

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Canopy cover and groundlayer vegetation dynamics in a fire managed eastern sand savanna

Marlin Bowles^{a,*}, Steven Apfelbaum^b, Alan Haney^c, Susan Lehnhardt^b, Tom Post^d

^aThe Morton Arboretum, Lisle, IL 60532, USA

^bApplied Ecological Services, Brodhead, WI 53520, USA

^cCollege of Natural Resources, University of Wisconsin-Stevens Point, Stevens Point, WI 54481, USA

^dDivision of Nature Preserves, Indiana Department of Natural Resources, Medaryville, IN 47957, USA

ARTICLE INFO

Article history:

Received 26 May 2011

Received in revised form 20 August 2011

Accepted 21 August 2011

Keywords:

Canopy cover gradient

Functional groups

Species richness

Topographic gradient

Repeated burning

Temporal change

ABSTRACT

Savanna vegetation is characterized by high and variable ground layer species richness regulated by functional group interactions with fire regimes and canopy cover. Frequent fire selects for C4 grasses and prairie forbs in canopy openings and C3 graminoid species and shade-adapted forbs and shrubs in canopy shade. Frequent fire also maximizes heterogeneity in partial canopy cover and species richness across the full canopy gradient. However, few studies have linked fire induced change in tree canopy cover with groundlayer vegetation dynamics in relation to this model. In 1986 and in 2007, we measured canopy cover and sampled groundlayer vegetation in 1 m² plots along 53 transects at the Tefft Savanna, a fire managed 197 ha eastern sand savanna with strong canopy cover and elevation gradients. We analyzed temporal change in canopy cover and groundlayer vegetation, correlating percent change in canopy cover with change in ground layer functional groups. After 20 years of burning at 3 fires/decade, elevation accounted for 62% of the variation in an NMS ordination of groundlayer vegetation. However, canopy cover, which averaged 24–86% in 2007, had a significant secondary effect on the ordination. Five vegetation types classified by TWINSPLAN varied significantly in elevation and canopy cover. Woody vegetation comprised 8 of the 12 species with greatest niche breadths, and tended to predominant in woodland or forest, where tree cover averaged 50% or more. Forbs had greater richness in savanna, which averaged less than 30% canopy cover. The C3 sedge *Carex pensylvanica* was the dominant graminoid species under woodland canopy cover, and was co-dominant with the C4 grasses *Andropogon scoparius* and *Sorghastrum nutans* under savanna canopy cover. As in other savannas, N-fixing species sorted across shade and canopy openings, and heterogeneity among transects was maximized at mid-canopy cover. Over time, canopy cover decreased up to 50%, creating more open savanna conditions at mid to high elevations. This decrease was associated with a 20–100 % increase in species richness and was significantly correlated with increasing richness and cover of C4 grasses and summer flowering prairie and woodland forbs. These results support a canopy cover model of fire-maintained savanna vegetation, with greater abundance of C4 grasses and prairie forb species associated with lower canopy cover, greater heterogeneity at mid-canopy cover, and species richness maximized across the light gradient. They also indicate that decreasing canopy cover caused by repeated burning increases species richness and abundance of C4 and prairie forb species.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Savanna vegetation in midwestern North America is usually defined as scattered oaks (*Quercus* sp.) over a forb-rich grassland that is floristically transitional between forest and prairie (Anderson and Bowles, 1999; Curtis, 1959; Leach and Givnish, 1999). The canopy transition from savanna to forest can be conceptualized as a shift from tree islands in a grassland matrix to canopy gap islands

in a canopy matrix (Belsky and Canham, 1994; Pavlovic et al., 2006). Across this gradient, savanna is often described as <50% canopy cover, and woodland as transitional to forest, ranging from 50% to <100% canopy cover (e.g. Pavlovic et al., 2006). However, savanna is also used to collectively describe the savanna–woodland gradient. This fire-dependent vegetation was formerly widespread across much of central North America (Anderson, 1983; Anderson and Bowles, 1999; Curtis, 1959). Savanna vegetation declined greatly following European settlement as a result of fire suppression and now is one of the most endangered ecosystems in the Midwest (Anderson and Bowles, 1999; Apfelbaum and Haney,

* Corresponding author. Tel.: +1 630 719 2422; fax: +1 630 719 2433.

E-mail address: mbowles@mortonarb.org (M. Bowles).

1995; Bowles and McBride, 1998; Curtis, 1959; Haney and Apfelbaum, 1990; Nuzzo, 1986; Taft, 1997). Because of its fire-dependency, understanding fire management effects on oak savanna is important for restoring this vegetation (Haney et al., 2008). In general, lower fire frequency and reduced fire intensity allow a shift toward more closed canopy woodland, causing decline of light-dependent species and increase of shade-tolerant species; while higher fire frequency and greater intensity cause a shift toward more open canopy savanna, and increase of shade-intolerant species (Bowles and McBride, 1998; Bray, 1958; Faber-Langendoen and Davis, 1995; Haney et al., 2008).

The distribution of savanna ground layer vegetation is controlled by light availability caused by canopy openness gradients (Bowles and McBride, 1998; Bray, 1958; Leach and Givnish, 1999; Meisel et al., 2002; Pavlovic et al., 2006). As a result, savanna ground layer vegetation is characterized by high and variable levels of species richness and heterogeneity caused by interactions between vegetation functional groups, fire regimes and canopy cover gradients (Leach and Givnish, 1999; Pavlovic et al., 2006; Peterson et al., 2007; Peterson and Reich, 2008). For example, cool season C3 graminoid species are most abundant under greater canopy cover, while warm season C4 grasses predominate in full sun, where they may competitively reduce forb richness (Pavlovic et al., 2006; Peterson et al., 2007). As a result, forb richness is thought to peak in partial shade, except in drier open sites on sandy soils (Leach and Givnish, 1999) or in canopy openings of unburned mesic sites (Bowles and McBride, 1998). Because of these interactions, fire regimes that cause spatially variable canopy cover maximize species richness, with greatest heterogeneity at intermediate canopy cover, and greater cover of nitrogen-fixing and cool season (C3) species in partial shade (Peterson et al., 2007; Peterson and Reich, 2008).

Among sites, or within large scale sites, edaphic factors may have greater effects than a canopy light gradient on vegetation (Leach and Givnish, 1999; Meisel et al., 2002), and available soil moisture usually comprises the primary ecological factor affecting the landscape-scale distribution of vegetation (e.g. Curtis 1959). For example, eastern sand savanna vegetation may comprise a black oak (*Quercus velutina*) – white oak (*Q. alba*) – pin oak (*Q. palustris*) transition across a gradient of decreasing soil drainage (Brewer and Vankat, 2004; Haney et al., 2008). Despite the general knowledge that fire frequency and intensity structure the savanna canopy and spatially pattern the distribution of groundlayer species and functional groups, few studies have documented temporal change in savanna groundlayer vegetation in response to changing canopy cover in fire-managed savanna. Because of the potential effects of elevation and canopy cover gradients on vegetation pattern, fire-managed sites with strong gradients may have complex groundlayer vegetation patterns that vary among functional groups. Understanding how fire management affects these patterns should facilitate savanna restoration management.

In contrast to the almost complete loss of savanna that has occurred on deep fine textured soils, more savannas have survived on sand soils because of their low soil fertility and greater susceptibility to fire (Haney et al., 2008). As a result, they provide an important resource for conservation and fire-management research (Anderson and Bowles, 1999; Faber-Langendoen and Davis, 1995; Will-Wolf and Stearns, 1999). In this paper, we examine composition, structure and long-term change in ground layer vegetation across elevation and changing canopy cover gradients in a large-scale eastern sand savanna burned at 3 fires/decade for 20 years (Haney et al., 2008). Eastern sand savannas differ geographically and compositionally from northern sand savanna, but are less well known and apparently similarly fragmented and degraded from fire protection (Will-Wolf and Stearns, 1999). With respect to the broad elevation and canopy gradients present at Tefft, and its history of fire-management, we ask:

- 1) How is ground layer vegetation distributed across these gradients after repeated burning?
- 2) How have canopy cover, species richness and heterogeneity, and richness and cover of functional groups changed over time across these gradients?
- 3) Does temporal change in canopy cover correlate with change in species richness and richness and cover of functional groups?

If groundlayer vegetation at Tefft Savanna fits a savanna canopy cover model, we would expect greater abundance of C4 grasses and prairie species with less canopy cover and greater abundance of C3 graminoid species and woody species with greater canopy cover. We also expect that a temporal decrease in canopy cover would select for greater abundance of light sensitive C4 grasses and prairie species, which would affect the distribution and pattern of vegetation.

2. Study area

Our study was conducted at Tefft Savanna Nature Preserve, a 197 ha eastern sand savanna remnant located at 41°10' N latitude and 86°58' W longitude, within the 3239 ha Jasper–Pulaski State Fish and Wildlife Area, Jasper Co., Indiana (see Fig. 1 in Haney et al., 2008). Soils tend to be acidic (pH < 7.0), are developed in Wisconsin-aged outwash and lacustrine sands, and belong primarily to the Oakville (mixed, mesic typic Udipsamment), Morocco (mixed, mesic aquic Udipsamment) and Newton (sandy, mixed, mesic typic Humaquept) soil series, which represent an excessive,

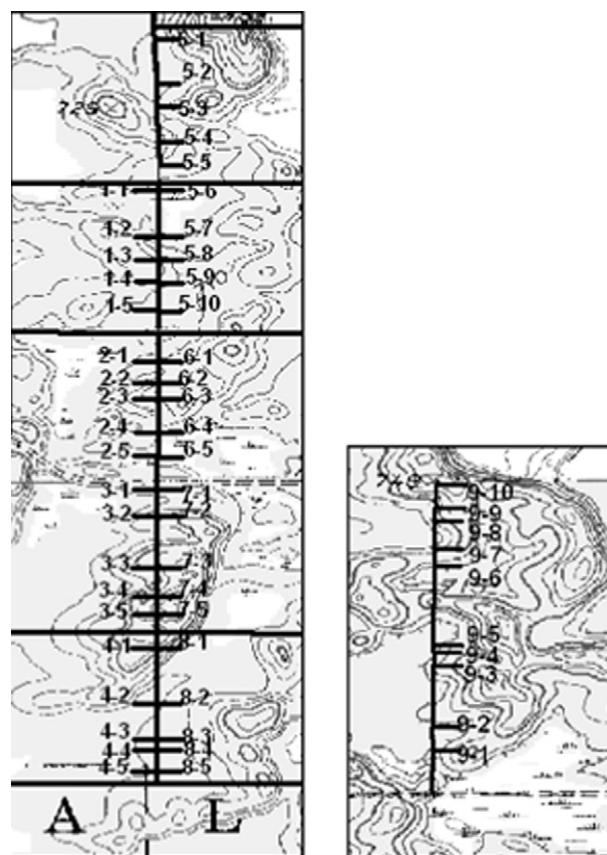


Fig. 1. Locations of 50 m sampling transects within the Tefft Savanna Nature Preserve, San Pierre, Indiana USGS Quadrangle Map. Transects are represented by solid horizontal lines labeled by management block and transect numbers. Unlabeled lines represent fire lanes. See Haney et al. (2008) for landscape location of blocks.

somewhat poorly and very poorly drained topographic gradient (Soil Survey Staff et al., 2004). These sands have been worked into aeolian dunes that grade into depressional wetlands, with elevation ranging from about 210–230 m above sea level (Fig. 2 in Haney et al., 2008). Dominant tree species respond to this elevational gradient, with *Q. velutina* at well-drained high elevations, *Q. alba* at intermediate elevations, and *Q. palustris* at poorly drained low elevations (Haney et al., 2008). The continental climate has average temperatures ranging from -4.5°C in January to 23.2°C in July, and 930 mm annual precipitation, 52% of which falls during the May through September growing season (Smallwood and Osterholz, 1990). The study area is located in the Prairie Peninsula (Transeau, 1935), a region of North America with unpredictable summer drought, as well as dry fall and early spring seasons, favoring fire-maintained prairie and savanna vegetation (Anderson, 1983; Anderson, 1991).

In the early 1800's, Tefft Savanna was predominantly *Q. velutina*-dominated "barrens" with <50 trees/ha; but tree density had

reached >400 stems/ha by the mid 1980's (Haney et al., 2008). This change apparently resulted from an extended period of fire suppression. To restore more open savanna similar to presettlement conditions, the Indiana Department of Natural Resources began prescribed burning in 1982, using dormant-season spring fires applied randomly to nine blocks at a rate of 3 fires/decade. Fires tended to consume most of the fuel layer, especially at higher elevations where sand soils promoted rapid drainage and drying of fuels. Scorch height was used to estimate fire intensity because of its relationship with tree mortality (Loomis, 1973). Initial high intensity fires averaged $1.90 (\pm \text{se } 0.11 \text{ se})$ m scorch height and significantly reduced oak canopy cover and basal area, which was further reduced by cumulative effects of repeated low intensity burns that averaged $1.03 (\pm \text{se } 0.055 \text{ se})$ m scorch height (Haney et al., 2008). Repeated burning also caused greater reduction of canopy cover at higher elevations, presumably due to increased flammability of fuel resulting from the drying effect of greater drainage (Haney et al., 2008).

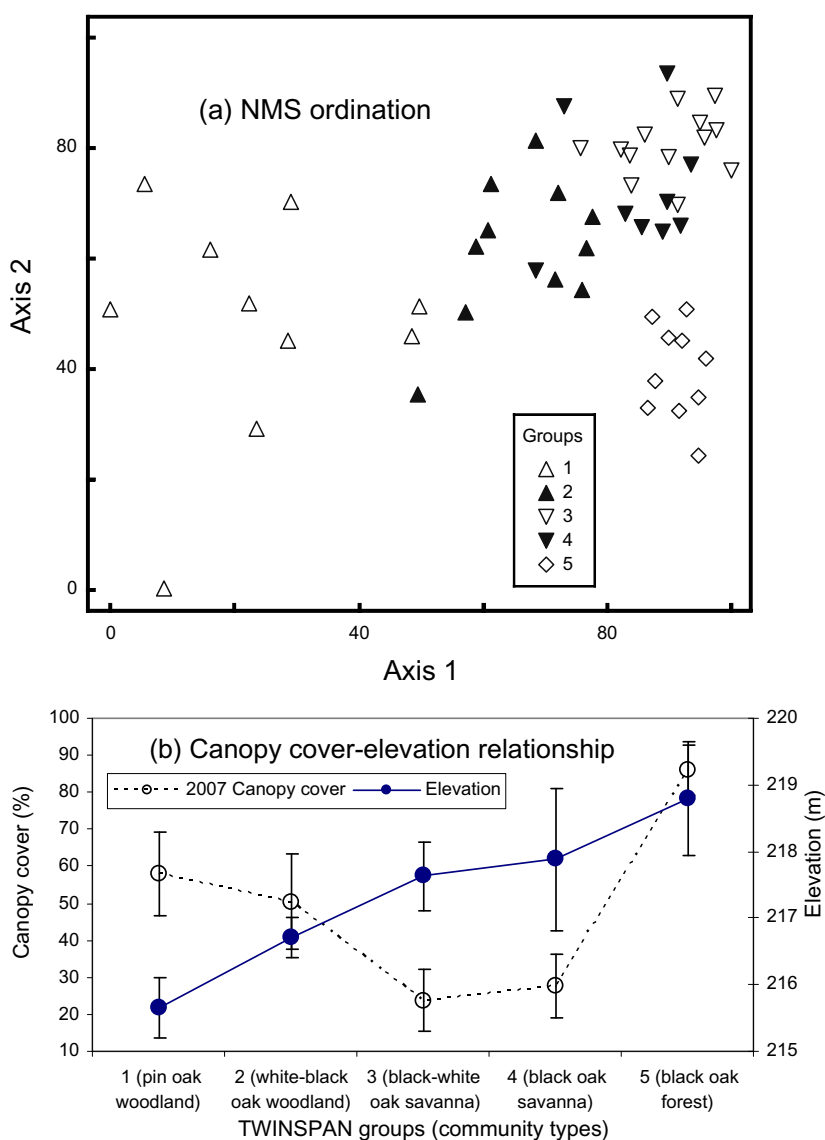


Fig. 2. (a) NMS ordination and TWINSpan classification of Tefft Savanna groundlayer vegetation. $P < 0.05$ of 250 random runs with stress less than observed stress; cumulative r^2 between ordination distances and distances in the original n -dimensional space: Axis 1 (0.617), Axis 2 (0.827). Environmental correlations: Axis 1 (elevation Spearman $r = 0.6405$, $P < 0.0001$), Axis 2 (tree cover Spearman $r = -0.4978$, $P = 0.000$). (b) relationship between elevation (median $\pm 95\%$ ci) and canopy cover (mean \pm se) gradients in 2007. TWINSpan groups and vegetation types correspond to NMS Axis 1. Kruskal–Wallis test of elevation: ($X^2 = 18.22083$, $P = 0.0012$); One-way ANOVA of canopy cover ($F = 7.72$, $P = 0.00007$).

3. Methods

Vegetation was sampled from permanently marked transects set at 50 m lengths to minimize crossing of contours. Transects were parallel and orientated east or west from north-south baselines located on fire lanes separating management blocks (Fig. 1). Five transect locations were randomly stratified within each 40 ha block, averaging 268 m distance between each transect. A 10 m buffer was set before the initial plot on each transect. Transects were used as replicates, as this study did not aim to detect different fire intensity treatments applied initially at the block level (Haney et al., 2008). Initial data were collected from 36 transects in 1986, with 23 transects sampled in 1988. For this reason, we refer to initial results as occurring in 1986–88. To assess repeated burning effects, we re-sampled 55 of these transects in June, 2007 (Fig. 1). Two transects were excluded from analysis due to flooding, leaving a total of 53 transects.

Each transect served as a line intercept to measure linear overstory canopy cover of tree species with stems >5 cm dbh and >1 m high, as well as understory shrub canopy cover of woody species with stems <5 cm dbh and >1 m high. These values were divided by transect length to estimate percent canopy cover of trees and shrubs. In 2007, to assess precision of tree canopy cover measured by line intercept, we also measured photosynthetically active radiation (PAR, micro-mol/second/m²) under clear sky conditions from five points at 10 m intervals along each transect. PAR was recorded using a 15-second average reading from a Li-Cor LI-190 SA Quantum Sensor (<http://www.licor.com>, Biggs et al., 1971) held 1 m above the transect line. To estimate the percentage of PAR intercepted by the tree canopy, each measure of PAR was divided by PAR measured in open habitat, and subtracted from 100. Canopy cover and intercepted PAR were significantly correlated ($r = 0.748$, $P < 0.001$), which indicates that our measures of linear canopy cover are acceptable estimates of the gradient of light energy available for assimilation by plants.

Presence and an ocular cover estimate were recorded for all herbaceous and woody (<1 m high) species within each of five 1 m² plots at 10-m intervals along each transect. Species frequencies were calculated as the percentage of plots occupied on each transect, and their percent cover was averaged across these transects. Species richness was calculated as the average number of species per plot within transects, and as total richness across each transect. The plot level measure represents species density, while the transect-level measure estimates species richness over an area effectively larger than cumulative plot area because plots are non-contiguous along transects (Scheiner, 2003). Transect-level cover and richness were also calculated within functional groups representing graminoid species using the C3 and C4 photosynthetic pathways, spring-flowering forbs (before 1 July), summer-flowering forbs (after 1 July), N-fixing species (legumes and *Ceanothus* species), and woody species. Flowering dates and nomenclature are based on Swink and Wilhelm (1994). These groups represent a combination of functional groups (C3, C4, N-fixing species), as well as phenological (spring and summer forbs), and woody species guilds. Non-native species were very rarely sampled, and were not significant to our analysis. We calculated heterogeneity as dissimilarity among transects based on proportional similarity (Bray and Curtis, 1957), where dissimilarity = $[(x_i - y_i)/(x_i + y_i)]$, and x_i and y_i are the abundances of species i in each transect. This method is more precise than the Sørensen similarity index, which does not take into account species abundance.

To address question 1 (how vegetation is distributed after repeated burning), transects were ordinated based on their 2007 species frequencies with Non-metric Multi-dimensional Scaling using a Sørensen distance measure in PCORD (McCune and Meford, 2006). We did not ordinate temporal change because of variable responses among the large number of replicates. TWINSpan was used to classify five groups, or vegetation types ($N = 9, 10, 10, 11, 13$ transects), using default settings in PCORD (McCune and Meford, 2006). Indicator species analysis (Dufrene and Legendre, 1997) was used to determine significant indicator species for each vegetation type using 2007 data in PCORD. The 2007 data were also used to calculate species niche breadth for dominant species as $e^{H'}$, where H' is the Shannon index of diversity based on species cover (Leach and Givnish, 1999). To determine whether species distributions corresponded to an elevation gradient, transect locations were digitized on the San Pierre, Indiana digital elevation model USGS quadrangle map and analyzed for average elevation on ARCVIEW software (<http://www.esri.com>). Linear regression was used to test whether average transect elevation and canopy cover were significantly related to the first and second axis scores of the NMS ordination. To test null hypotheses of no differences in elevation and canopy cover among the vegetation types classified by TWINSpan, we used a Kruskal-Wallis one-way analysis of variance (ANOVA) of rank transect elevation, and one-way ANOVA of transect canopy cover data that were square-root arcsine transformed to achieve normality (Zar, 1974). Vegetation-type names were assigned to each of the five TWINSpan groups based on combinations of co-dominant oaks and average canopy cover in 2007 representing savanna (<50% cover), woodland (50–80% cover) or forest (>80% cover). We also used a two-factor ANOVA in a General Linear Model (GLM) to test whether species richness differed among functional groups and TWINSpan vegetation types. In this test, a significant interaction would indicate a shift in functional group richness among vegetation types.

We used Repeated Measures ANOVA to address question 2 (how canopy cover, species richness and functional groups have changed over time). This procedure tested a null hypothesis of no temporal difference between 1986–88 and 2007 in these measures among TWINSpan groups. As elevation and canopy cover differed significantly among TWINSpan groups (see below), they serve as relevant categorical factors. We used a GLM to test whether heterogeneity differed among TWINSpan groups, using year (1986–88 vs 2007) as an additional factor. To achieve normality, percent canopy cover was square-root arcsine transformed, and functional group cover and richness were log-transformed.

To address question 3 (does canopy cover change correlate with change in species richness and functional group richness), we conducted linear regression of percent change in canopy cover vs change in species richness, and cover and richness of functional groups, testing a null hypothesis of no significant relationship as shown by the slope of regression line. Percent change in canopy cover was calculated as % change = $[(\text{Value}_{2007} - \text{Value}_{1986-88})/\text{Value}_{1986-88}]$; change in groundlayer cover or richness was calculated as change = $(\text{Value}_{2007} - \text{Value}_{1986-88})$. Canopy cover values were square-root transformed to achieve normality, which also increased r^2 and significance levels. These analyses result in a negative correlation between decreasing canopy cover and increasing species richness or cover. For both 1986–88 and 2007, we also used regression analysis to test the relationship between shrub layer cover and cover of C4 graminoid species, as well as the relationship between C4 cover and richness of summer flowering forbs. Temporal change in shrub cover was not used as a factor because

it returns to pre-burn conditions within 4 years (Haney et al., 2008).

4. Results

4.1. Vegetation ordination and classification

NMS ordination produced a 2-dimensional solution with stress < observed stress (Fig. 2). Axis 1 accounted for 62% of NMS variation and was significantly correlated with elevation (Spearman $r = 0.6405$, $P < 0.0001$); axis two accounted for an additional 21% variation, and was significantly correlated with canopy cover (Spearman $r = -0.4978$, $P < 0.0001$). The five TWINSpan groups differed significantly in relation to elevation and tree canopy cover (Fig. 2). We refer to these groups as the following woodland, savanna, or forest vegetation types. Pin oak woodland (TWINSpan group 1) had a median elevation of 215.5 m and averaged 58.1% canopy cover in 2007. White oak-black oak woodland (group 2) median elevation was 217 m, with 50.5% canopy cover. Black oak-white oak savanna (group 3) median elevation was 217.5 m, with 23.8% canopy cover. Black oak savanna median elevation was 218 m, with 27.5% canopy cover. Black oak forest median elevation was 219 m, with 86.1% canopy cover. Variation around means and medians is shown in Fig. 2.

A total of 142 species were sampled at Tefft Savanna. In 2007, 62 of these species occurred at >10% frequency within at least one vegetation type, 71% of which were significant indicator species of different types (Table 1). Indicator species were non-randomly distributed ($\chi^2 = 28.56$, $P < 0.0001$), with 75% occurring in two vegetation types. Over 65% of the indicator species are also typically found in prairie or savanna habitats (Swink and Wilhelm, 1994). In 2007, there was a significant (Pearson $r = 0.8310$, $P < 0.001$) positive correlation between species niche breadth and the number of vegetation types occupied. Also in 2007, functional group species richness varied significantly within and among TWINSpan groups (Fig. 3). Woody species were the leading group at lower elevations, which supported woodland vegetation, but were second to summer flowering herb species at mid-elevations, which supported savanna vegetation. Richness of spring flowering forbs and C4 grasses were also greater in mid-elevation savanna, while richness of N-fixing species was extremely low at low-elevations in woodland, and higher at mid-elevations in savanna and forest vegetation. Richness of C3 graminoid species had little variation across the elevation gradient and among community types.

In 2007, the C3 sedge *Carex pensylvanica*, and the woody species *Q. velutina* were dominant in four of five vegetation types and ranked 1st and 2nd in niche breadth (Table 1). Also, 8 of 12 species with greatest niche breadth were woody species. In pin oak woodland, the woody species *Rubus hispidus*, *Gaylussacia baccata* and *Aronia melanocarpa* were most frequent, and were replaced by *Q. velutina* and *Vaccinium* species in white oak-black oak woodland. *Q. velutina* was also the most abundant woody species in savanna, followed in abundance by *Rosa carolina* and *Rhus copallina*. *Rubus allegheniensis* and *Sassafras albidum* were the leading woody vegetation in black oak forest. The summer forbs *Helianthus divaricatus*, *Tradescantia ohiensis*, and *Euphorbia corollata* were the leading species in savanna, and were replaced by *Smilacina racemosa*, *Circaea lutetiana* and *Amphicarpa bracteata* in forest. Leading spring-flowering forbs in savanna included *Comandra richardsoniana*, *Phlox pilosa* and *Lupinus perennis*. The most abundant species shifted from *L. perennis*, *Lespedeza capitata* and *Cassia fasciculata* in savanna to *A. bracteata* and *Desmodium* species in forest. *Andropogon scoparius* and *Sorghastrum nutans* were the leading C4 graminoid species under savanna canopy cover.

4.2. Temporal change in canopy cover, species richness, and functional groups

Percent canopy cover decreased significantly over time (Table 2). The greatest change was a 55% decrease in cover at mid-elevation (Fig. 4), leaving <30% canopy cover in both black oak-white oak savanna and black oak savanna. Species richness differed significantly across the elevation gradient at the plot and transect scales (Table 2) and increased over time (Fig. 4). At mid-elevations in savanna, species richness increased 100% at the plot level (data not shown), and 40–70% at the transect level (Fig. 4), resulting in maximums of 11.4 (± 0.84 se) species/plot and 25.6 (± 1.21 se) species richness at the transect level.

Vegetative cover and richness were significantly correlated within all functional groups (Pearson's $r > 0.4600$, $P < 0.001$) except C3 graminoid species ($r = 0.0153$, $P = 0.2027$). Woody species had comparatively high cover, C3 graminoid species and summer forbs had intermediate cover, and C4, N-fixing species and spring forbs had low cover (Fig. 5). Richness was comparatively high in summer forbs and woody species and low in other groups (Fig. 5). Over time, there were significant increases in cover and richness of all functional groups except spring forbs and cover of N-fixing species (Fig. 5, Table 2). With the exception of C3 richness and spring forb cover, all functional groups also differed significantly across vegetation types (Table 2). However, significant group \times year interactions occurred only for C4, spring forb and summer forb cover (Table 2).

Heterogeneity did not change significantly over time, but differed significantly among vegetation types (Table 2). Across an increasing canopy cover gradient, heterogeneity had a unimodal distribution, reaching maximum values at mid-canopy cover, while species richness had an inverse relationship (Fig. 6). High C4 vegetation cover was essentially restricted to the low canopy cover, while C3 vegetation, as well as richness of spring, summer, and species was lower at mid-canopy cover (Fig. 6). In contrast, woody vegetation cover peaked under mid-canopy cover (Fig. 6).

4.3. Correlation between change in canopy cover and groundlayer vegetation

In 1986, canopy cover was not significantly correlated with plot species richness, nor with species richness at the transect scale. However, in 2007, there were significant negative relationships between canopy cover and species richness at the plot ($r = -0.2552$, $P = 0.0077$), and transect ($r = -0.2983$, $P = 0.0019$) scales. Percent change in canopy cover was significantly negatively correlated with change in species richness and with richness and cover of C4 graminoid species and summer forbs, indicating that these measures increased with decreasing canopy cover (Table 3). Change in richness of N-fixing species, as well as woody cover, was also negatively correlated with canopy change. However, change in richness of woody species had a significant positive correlation, suggesting that woody species richness may increase with increasing canopy cover (Table 3). There were significant negative correlations between shrub layer cover and cover of C4 grasses in 1986–88 (Spearman $r = -0.2959$, $P = 0.0314$) and in 2007 (Spearman $r = -0.370$, $P = 0.006$). There were also significant positive relationships between C4 grass cover and richness of summer flowering forbs in both 1986–88 ($r^2 = 0.2578$, $P = 0.0001$) and 2007 ($r^2 = 0.3941$, $P < 0.0001$).

5. Discussion

Our data provide further understanding of the fire-driven dynamic relationship between the savanna canopy light gradient

Table 1

Temporal frequencies of species occurring at >10% average frequency among TWINSPAN groups and vegetation types groups ordered by median elevation rounded to 0.5 (+95% ci). Canopy cover is average percent canopy cover rounded to nearest whole number. Functional Groups: C3 (C3 graminoid) C4 (C4 graminoid), SP (spring flowering forb), SU (summer flowering forb), W (woody), N (N-fixing species). Numbers in bold with asterisks indicate significant indicator species at $P < 0.05$ based on 2007 frequencies. Species ranked within functional groups by niche breadth calculated from 2007 data as e^H .

Species-Functional Group		TWINSPAN Group										Niche breadth 2007
		1		2		3		4		5		
Elevation		215.5 (0.56)		217 (0.30)		217.5 (0.51)		218 (1.07)		219 (0.86)		
Vegetation		Pin oak		White oak-black		Black oak-white		Black oak		Black oak		
Type		woodland		oak woodland		oak savanna		savanna		forrest		
Year		1986	2007	1986	2007	1986	2007	1985	2007	1986	2007	
Canopy cover		75	58	54	50	53	24	34	27	97	86	
<i>Carex pensylvanica</i>	C3	0	9.1	52.7	65.5	71.1	75.6	90.8	80	70	*84.0	42.6
<i>Carex</i> sp.	C3	14	*25.5	10.9	9.1	6.7	0	0	0	0	0	8.5
<i>Carex muhlenbergii</i>	C3	0	0	0	0	0	4.4	0	*13.8	1.7	0	5.2
<i>Calamagrostis canadensis</i>	C3	18	3.6	5.5	3.6	0	0	0	0	1.7	0	3.0
<i>Andropogon scoparius</i>	C4	0	0	1.8	5.5	8.9	26.7	12.3	*56.9	0	0	18.3
<i>Sorghastrum nutans</i>	C4	0	0	3.6	7.3	4.4	2.2	3.1	*20.0	0	0	11.9
<i>Comandra richardsoniana</i>	SP	0	0	5.5	7.3	24.4	31.1	29.2	*44.6	0	0	17.6
<i>Fragaria virginiana</i>	SP	0	0	0	1.8	6.7	11.1	1.5	10.8	0	6	11.9
<i>Antennaria plantaginifolia</i>	SP	0	7.3	1.8	5.5	6.7	6.7	7.7	15.4	0	0	10.9
<i>Phlox pilosa</i>	SP	0	0	1.8	0	2.2	13.3	13.8	*21.5	0	0	6.5
<i>Osmunda cinnamomea</i>	SP	4	*12.7	1.8	0	0	0	0	0	0	0	4.7
<i>Galium</i> sp.	SP	0	3.6	0	0	0	0	0	0	30.1	16	4.0
<i>Osmunda regalis</i>	SP	14	*12.7	0	1.8	0	0	0	0	0	0	3.4
<i>Viola lanceolata</i>	SP	2	14.5	0	0	0	2.2	0	0	0	0	2.8
<i>Geranium maculatum</i>	SP	0	0	0	0	0	0	0	0	3.3	10	1.6
<i>Claytonia virginica</i>	SP	0	0	3.6	0	22.2	0	18.5	4.6	13.4	0	1.0
<i>Lupinus perennis</i>	SP/N	0	1.8	0	0	11.1	*33.3	9.2	21.5	0	0	9.8
<i>Helianthus divaricatus</i>	SU	0	0	3.6	14.5	24.4	42.2	23.1	*53.8	18.4	24	29.6
<i>Pteridium aquilinum</i>	SU	6	1.8	18.2	40	8.9	22.2	16.9	24.6	21.7	24	26.1
<i>Smilacina racemosa</i>	SU	4	3.6	18.2	16.4	24.4	17.8	15.4	7.7	68.3	*62.0	20.0
<i>Tradescantia ohioensis</i>	SU	0	0	5.5	0	26.7	24.4	23.1	*38.5	6.8	18	18.3
<i>Euphorbia corollata</i>	SU	0	0	5.5	3.6	11.1	26.7	24.6	*33.8	1.7	0	16.3
<i>Potentilla simplex</i>	SU	0	0	3.8	14.5	4.4	8.9	0	9.2	16.7	*22.0	15.9
<i>Aster linariifolius</i>	SU	0	0	1.8	5.5	8.9	4.4	12.3	*33.8	0	0	14.4
<i>Helianthemum canadense</i>	SU	0	0	0	1.8	0	17.8	0	*27.7	0	0	13.3
<i>Coreopsis palmata</i>	SU	0	0	0	1.8	11.1	8.9	18.5	*32.3	0	0	13.1
<i>Solidago nemoralis</i>	SU	0	0	0	0	0	*22.2	0	21.5	0	0	12.2
<i>Aster azureus</i>	SU	0	0	0	1.8	0	8.9	3.1	*23.1	0	2	11.0
<i>Smilacina stellata</i>	SU	0	0	0	0	0	4.4	0	10.8	30	14	10.0
<i>Solidago speciosa</i>	SU	0	0	0	0	4.4	8.9	7.7	10.8	0	0	7.5
<i>Circaea lutetiana</i>	SU	0	0	0	0	0	0	0	0	1.7	*30.0	7.3
<i>Liatris aspera</i>	SU	0	0	0	0	8.9	0	1.5	*12.3	0	0	5.3
<i>Polygala polygama</i>	SU	0	0	0	3.6	0	2.2	0	10.8	0	0	5.0
<i>Prenanthes alba</i>	SU	0	0	0	0	0	0	0	0	3.3	*12.0	4.8
<i>Scrophularia marilandica</i>	SU	0	0	0	0	0	0	0	0	1.7	*10.0	2.6
<i>Smilax</i> sp.	SU	0	0	0	0	0	0	0	0	21.7	*12.0	1.9
<i>Lespedeza capitata</i>	SU/N	0	0	0	0	2.2	15.6	0	*18.5	0	0	11.1
<i>Amphicarpa bracteata</i>	SU/N	0	0	0	3.6	0	0	1.5	3.1	6.7	*66.0	11.0
<i>Cassia fasciculata</i>	SU/N	0	0	0	0	0	20	4.6	*21.5	0	0	10.3
<i>Desmodium glutinosum</i>	SU/N	0	0	0	0	0	0	0	0	33.3	22	3.7
<i>Desmodium paniculatum</i>	SU/N	0	0	0	0	0	0	0	0	10	4	1.0
<i>Quercus velutina</i>	W	10	3.6	12.7	60	24.4	64.4	23.1	*70.8	40	28	37.5
<i>Rosa carolina</i>	W	0	1.8	12.7	12.7	40	53.3	36.9	*66.2	21.8	18	27.6
<i>Sassafras albidum</i>	W	12	18.2	7.3	21.8	15.6	26.7	0	1.5	40.2	*38.0	24.7
<i>Quercus alba</i>	W	12	14.5	34.5	*36.4	4.4	15.6	6.2	12.3	11.8	18	23.3
<i>Rhus copalina</i>	W	0	0	3.6	30.9	2.2	35.6	7.7	*53.8	0	2	22.6
<i>Rubus hispidus</i>	W	2	32.7	10.9	36.4	0	20	1.5	9.2	0	2	21.1
<i>Rubus allegheniensis</i>	W	0	0	0	10.9	0	33.3	0	4.6	0	*34.0	18.7
<i>Vaccinium angustifolium</i>	W	10	21.8	41.8	*47.3	0	17.8	10.8	9.2	1.7	0	18.5
<i>Prunus serotina</i>	W	0	0	5.5	12.7	6.7	8.9	7.7	1.5	18.4	16	16.2
<i>Vaccinium pallidum</i>	W	0	7.3	14.5	*50.9	0	15.6	4.6	32.3	1.7	2	14.5
<i>Gaylussacia baccata</i>	W	12	27.3	32.7	29.1	0	6.7	10.8	7.7	0	0	13.4
<i>Aronia melanocarpa</i>	W	50	*27.3	27.3	18.2	0	0	4.6	0	0	0	10.3
<i>Rubus occidentalis</i>	W	0	0	0	0	0	0	0	0	26.7	*52.0	7.7
<i>Nyssa sylvatica</i>	W	8	*25.5	10.9	3.6	0	0	0	0	0	0	7.1
<i>Vitulus labrusca</i>	W	0	0	0	0	0	0	0	0	0	*28.0	6.7
<i>Quercus palustris</i>	W	8	10.9	1.8	10.9	0	0	0	0	0	0	5.3
<i>Acer rubrum</i>	W	0	12.7	0	5.5	0	0	0	0	0	0	5.0
<i>Rhus radicans</i>	W	0	0	0	0	0	0	0	0	8.3	*22.0	4.7
<i>Corylus americana</i>	W	0	0	0	0	0	0	0	0	10.1	*16.0	4.5
<i>Populus grandidentata</i>	W	0	0	0	*10.9	0	0	1.5	0	1.7	2	3.6
<i>Rubs</i> sp.	W	12	9.1	7.3	0	6.7	0	0	0	0	0	1.0
<i>Tephrosia virginiana</i>	W/N	0	0	0	0	6.7	11.1	4.6	*20.0	0	0	9.7

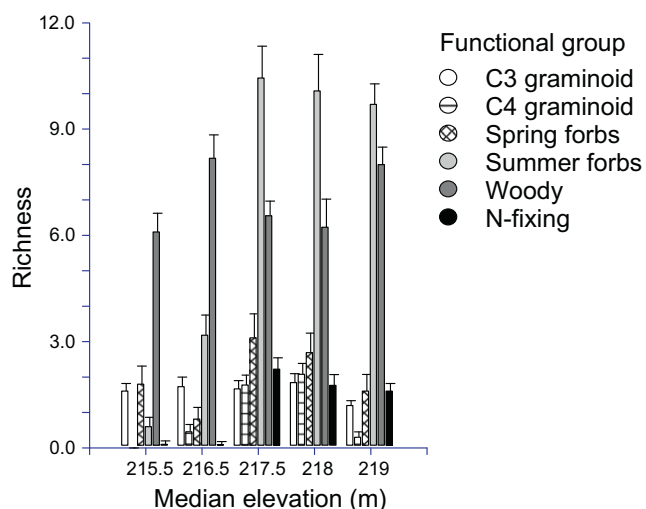


Fig. 3. Functional group richness (mean ± se) in 2007 across the Tefft Savanna elevation gradient. Elevations represent median transect elevation for each vegetation type classified by TWINSpan. ANOVA: TWINSpan group ($F = 47.06$, $P < 0.0001$), functional group ($F = 138.43$, $P < 0.0001$), interaction ($F = 10.90$, $P < 0.0001$).

and groundlayer vegetation. Observations of this relationship based on single time periods have not directly linked compositional change with fire-caused reduction in canopy cover (e.g., Bowles and McBride, 1998; Leach and Givnish, 1999; Peterson et al., 2007; Peterson and Reich, 2008). Our results support a fire-driven canopy-groundlayer dynamics model by linking temporal change in groundlayer species richness and functional groups with changing canopy cover under a repeated fire regime. They demonstrate that functional groups respond to changing canopy cover in an expected manner, with increasing abundance of C4 graminoid species and prairie species under canopy openings, and an overall increase in forb richness across the canopy gradient. Our finding that heterogeneity is maximized in intermediate (50–60%) canopy cover also supports previous work that has found maximum dissimilarity under intermediate canopy cover, where greater variation would occur among species with different light adaptations (Peterson et al., 2007). The lack of temporal change in heterogeneity suggests that it may be more stable than species richness, at least under the range of canopy cover change in our study. This

scale-dependent measure also may have maximized at mid-cover because our 50 m transect lengths would tend to cross boundaries of woodland canopy gaps in sand savanna (Pavlovic et al., 2006).

5.1. Vegetation response to elevation and canopy gradients

Our data comprise one of the most extensive canopy-ground-layer vegetation gradients for eastern sand savanna vegetation (see also Brewer and Vankat, 2006; Catling and Catling, 1993). These data suggest that low-diversity woodland may develop following fire exclusion and persist with repeated burning in poorly drained sand savanna, with groundlayer dominance by post-fire sprouting woody vines, Ericaceous shrubs, and trees, ferns and *Carex* species. *Q. palustris* is often a dominant canopy species in these habitats (Brewer and Vankat, 2004; Haney et al., 2008). Although high density and cover of woody vegetation also may persist in more well drained habitats, our data indicate that when burning opens canopy cover to <50%, it increases abundance of prairie forbs and C4 grasses. Dominance of shade-adapted forbs and *C. pensylvanica* under forest canopy conditions at higher elevations at Tefft appears to be a result of both historic fire protection, as well as recent fire history. Even though canopy cover of this habitat decreased over time, it had not burned since 2003. This recent fire-free interval probably allowed return of shrublayer cover and stem density (e.g., from *S. albidum*) to pre-burn conditions (Haney et al., 2008), contributing to a retention of forest canopy cover and greater expression of shade-adapted groundlayer vegetation. Nevertheless, species richness increased over time in this habitat due to an increase in summer forbs.

Forb-dominance of open-canopied savanna habitat at Tefft is consistent with Wisconsin savannas (Leach and Givnish, 1999; Meisel et al., 2002). Leach and Givnish (1999) recorded 16.1 species/1 m² in Wisconsin savannas. The lower maximum richness (11.4 species/m²) at Tefft may result from historic and current fire regimes. For example, richness was positively correlated with fire frequency in Minnesota savanna, where it peaked with 7–8 fires/decade at mid-canopy cover (Peterson and Reich, 2001). Although grasses may compete with forbs at high fire frequencies, C4 grass cover and richness of summer flowering forbs were positively correlated at Tefft, suggesting lack of such competition under the current fire regime. Infertile sand soils, which characterize open savanna at Tefft, also may reduce competitiveness of C4 grasses and increase forb richness (Leach and Givnish, 1999; Peterson and Reich, 2008).

Table 2
Analysis of Variance F-statistics and probabilities for temporal change in cover, heterogeneity, plot and transect richness, and cover and richness of functional groups across vegetation types classified by TWINSpan groups. Figs. 3 and 4 indicate magnitude and direction of change. Significant ($P < 0.05$) probabilities are in bold. Richness and functional group tests are Repeated ANOVA, heterogeneity test is General Linear Model.

Variable	Vegetation type TWINSpan group		Year 1986–88 vs 2007		Interaction Group × year	
	F-statistic	Probability	F-statistic	Probability	F-statistic	Probability
Canopy cover (%)	7.69	<0.00001	8.59	0.0055	0.97	0.431427
Heterogeneity	35.7	<0.00001	2.49	0.11539	0.18	0.94919
Plot richness	26.05	<0.00001	82.37	<0.00001	9.29	<0.00001
Total richness	24.62	<0.00001	46.07	<0.00001	2.55	0.05092
C3 cover	7.6	0.00008	4.14	0.04740	1.43	0.23751
C3 richness	1.71	0.16433	5.82	0.01974	0.75	0.56020
C4 cover	8.6	0.00003	7.56	0.00838	2.98	0.02823
C4 richness	18.71	<0.00001	6.45	0.01439	1.83	0.13922
Spring forb cover	2.37	0.06600	3.54	0.06608	4.46	0.00383
Spring forb richness	5.16	0.00154	0.38	0.54175	2.56	0.05043
Summer forb cover	24.83	<0.00001	14.29	0.00043	2.88	0.03221
Summer forb richness	57.69	<0.00001	16.62	0.00017	1.76	0.15228
Woody cover	5.24	0.00138	39.09	<0.00001	0.77	0.55154
Woody richness	6.87	0.00019	28.35	<0.00001	0.83	0.51562
N-fixing cover	31.3	<0.00001	3.35	0.07345	1.64	0.17992
N-fixing richness	45.77	<0.00001	6.57	0.01353	2.28	0.07434

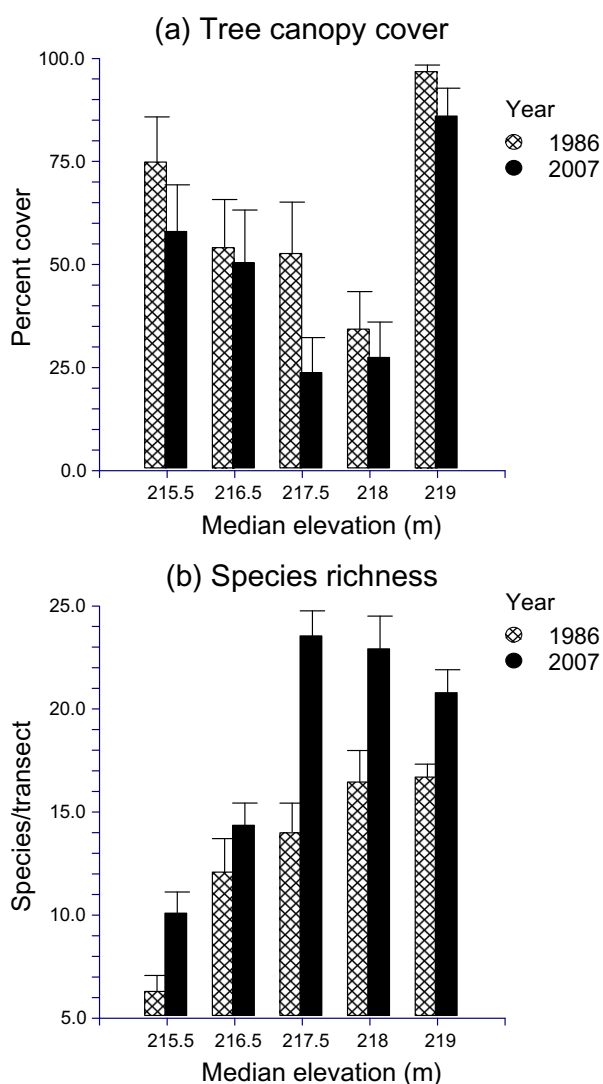


Fig. 4. Temporal change in (a) canopy cover (mean \pm se) and (b) species richness (mean \pm se) at the transect level across the Tefft Savanna elevation gradient. Elevations represent median transect elevation for each vegetation type classified by TWINSpan. Canopy cover: TWINSpan group ($P < 0.00001$), year ($P = 0.0055$), interaction ($P = 0.431427$). Species richness: TWINSpan group ($P < 0.00001$), year ($P < 0.00001$), interaction ($P = 0.05092$). 1986 represents 1986–88. See Table 2 for complete ANOVA.

While though cover and richness were correlated in other groups, the lack of correspondence between richness and cover in C3 graminoid species is due to the dominance of C3 species by *C. pensylvanica*. This sedge was the most frequent species in Wisconsin (Leach and Givnish, 1999) and Ohio (Abella et al., 2004) savannas. It appears adapted to the dynamic and variable canopy structure of savanna, as it is more shade tolerant than C4 grasses, but also tolerates full sun. It may have spread during the period of fire suppression at Teft, and now persists where burning has opened canopy cover.

Vegetation response to the canopy cover gradient at Teft is also consistent with conclusions that savanna vegetation represents an assemblage of fire-tolerant species adapted to a continuum of open, intermediate, and more closed canopy conditions (e.g. Bowles and McBride, 1998; Leach and Givnish, 1999; Meisel et al., 2002; Pavlovic et al., 2006). At Teft, this gradient interacts with elevation, with greater canopy openness at mid-elevations supporting greater numbers of shade-intolerant prairie grasses (e.g., *A. scoparius*, *S. nutans*) and forbs, and greater canopy cover at lower

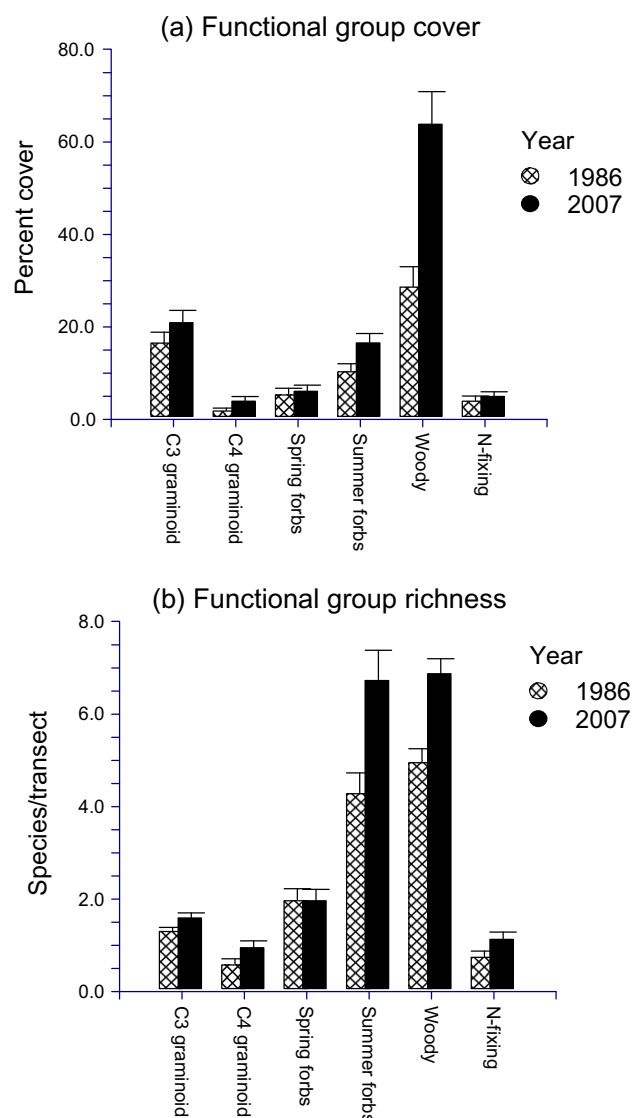


Fig. 5. Temporal change in (a) functional group cover (mean \pm se) and (b) transect-level species richness (mean \pm se) at Tefft Savanna. Cover: C3 ($P = 0.04740$), C4 ($P = 0.00838$), N-fixing ($P = 0.07345$), Spring forbs ($P = 0.06608$), Summer forbs ($P = 0.00043$), Woody ($P < 0.00001$). Richness: C3 ($P = 0.01974$), C4 ($P = 0.01439$), N-fixing ($P = 0.01353$), Spring forbs ($P = 0.54175$), Summer forbs ($P = 0.00017$), Woody ($P < 0.00001$). 1986 represents 1986–88. Table 2 for complete ANOVA.

elevations associated with Ericaceous shrubs and ferns. More closed canopy conditions at upper elevations allow dominance by more typical forest or woodland forbs (e.g. *Smilacina recemosa*, *A. bracteata*, *C. lutetiana*, *Prenanthes alba*), as well as woody species (e.g. *S. albidum*, *Vitis labrusca*, *Rhus radicans*, *Corylus americana*, *Rubus occidentalis*).

5.2. Functional group spatial structure and diversity

Our data also support a functional group model for fire-maintained savanna (Leach and Givnish, 1999; Peterson et al., 2007). As expected, C4 grasses and prairie species were most abundant at low canopy cover because of their shade intolerance, while C3 species, in this case *C. pensylvanica*, had a broader distribution. To some extent, our data support sorting of N-fixing forbs based on shade tolerance. As found by Leach and Givnish (1999), *A. bracteata* and *Desmodium* species occupied shaded habitat, while the prairie species *L. capitata* preferred open conditions. The low

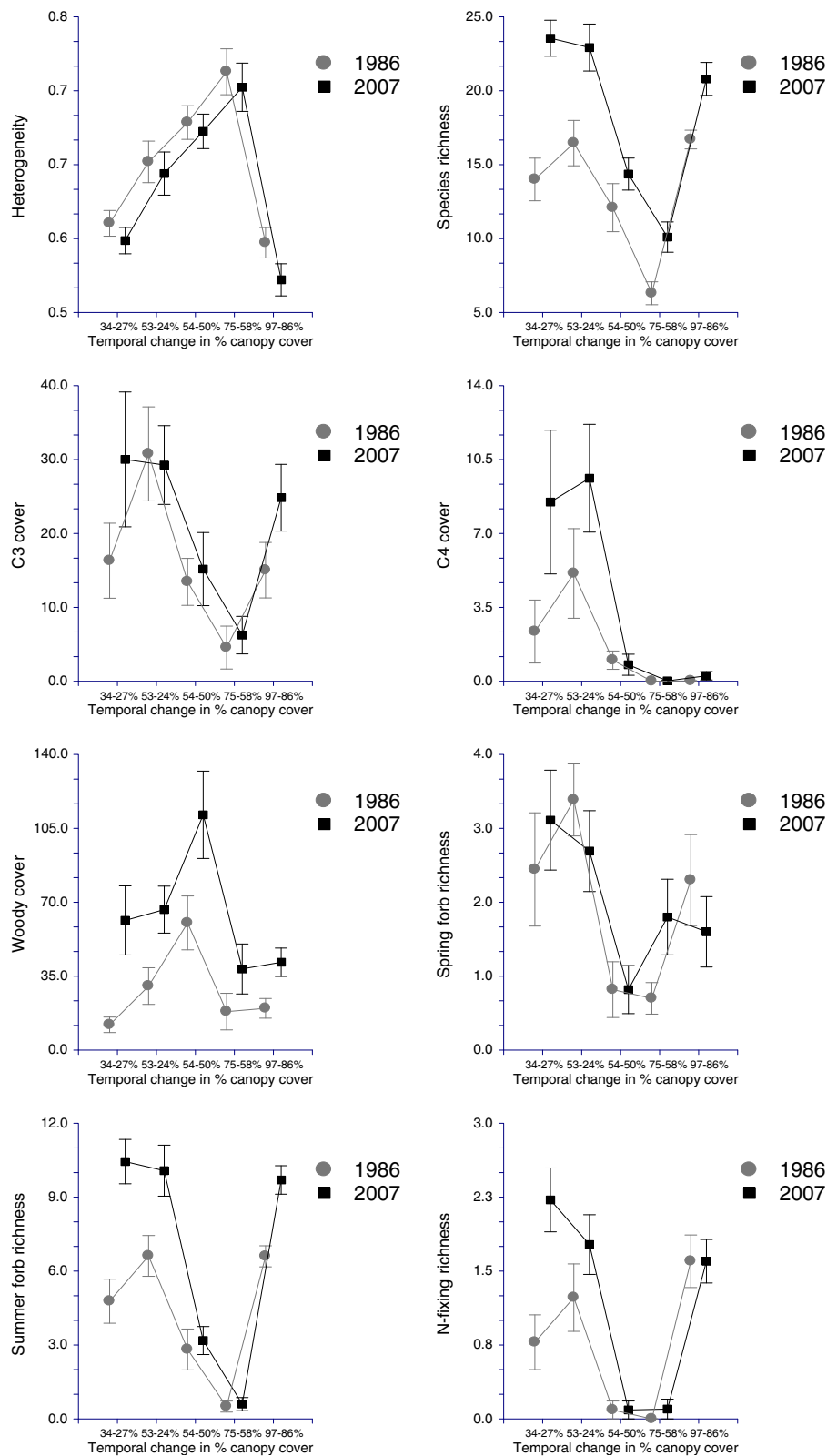


Fig. 6. Temporal changes in mean (\pm se) heterogeneity, species richness, graminoid and woody cover, and forb and N-fixing functional group richness across the Tefft Savanna canopy cover gradient. Hyphenated percentages on horizontal axes indicate change in average cover between 1986–88 and 2007 for each vegetation type classified by TWINSpan. Temporal change: $P < 0.05$ for all variables except spring forb richness; TWINSpan groups: $P < 0.01$ for all variables; interaction: $P < 0.05$ only for C4 species. 1986 represents 1986–88. See Table 2 for complete ANOVA.

richness of N-fixing species under intermediate canopy cover at Tefft may have resulted from inadequate fire coverage in this poorly drained habitat, which could have selected for lower

representation of this fire-adapted functional group (e.g., Hiers et al., 2003). The widespread dominance of woody species at Tefft reflects its history of fire exclusion and recent fire regime, which

Table 3

Temporal relationship between change in percent tree canopy cover between 1986–88 vs 2007 and change in richness and cover of functional groups. Probabilities are that the slope of each linear regression is not different from zero. Levels in bold are <0.10, those with asterisks indicate <0.05*, and <0.01**. Negative *r*-values indicate that richness or cover increase with decreasing canopy cover.

Variable	Statistic	Pearson correlation coefficient	Coefficient of determination (R-Squared)	Spearman correlation coefficient
Richness	Value	−0.4325	0.1871	−0.369
	Probability	0.0012**	0.0012**	0.0066**
C3 richness	Value	−0.0842	0.0071	−0.1472
	Probability	0.549	0.549	0.2928
C3 cover	Value	−0.116	0.0135	−0.0763
	Probability	0.4081	0.4081	0.5874
C4 richness	Value	−0.3164	0.1001	−0.274
	Probability	0.021*	0.021*	0.0471*
C4 cover	Value	−0.3404	0.1159	−0.3342
	Probability	0.0126*	0.0126*	0.0145*
Spring forb richness	Value	−0.1453	0.0211	−0.0944
	Probability	0.2993	0.2993	0.5011
Spring forb cover	Value	−0.1571	0.0247	−0.2391
	Probability	0.2614	0.2614	0.0846
Summer forb richness	Value	−0.3522	0.124	−0.4031
	Probability	0.0097**	0.0097**	0.0028**
Summer forb cover	Value	−0.3972	0.1578	−0.3666
	Probability	0.0032**	0.0032**	0.0069**
N-fixing richness	Value	−0.3369	0.1135	−0.2001
	Probability	0.0136*	0.0136*	0.1508
N-fixing cover	Value	−0.1914	0.0366	−0.116
	Probability	0.1699	0.1699	0.4081
Woody richness	Value	0.2982	0.0889	0.2053
	Probability	0.0301*	0.0301*	0.1402
Woody cover	Value	−0.2649	0.0701	−0.198
	Probability	0.0553	0.0553	0.1553

allows rapid recovery of shrub layer density and cover (Haney et al., 2008). As a result, 6 of the 10 species with niche breadths >20 are trees or shrubs associated with savanna or forest vegetation. Even mid-elevation habitat with greatest canopy openness is co-dominated by woody species. *Q. velutina*, a dominant canopy tree species at Tefft, is the leading indicator species of this habitat where it occurs as post-fire sprouting stems. This gives this habitat a barrens-like aspect caused by past high intensity fire followed by repeated low intensity burning (Haney et al., 2008).

6. Conclusions and management implications

Because of its fire-dependency, understanding fire management effects in oak savanna is important for restoring this ecosystem (Haney et al., 2008). The results of 20 years of repeated burning at Tefft Savanna support the long-held assumption that repeated burning can reduce canopy cover and drive vegetation change. Our analysis shows that reducing canopy cover below a lower threshold of at least 50% is important for increasing cover of C4 graminoid species and richness of prairie forbs, which can increase species richness in canopy openings. The comparatively low correlation coefficients between percent change in canopy cover and change in species richness or functional groups suggest that other unmeasured factors also affect these changes. These factors probably include species-level demographic responses to fire, which can increase population growth rates of grassland plants through greater rates of flowering, fecundity and seedling survivorship (Menges and Dolan 1998; Kaye et al., 2001; Kesler et al., 2008). Fire may facilitate this process through seed scarification, removal of litter that would shade light-dependent germinating seeds and seedlings, and release of compounds in smoke that induce germination (Baskin and Baskin 1998; Dixon et al., 1995). Increased fuel loading also may be an important factor. Cover of C4 graminoid species comprises a fuel matrix that increases with burning and facilitates fire effects in a feed-back process (Collins et al., 1995). Because C4 graminoids are shade-intolerant, this increase would occur primarily in habitat with low canopy cover.

Shrublayer vegetation at Tefft has not been reduced because of the rapid rate at which it recovers by post-fire sprouting (Haney et al., 2008). The negative relationship between shrublayer cover and C4 cover suggests that this process may dampen the response of C4 vegetation to fire. This concurs with suggestions that greater fire frequency, up to biennial burning, is needed to maintain species diversity among functional groups by stabilizing woody vegetation (Peterson and Reich, 2008). Supplemental removal of canopy trees has been suggested as necessary to further reduce canopy cover where trees have exceeded thresholds of fire sensitivity (Nielsen et al., 2003). In the case of Tefft, high intensity fires have significantly reduced canopy cover (Haney et al., 2008) and could be used as an alternative to mechanical removal. Nevertheless, they are not a replacement for frequent fire needed to control woody vegetation in the ground and shrub layer.

Acknowledgments

We thank the Indiana Department of Natural Resources, Division of Nature Preserves for funding support and cooperation. We also thank Jenny McBride for GIS assistance, and Tim Bell, Bob Fahey, Noel Pavlovic, Bryant Scharenbroch, and two anonymous reviewers for valuable comments.

References

- Abella, S.R., Jaeger, J.F., Brewer, L.G., 2004. Fifteen years of plant community dynamics during a northwest Ohio oak savanna restoration. *Mich. Bot.* 43, 117–127.
- Anderson, R.C., 1983. The eastern prairie-forest transition – an overview. In: Brewer, R. (Ed.), *Proceedings of the Eighth North American Prairie Conference*. Western Michigan University, Kalamazoo, MI, USA, pp. 86–92.
- Anderson, R.C., 1991. Presettlement forests of Illinois. In: Burger, G.V., Ebinger, J.E., Wilhelm, G.S. (Eds.), *Proceedings of the Oak Woods Management Workshop*. Eastern Illinois University, Charleston IL, USA, pp. 9–19.
- Anderson, R.C., Bowles, M.L., 1999. Deep-soil savannas and barrens of the Midwestern United States. In: Anderson, R.C., Fralish, J.S., Baskin, J.M. (Eds.), *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge University Press, New York, NY, USA, pp. 155–170.

- Apfelbaum, S.I., Haney, A. 1995. Characterization of midwestern oak savannas, in: Holland, K., Stearns, F. (eds) Proceedings of the Midwest Oak Savanna Conference. <<http://www.epa.gov/ecopage/upland/oak/oak93/haney.htm>>.
- Baskin, C.C., Baskin, J.M., 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, New York.
- Belsky, A.J., Canham, C.D., 1994. Forest gaps and isolated savanna trees. *Bioscience* 44, 77–84.
- Biggs, W.W., Edison, A.R., Easton, J.D., Brown, K.W., Maranville, J.W., Clegg, M.D., 1971. Photosynthesis light sensor and meter. *Ecology* 52, 125–131.
- Bowles, M.L., McBride, J.L., 1998. Vegetation composition, structure, and chronological change in a decadent Midwestern North American savanna remnant. *Nat. Areas J.* 18, 14–27.
- Bray, J.R., 1958. The distribution of savanna species in relation to light intensity. *Can. J. Bot.* 36, 671–681.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 325–349.
- Brewer, L.C., Vankat, J.L., 2004. Description of the oak openings of northeastern Ohio at the time of Euro-American settlement. *Ohio J. Sci.* 104, 76–85.
- Brewer, L.C., Vankat, J.L., 2006. Richness and diversity of oak savanna in northwestern Ohio: proximity to possible sources of propagules. *Am. Midland Nat.* 155, 1–10.
- Catling, P.M., Catling, V.R., 1993. Floristic composition, phytogeography and relationships of prairies, savannas and sand barrens along the Trent River, Eastern Ontario. *Can. Field-Naturalist* 107, 24–45.
- Collins, S.L., Glenn, S.M., Gibson, D.J., 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76, 486–492.
- Curtis, J.T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, University of Wisconsin, Madison, Wisconsin, USA.
- Dixon, K.W., Roche, S., Pate, J.S., 1995. The promotive effect of smoke derived from burnt native vegetation on seed germination of western Australian plants. *Oecologia* 101, 185–192.
- Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67 (3), 345–366.
- Faber-Langendoen, D., Davis, M.A., 1995. Effects of fire frequency on tree canopy cover at Allison Savanna, east-central Minnesota, USA. *Nat. Areas J.* 15, 319–328.
- Haney, A., Apfelbaum, S.I., 1990. Structure and dynamics of Midwest oak savannas. In: Sweeney, J.M. (Ed.), Management of Dynamic Ecosystems. North Central Section, The Wildlife Society, Lafayette, Indiana, pp. 19–30.
- Haney, A., Bowles, M., Apfelbaum, S., Lain, E., Post, T., 2008. Gradient analysis of an eastern sand savanna's woody vegetation, and its long-term responses to restored fire processes. *For. Ecol. Manage.* 266, 1560–1571.
- Hiers, J.K., Mitchell, R.J., Boring, L.R., Hendricks, J.J., Wyatt, R., 2003. Legumes native to longleaf pine savannas exhibit capacity for high N₂-fixation rates and negligible impacts due to timing of fire. *New Phytol.* 157, 327–338.
- Kaye, T.N., Pendergrass, L.L., Finley, K., Kauffman, J.B., 2001. The effect of fire on the population viability of an endangered prairie plant. *Ecol. Appl.* 11, 1366–1380.
- Kesler, H.C., Trusty, J.L., Hermann, S.M., Guyer, C., 2008. Demographic responses of *Apinguicula ionantha* to prescribed fire: a gression-design LTRE approach. *Oecologia* 156, 545–557.
- Leach, M.K., Givnish, T.J., 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. *Ecol. Monogr.* 69, 353–374.
- Loomis, R. M. 1973. Estimating fire-caused mortality and injury in oak-hickory forests. United States Forest Service, North Central Forest Experiment Station, Research Paper NC-94.
- McCune, B., Mefford, M.J. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5.04 MjM Software, Gleneden Beach, Oregon, U.S.A.
- Meisel, J., Trushenski, N., Weiher, E., 2002. A gradient analysis of oak savanna community composition in western Wisconsin. *J. Torr. Bot. Soc.* 129, 115–124.
- Menges, E., Dolan, R.W., 1998. Demographic viability of populations of *Silene regia* in Midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. *J. Ecol.* 86, 63–78.
- Nielsen, S., Kirschbaum, C., Haney, A. 2003. Restoration of Midwest oak barrens: Structural manipulation or process-only? *Conserv. Ecology* 7(2), 10. [online] URL: <<http://www.consecol.org/vol7/iss2/art10>>.
- Nuzzo, V.A., 1986. Extant and status of Midwest oak savanna: presettlement and 1985. *Nat. Areas J.* 6, 6–36.
- Pavlovic, N.B., Grundel, R., Sluis, W., 2006. Groundlayer vegetation gradients across oak woodland canopy gaps. *J. Torr. Bot. Soc.* 133, 225–239.
- Peterson, D.W., Reich, P.B., 2008. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecol. Appl.* 11, 914–927.
- Peterson, D.W., Reich, P.B., Wrage, K.J., 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *J. Veg. Sci.* 18, 3–12.
- Scheiner, S.M., 2003. Six types of species-area curves. *Glob. Ecol. Biogeogr.* 12, 441–447.
- Smallwood, B.F., Osterholz, L.C. 1990. Soil survey of Jasper County. United States Department of Agriculture, Soil Conservation Service.
- Soil Survey Staff et al. 2004. Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Official Soil Series Descriptions [Online WWW]. Available URL: <<http://soils.usda.gov/technical/classification/osd/index.html>> [Accessed 10 February 2004]. USDA–NRCS, Lincoln, NE.
- Swink, F., Wilhelm, G. 1994. Plants of the Chicago region. Indiana Academy of Science. Indianapolis, Indiana.
- Taft, J.B., 1997. Savanna and open-woodland communities. In: Schwartz, M. (Ed.), Conservation in Highly Fragmented Landscapes. Chapman and Hall, New York, USA, pp. 24–54.
- Transeau, E.N., 1935. The prairie peninsula. *Ecology* 16, 423–437.
- Will-Wolf, S., Stearns, F., 1999. Dry soil oak savanna in the Great Lakes Region. In: Anderson, R.C., Fralish, J.S., Baskin, J.M. (Eds.), Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press, New York, NY, USA, pp. 135–154.
- Zar, J.H., 1974. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey.