.1	39.6 \pm 4.7	4.4
<i>Rubus allegheniensis</i>	2.4 \pm 0.003	52.43 \pm 5.3	4.25
<i>Allium</i> spp.	5.1 \pm 0.1	43.5 \pm 8.6	4.1
<i>Solidago altissima</i>	3.5 \pm 0.1	31.0 \pm 3.8	3.9
<i>Polygonum virginianum</i>	2.9 \pm 0.1	33.54 \pm 5.6	3.5
<i>Alliaria petiolata</i>	2.5 \pm 0.1	32.3 \pm 6.4	3.3
<i>Oxalis stricta</i>	1.9 \pm 0.1	31.0 \pm 5.1	2.9
<i>Carex pensylvanica</i>	3.9 \pm 0.2	13.2 \pm 5.4	2.8
<i>Anemonella thalictroides</i>	2.4 \pm 0.1	15.3 \pm 5.6	2.5
<i>Geranium maculatum</i>	1.5 \pm 0.003	24.0 \pm 2.8	2.3
<i>Solidago graminifolia</i>	2.1 \pm 0.1	14.7 \pm 3.4	2.1
<i>Rhamnus frangula</i>	1.2 \pm 0.005	20.4 \pm 7.1	1.8
<i>Helianthus strumosus</i>	1.8 \pm 0.1	12.4 \pm 4.2	1.7
<i>Polygonatum canaliculatum</i>	1.0 \pm 0.004	16.0 \pm 6.0	1.5
<i>Potentilla simplex</i>	0.9 \pm 0.004	14.4 \pm 4.2	1.3
<i>Smilacina racemosa</i>	0.7 \pm 0.002	14.3 \pm 2.2	1.2
<i>Rosa carolina</i>	0.6 \pm 0.002	16.3 \pm 4.8	1.2
<i>Prunus serotina</i>	0.6 \pm 0.003	14.2 \pm 5.5	1.2
<i>Aster sagittifolius</i>	0.5 \pm 0.002	14.9 \pm 3.9	1.1
<i>Fragaria virginiana</i>	0.6 \pm 0.003	10.3 \pm 3.1	1.0

loides, and *Geranium maculatum* had strongly bimodal distributions, with high frequencies at low light levels and in light gaps. In contrast, none of the important high light level species were frequent in the lowest light level categories. Important woodland species at higher light levels were the blackberry *Rubus allegheniensis*, the sunflower *Helianthus strumosus*, and the sedge *Carex pensylvanica*. Other species that were most abundant at higher light levels, and which often occur in prairies, were the shrub *Rosa carolina*, and the herbaceous species *Potentilla simplex*, *Fragaria virginiana*, *Solidago altissima*, and *S. graminifolia*. As no species had higher frequencies at intermediate light levels, the nine species in this category appear to be generalists within the range

of light available at WRP. Three invasive woody species were in this generalist category: the native shrub *Cornus racemosa* and tree *Prunus serotina*, and the alien shrub *Rhamnus frangula*. Intermediate herbaceous species were *Aster sagittifolius*, *Eupatorium rugosum*, *Oxalis stricta*, *Allium* spp., *Smilacina racemosa*, and *Polygonatum canaliculatum*.

The 66 less important species (IV <1.0) were distributed discontinuously across the light gradient (Table 3). Only seven of these species are present in all four light categories, and few appear to be restricted to the intermediate light level at WRP. Thirty-eight of the less important species, 20 of which were typical prairie species, as determined from Swink and Wilhelm

(1994), were most frequent in the two highest light levels. Thus, half of the uncommon species contributed to species richness under higher light levels, and the majority are prairie species. In addition, all but two prairie species had their highest frequencies in the two highest light categories, and nine of the ten species restricted to the highest light category were prairie species, including the characteristic prairie grasses *Andropogon gerardii* and *A. scoparius*. Other grass species (*Elymus virginicus*, *Panicum implicatum*, and *Poa* sp.) were also restricted to the two highest light categories. Among woody plants, the prairie shrub *Salix humilis*, the grape vine *Vitis riparia*, and the alien shrub *Lonicera tatarica* were most abundant at higher light levels. *Corylus americana*, *Smilax lasion-eura*, *Parthenocissus quinquefolia*, and *Rhus radicans*, were most frequent at lower light levels. However, *C. americana* was light sensitive, occurring along the edge of the largest light gap and as small clones under subcanopy shade or in smaller canopy openings.

DISCUSSION

Temporal Persistence and Change in Savanna Vegetation Structure

Savanna has persisted in the same position at Wolf Road Prairie as recorded by the Public Land Survey in 1820. Tree density also appears to have been stable until about 1955, probably due to fire resistance of the adult trees and, possibly, reduced fuel loads under tree canopies (Anderson and Brown 1983). Although a gradual increase in tree density had begun by the 1950s, the most dramatic change occurred after 1965, when the savanna oak grubs rapidly developed into a *Quercus macrocarpa*-dominated subcanopy. This rapid change in a formerly stable community correlates with reduced fire frequencies (Cole and Taylor 1995).

Fire history and the condition of surrounding vegetation suggest that spatial structure of the savanna ground layer at WRP may have been relatively stable until the mid-1960s. Although no data are available on the historic composition of the savanna ground layer, frequent fires and high light

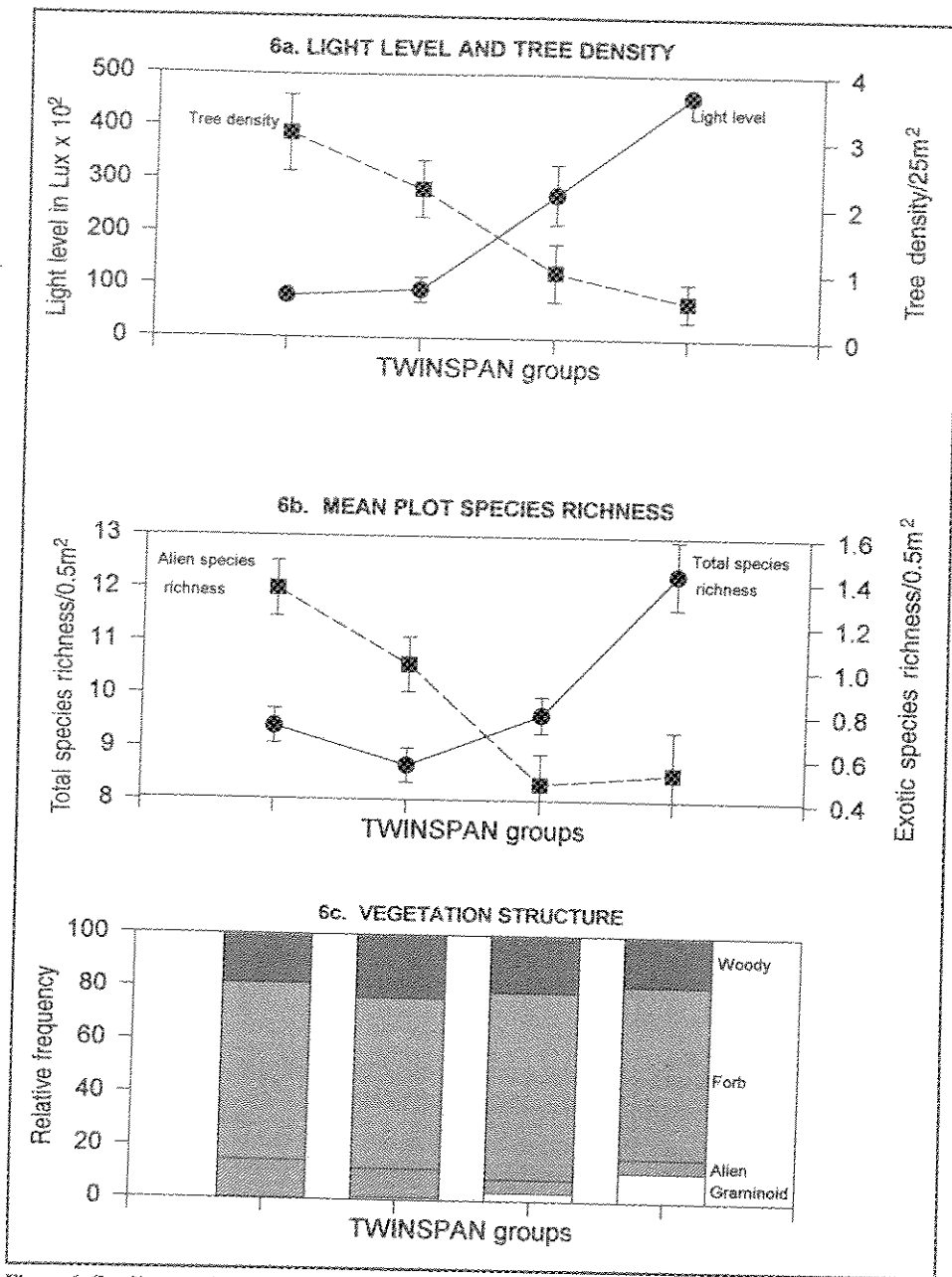


Figure 6. Gradient analysis of relationships between mean light intensity and tree density (6a), and their effects on plot species richness and plot alien species richness (6b) and vegetation structure (6c) among four TWINSpan groups across the horizontal axis. Bars indicate standard errors. Significant differences occur among groups for mean light levels ($F_{3, 137} = 13.7, P < 0.0001$), mean tree density ($F_{3, 66} = 4.29, P = 0.0079$), mean plot species richness ($F_{3, 137} = 11.21, P < 0.0001$), and mean plot alien richness ($F_{3, 137} = 7.10, P = 0.0002$).

levels associated with an open canopy probably selected for high graminoid cover and reduced woody vegetation (Skarpe 1992). We presume that prairie species were important because they remain present in larger canopy gaps and comprise the adjacent prairie. However, oak grubs were apparently a strong component of the savanna, as trees occurred in

69% of all tree sample plots and 40.6% of all trees had multiple stems, suggesting they arose from grub sprouts.

The change in structure from an open matrix with few canopy trees in 1965 to a closed canopy matrix with few gaps by 1995 has shifted community patch dynamics from savanna (shade gap) toward forest (light gap)

processes (Belsky and Canham 1994). The present ground layer composition probably resulted from a vegetation shift corresponding to this change, with an expansion of species adapted to lower and intermediate light levels and loss of high light level species. This process would have restricted a strong prairie component to the few savanna light gaps, causing the current rarity of most of these species. Reduced fire frequency also may have directly affected the abundance of prairie and graminoid species. Pruka (1994a) found that sedges replaced grasses under reduced light levels in a Wisconsin savanna, but this transition is weak at WRP. Bray (1958) recorded prairie species even in the lowest light regime in Wisconsin savannas, and at least some of his study sites had been burned (G. Ware, Morton Arboretum, Illinois, pers. com.). Prairie grasses and forbs increase with increased burning frequency of sand savannas (Tester 1989), and frequent fire increases cover of graminoid fuel species in prairie (Collins and Glenn 1988, Collins and Gibson 1990) and fen (Bowles et al. 1996) vegetation. As a result, we hypothesize that, in addition to direct shading, 20 years of low fire frequency at WRP contributed to the loss of prairie species, as well as other graminoid species such as *Carex pensylvanica*, from areas of reduced light.

Relationship Between Canopy Light Gradient and Species Distribution

The range of mean light intensities (8,000–46,000 lux) in savanna at WRP corresponds to the range of light intensities (~800–4,600 FC) that Bray (1958) found for partial shade-adapted Wisconsin savanna species. The highest mean light category at WRP is approximately the midpoint of Bray's intermediate light category for savanna (Table 18 in Curtis 1959).

This restricted savanna light gradient at WRP now controls its ground-layer composition and structure. The positive association between species richness, high light levels, and low tree stem densities at WRP correlates with other findings that fire protection reduces ground-layer species richness in oak savanna (Pruka 1994a, 1994b) and flatwoods (Taft et al. 1995) by reducing light levels in these habitats. Higher alien species richness in reduced light is

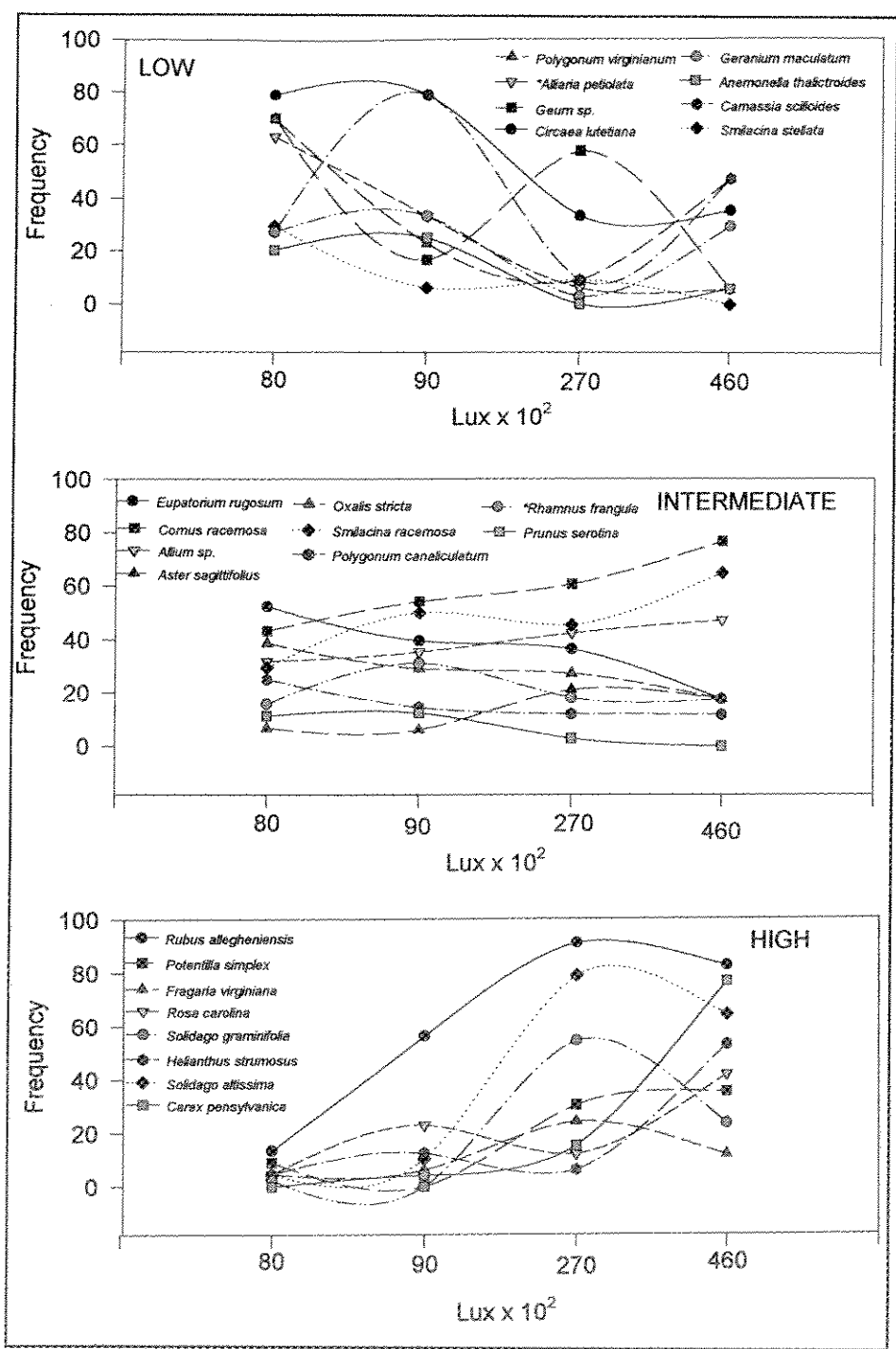


Figure 7. Frequency distribution of common ($IV > 1.0$) vegetation along a savanna light gradient at Wolf Road Prairie. Sample size: 80×10^2 Lux ($N = 44$ plots), 90×10^2 Lux ($N = 48$ plots), 270×10^2 Lux ($N = 33$ plots), 460×10^2 Lux ($N = 17$ plots). All P values are < 0.05 for LOW and HIGH light level species, and > 0.05 for INTERMEDIATE light level species. Alien species are indicated by an asterisk.

due primarily to concentrations of the garlic mustard (*Alliaria petiolata*), which colonizes bare ground at the bases of subcanopy trees, and greater occurrences of *Solanum dulcamara* under low light levels. However, the invasive alien shrub

Rhamnus frangula occurs across the light gradient at WRP savanna. This species, as well as the native dogwood *Cornus racemosa*, is bird dispersed; both species probably increased with use of the subcanopy by birds. As indicated, *Corylus americana*,

na, a characteristic savanna shrub (Cottam 1949, McAndrews 1966, Bowles and McBride 1994), is much less frequent and more restricted to canopy gaps at WRP.

Although prairie species, especially grasses, are essentially restricted to canopy gaps, these habitats are dominated by nonprairie species that probably shifted into this habitat as fire protection increased shade and reduced graminoid competition. Indeed, only four high-light-preferring species, *Potentilla simplex*, *Rosa carolina*, *Helianthus strumosus*, and *Carex pensylvanica*, are most abundant in canopy gaps. Two of these species, *P. simplex* and *H. strumosus*, are strongly rhizomatous, which may facilitate rapid exploitation of this habitat. For example, *Rubus allegheniensis*, the most important canopy-gap species, is slightly more abundant at lower light levels and could have easily spread into canopy gaps by its arching canes. The other strongly rhizomatous or clonal species, *Cornus racemosa*, *Solidago altissima*, and *S. graminifolia*, also predominate in the second highest light level.

Species that occur in lower and intermediate light levels at WRP, such as *Anemone thalictroides*, *Circaea lutetiana*, *Geranium maculatum*, *Smilacina racemosa*, *S. stellata*, *Polygonum canaliculatum*, and *Polygonum virginianum*, may be spatially stable "light-flexible herbs" (Collins et al. 1985). Such species tolerate shade, use light flecks, and flower and fruit more frequently in relation to inherent size or as canopy gaps or edge develop (e.g., Zangerl and Bazzaz 1983, Lee et al. 1986, Dahlem and Boerner 1987, Piper 1989). However, many of these species require disturbance gaps for regeneration (Thompson 1980), and their current spatial patterns may reflect past events and differing life-history strategies. The bimodal distribution of *Camassia scilloides*, *G. maculatum*, and *P. virginianum*, with high frequencies in shade and light categories, suggests that they can tolerate dynamic canopy change. Although not measured, shrub layer cover above 1 m, especially from *Rubus allegheniensis*, becomes extensive in parts of the savanna by midsummer and probably further reduces ground-layer light levels. As a result, ephemeral growth also may char-

acterize some savanna species, allowing completion of much of their growth cycle before canopy closure (Gustafson and Anderson 1994). For example, *C. scilloides* and *Allium canadense* flower, disperse seed, and senesce by midseason. *Allium cernuum* flowers later and often occurs in prairie (Swink and Wilhelm 1994). The absence of species restricted to an intermediate light level at WRP suggests that many nonprairie species that occur in savanna are generalists. However, the restricted range of light at WRP prevents determining how such species are distributed across the wider range of light that Bray found in Wisconsin savannas. Some bimodal species (such as *C. scilloides*) are clearly not typical forest or prairie species and may be adapted to savanna habitat.

Restoration Needs and Implications

Wolf Road Prairie contains one of the few remaining tracts of original midwestern savanna and has high conservation value (Shafer 1995). While vegetation change is natural and expected (Pickett et al. 1992), and high fire frequencies that stabilized savanna at the time of European settlement were anthropogenic (Curtis 1959, Cole and Taylor 1995), it is important to restore the fire regime and open savanna canopy structure to that which occurred at WRP prior to 1955. Because of the positive relationship between light level and species richness and the negative relationship between light level and alien species richness at WRP, such management would increase small-scale species richness and alpha diversity while reducing alien species in a locally rare natural area. Such restoration also could provide components of a necessary reference system for community restoration (Aronson et al. 1995), which currently is lacking for midwestern savanna (Leach and Ross 1995). Perhaps the greatest impediment to restoration is the 2-ha size and fragmented nature of savanna at WRP, which prevent restoration of landscape-scale processes (Hobbs and Norton 1996).

A primary management objective should be to restore former savanna canopy and grub structure, while allowing for recruitment of new canopy trees. Many of the

Table 3. Frequency distribution of uncommon species (IV <1.0) arranged by TWINSpan plot groups along a savanna light gradient at Wolf Road Prairie. A = alien, G = graminoid, P = prairie species, W = woody. See Figures 6 and 7 for further description of light gradient. N = number of plots in each group. Mean FC calculated from the formula: $1FC = 10.76 \text{ lux}$. Mean instantaneous PAR approximated by the formula: $\text{lux} \times 0.018 = \text{mol m}^{-2} \text{ s}^{-1}$ (Biggs 1984).

		Light Gradient			
Mean Lux x 10 ² ±se		79.5 ±5.94	91.5 ±23.99	272.6 ±56.2	459.2 ±5.94
Mean FC		738.8	850.4	2533.5	4267.7
Mean PAR		-143.1	-164.7	-490.7	-826.6
		N = 44	N = 48	N = 33	N = 17
W	<i>Prunus virginiana</i>	11.4			
	<i>Chenopodium album</i>	4.5			
W	<i>Quercus ellipsoidalis</i>	4.5			
	<i>Erythronium albidum</i>	2.3			
W	<i>Fraxinus pennsylvanica</i>	2.3			
	<i>Sanicula gregaria</i>	2.3			
P	<i>Zizia aurea</i>	2.3			
W	<i>Crataegus</i> spp.	6.8	4.2		
W	<i>Corylus americana</i>	2.3	12.5		
A	<i>Epipactis helleborine</i>	6.8	2.1		
W	<i>Smilax lasioneura</i>	20.5	10.4		
A	<i>Arctium minus</i>		4.2		
W	<i>Sambucus canadensis</i>	2.3		3.0	
A	<i>Solanum dulcamara</i>	25.0	22.9	3.0	
	<i>Prenanthes alba</i>	8.3	6.1	5.9	
	<i>Hackelia virginiana</i>	9.1	2.1	3.0	
W	<i>Rhus radicans</i>	9.1	2.1	3.0	
	<i>Lilium michiganense</i>		6.2	3.0	
A,W	<i>Rhamnus cathartica</i>	18.2	4.2	3.0	5.9
	<i>Thalictrum dasycarpum</i>	15.9	6.2	12.1	11.8
W	<i>Parthenocissus quinquefolia</i>	6.8	2.1	5.9	
	<i>Solidago caesia</i>	2.3	2.1	21.2	
	<i>Convolvulus sepium</i>	4.5	8.3	18.2	
	<i>Bidens</i> sp.	9.1	2.1	12.1	
	<i>Aster lateriflorus</i>	6.8	2.1	9.1	
	<i>Hypericum</i> sp.		2.1	6.1	
	<i>Rubus occidentalis</i>	6.8	10.4	9.1	5.9
	<i>Viola</i> spp.	13.6	12.5	24.2	17.6
W	<i>Vitis riparia</i>	9.1	2.1	6.0	17.7
P	<i>Parthenium integrifolium</i>	4.5	2.1		5.9
W	<i>Acer negundo</i>	4.5			5.9
P	<i>Dodecatheon meadia</i>	4.5			5.9
P	<i>Silphium terebinthinaceum</i>	2.3	2.1	3.0	17.6
	<i>Agrimonia gryposepala</i>	4.5	2.1	3.0	11.8
	<i>Cirsium</i> spp.	4.5		3.0	5.9
G	<i>Elymus virginicus</i>			2.1	
G	<i>Panicum implicatum</i>			6.1	
	<i>Arisaema dracontium</i>			3.0	
P	<i>Aster laevis</i>			3.0	
G	<i>Cinna arundinacea</i>			3.0	
A	<i>Convallaria majalis</i>			3.0	

table continued

Table 3, continued

		Light Gradient			
Mean Lux x 10 ² ±se		79.5 ±5.94	91.5 ±23.99	272.6 ±56.2	459.2 ±5.94
Mean FC		738.8	850.4	2533.5	4267.7
Mean PAR		-143.1	-164.7	-490.7	-826.6
		N = 44	N = 48	N = 33	N = 17
P	<i>Eryngium yuccifolium</i>			3.0	
	<i>Eupatorium serotinum</i>			3.0	
	<i>Gaura biennis</i>			3.0	
	<i>Erigeron philadelphicus</i>			3.0	
A	<i>Taraxacum officinale</i>		2.1	6.1	11.8
P	<i>Tradescantia ohiensis</i>		2.1		17.6
	<i>Carex</i> spp.	2.3	2.1	9.1	23.5
	<i>Asclepias purpurascens</i>		2.1		5.9
G	<i>Poa</i> spp.			6.1	5.9
P,W	<i>Salix humilis</i>			6.1	5.9
A,W	<i>Lonicera tatarica</i>			3.0	5.9
P	<i>Silphium integrifolium</i>			3.0	5.9
P	<i>Solidago juncea</i>			3.0	17.6
W	<i>Vitis vulpina</i>			6.1	11.8
P	<i>Monarda fistulosa</i>			3.0	11.8
P	<i>Solidago gigantea</i>			6.1	29.4
G,P	<i>Andropogon scoparius</i>				5.9
A	<i>Daucus carota</i>				5.9
P	<i>Helianthus grosseserratus</i>				5.9
P	<i>Coreopsis tripteris</i>				11.8
P	<i>Prenanthes aspera</i>				11.8
G,P	<i>Andropogon gerardii</i>				17.6
P	<i>Oxypolis rigidior</i>				17.6

oaks present on the 1955 aerial photograph are still present in the savanna and should be retained while returning the 30-year-old cohort to a grub level. Because oaks sprout after fire (Curtis 1959, Anderson and Brown 1983, Lorimer 1987, Reich et al. 1990, Sieg and Wright 1996), burning would appear to facilitate restoration of the grub layer. However, several factors constrain this approach. Presettlement fires occurred in a landscape context, and may have been most effective on woody plants during drought conditions (Anderson 1982). As a result, their intensity may not be replicable in a fragmented preserve, especially under municipal fire restrictions. In a small preserve, annual burning also must be placed in context with the need to protect fire-sensitive or-

ganisms such as insects (Panzer 1988). Further, 30-year-old subcanopy oaks will probably be resistant to top-killing by fire. Two annual burns did not open a Wisconsin oak forest canopy (Kline and McClintock 1994) nor top-kill *Q. macrocarpa* saplings (Hruska and Ebinger 1995), and 13 annual spring burns did not affect greater than 25 cm dbh *Q. ellipsoidalis* (White 1983, Tester 1989). The low importance of graminoid fuel at WRP may further reduce fire effects on oaks. A necessary alternative appears to be cutting or girdling of the subcanopy oaks, which would result in resprouting and formation of a grub layer that could then be maintained by fire. Such treatments should be experimental, using plots at least 25 m² in size, in which we found canopy openings with

less than one tree to have significant effects on ground-layer vegetation. A critical need is to determine the appropriate fire frequencies and intensities needed to maintain oak grubs.

A second objective in opening the savanna canopy is to allow spatial adjustment of the WRP savanna ground-layer vegetation along the changing light gradient, including maximizing native species richness, and reducing aliens. These shifts in species abundance also should be experimentally monitored to provide important savanna restoration information. For example, what degree of canopy opening threatens native low light level species, and does bimodality in some species buffer against canopy reduction? The assemblage of species expected to colonize enlarged canopy gaps is likely to include strongly clonal species in adjacent vegetation, or species with wind or animal dispersed propagules. As grasses and sedges are nearly eliminated, they may fail to recolonize without introduction (Kline and McClintock 1994), and their absence may facilitate woody invasion of new canopy gaps. Few savanna species have appeared from soil seed banks after burning and canopy restoration (Packard 1988b), and late-successional prairie species which might occur in savanna are also poorly represented in soil seed banks (Johnson and Anderson 1986).

An important concern also is the need to remove the alien shrubs *R. frangula* and *R. cathartica* from the savanna, especially since they may expand into newly restored canopy gaps. Prescribed burning is not always effective in permanently reducing these species because they sprout after fire, and supplemental herbicide application may be required to remove them (Heidorn 1991). *Prunus serotina* also responds positively to light gaps (McCune and Cottam 1985) and may increase if burns are infrequent. Ideally, *Alliaria petiolata* should be reduced by increasing light levels, but it also may expand into new canopy gaps if they are free of competition (Anderson et al. 1996), such as from grasses. More information is needed on the abundance and diversity of ground-layer species along savanna light gradients in relation to dif-

fering burn frequencies in order to guide their recovery at WRP and other savanna restorations.

SUMMARY AND CONCLUSIONS

Because savannas on silt loam soils disappeared soon after European settlement of midwestern North America, the restoration management of savanna remnants is important; but precise savanna models are lacking and specific restoration goals are uncertain. Wolf Road Prairie contains one of only a few mesic savanna remnants, and its vegetation may have been relatively stable until the late 1960s. Recent fire protection has allowed *Q. macrocarpa* and *Q. ellipsoidalis* grubs to mature into a subcanopy that dominates the ground layer, a landscape-scale process that occurred a century earlier throughout the Midwest. Although savannas are often thought to have graminoid-dominated understories, the presence of former oak grubs at WRP suggests that this may have been a common savanna feature. The presence of oak grubs allows rapid conversion to forest after fire suppression. Because most of the WRP savanna canopy is now closed, its species align along only a portion of the savanna light gradient identified by Bray (1958) for Wisconsin savannas, and its community dynamics have shifted toward gap processes. Despite the almost total absence of graminoid species, forest species such as spring ephemerals also are rare at WRP. The herbaceous species that are present apparently provide a rare example of savanna ground-layer composition, such as dominance by *Camassia scilloides*. The positive relationship between light and species richness, and the negative relationship between light and alien richness strongly suggest that savanna management objectives at WRP should include a return to higher light levels and fire frequencies. However, the maturity of subcanopy trees and the lack of landscape-scale fire effects will limit attempts to restore former savanna structure without supplemental cutting. As a result, an experimental approach is needed to understand the different effects of fire and cutting on restoration of original savanna structure at WRP.

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