Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands

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Abstract

Questions: How do fire frequency, tree canopy cover, and their interactions influence cover of grasses, forbs and understorey woody plants in oak savannas and woodlands?

Location: Minnesota, USA.

Methods: We measured plant functional group cover and tree canopy cover on permanent plots within a long-term prescribed fire frequency experiment and used hierarchical linear modeling to assess plant functional group responses to fire frequency and tree canopy cover.

Results: Understorey woody plant cover was highest in unburned woodlands and was negatively correlated with fire frequency. C_4-grass cover was positively correlated with fire frequency and negatively correlated with tree canopy cover. C_3-grass cover was highest at 40% tree canopy cover on unburned sites and at 60% tree canopy cover on frequently burned sites. Total forb cover was maximized at fire frequencies of 4-7 fires per decade, but was not significantly influenced by tree canopy cover. Cover of N-fixing forbs was highest in shaded areas, particularly on frequently burned sites, while combined cover of all other forbs was negatively correlated with tree canopy cover.

Conclusions: The relative influences of fire frequency and tree canopy cover on understorey plant functional group cover vary among plant functional groups, but both play a significant role in structuring savanna and woodland understorey vegetation. When restoring degraded savannas, direct manipulation of overstorey tree canopy cover should be considered to rapidly reduce shading from fire-resistant overstorey trees. Prescribed fires can then be used to suppress understorey woody plants and promote establishment of light-demanding grasses and forbs.

Keywords: Cedar Creek Natural History Area; Disturbance ecology; Fire ecology; Forb;Prescribed fire; Grass; Savanna restoration; Woody plant.

Nomenclature: Barkley (1986).

Introduction

Savannas, with continuous understorey grass and forb layers and scattered overstorey trees, are native to many subtropical and temperate climatic regions where precipitation is sufficient to support dense forest vegetation. Frequent disturbances (usually fires) are important for maintaining savanna structure in these regions (Curtis 1959; Vogl 1974; McPherson 1997) and reductions in fire frequency have often led to rapid conversion of savannas to woodlands and forests (Curtis 1959; Vogl 1974). In central North America, oak savannas were once abundant in the transition zone between the tall-grass prairie and deciduous forest biomes, where they were maintained by frequent fires spreading from tall-grass prairie grasslands. However, high quality savanna sites are now rare in this region due to land-use changes and fire exclusion following modern settlement of the area in the past 150 years (Curtis 1959; Nuzzo 1986). Restoration-oriented management now appears necessary for long-term preservation of temperate oak (and many pine) savanna ecosystems, but requires improved understanding of the ways in which fire regulates understorey vegetation structure and composition in savannas.

Prescribed fire is a commonly accepted tool for restoring and managing temperate oak savannas and many other dry forest types. Prescribed fire has a long history of use in tall-grass prairie grassland restoration (Towne & Owensby 1984), and previous studies in oak and pine savannas suggest that high frequency prescribed fire regimes are effective for suppressing understorey shrubs and trees and promoting increased cover of grasses and forbs (White 1983; Tester 1989; Waldrop et al. 1992). However, prescribed fire treatments are slow to alter overstorey canopy structure because prescriptions are typically designed to produce low fire intensities and large overstorey trees typically have thick bark that protects them against basal heating (White 1983; Bond & van Wilgen 1996; Peterson & Reich 2001).

Fire effects on overstorey trees are important because

overstorey canopy structure can influence understorey vegetation structure and composition in savannas (Scholes & Archer 1997). Understorey species composition has been shown to vary across understorey light gradients associated with varying tree canopy cover in savannas and woodlands (Bray 1958; Scholes & Archer 1997; Leach & Givnish 1999), with grasses and many forbs most abundant in open or partially shaded patches. Mechanical thinning has received increasing attention as a savanna restoration treatment because it can be used to rapidly and selectively modify overstorey canopy structure and increase understorey light availability, thereby favoring establishment and increased abundance of light-demanding grasses and forbs.

To date, few studies have attempted to assess the combined effects of fire regimes and overstorey stand structure (and their interactions) on savanna understorey vegetation. To address this issue, we measured plant functional group cover within large permanent sampling plots established in a long-term, prescribed fire frequency experiment. We used fine-scale variability in tree canopy cover within and among sampling plots to evaluate and model plant functional group responses to tree canopy cover at different experimental fire frequencies. Plant functional groups studied included understorey woody plants (including shrubs, trees, and vines), forbs, grasses (including sedges), C_3-grasses, C_4-grasses, N-fixing forbs and other forbs.

Based on previous studies, we expected plant functional groups to vary in their responses to fire frequency and tree canopy cover (Tester 1989; Leach & Givnish 1999). For this study, we asked the following questions:

1. How do fire frequency and mean tree canopy cover influence variability in mean plant functional group cover among prescribed fire treatment units?
2. How much does tree canopy cover influence fine-scale variability in plant functional group cover within management units?
3. Does fire frequency alter tree canopy effects on plant functional group cover?

Background

Study site

The study site was the Cedar Creek Natural History Area and adjacent Helen Allison Savanna in east-central Minnesota, USA (45° 35' N, 93°10' W). The climate is humid continental, with mean daily temperatures range from –11 °C in January to 22 °C in July. Mean annual precipitation is 790 mm, with 64% falling from May to September. Soils are well drained fine sandy soils of the Sartell & Zimmerman series (Grigal et al. 1974).

Fires were common in the study area prior to 1940 (Pierce 1954), but details about Cedar Creek fire regimes are not well documented. Within the broader region, fires historically occurred mostly in autumn or spring, when grass litter was abundant and fuel moisture levels were low enough to carry fire (Gleason 1913; Curtis 1959). Humans probably started most fires, either intentionally or accidentally (Gleason 1913). Today, wildfires are rare and generally small, so high fire frequencies are realized only through prescribed fire programs.

Upland areas of Cedar Creek currently support a mosaic of forest, savanna, and old-field grasslands. Floristically, these communities closely resemble the southern dry forest, oak barren, and dry-mesic prairie types, respectively, described in Wisconsin by Curtis (1959). Dominant tree species are *Quercus ellipsoidalis* and *Q. macrocarpa*. Important shrubs include *Corylus americana*, *Rhus glabra* and *Prunus virginiana*. Other common understorey species include *Andropogon gerardii*, *Schizachyrium scoparius*, *Sorghastrum nutans*, *Poa pratensis*, *Parthenocissus vitacea*, *Amphicarpa bracteata*, *Rhus radicans* and *Carex pensylvanica*.

Fire frequency experiment

A prescribed fire study has been ongoing since 1962 at Cedar Creek and adjacent Helen Allison Savanna (owned and managed by The Nature Conservancy) to study fire frequency effects in oak savannas and woodlands. Managers established prescribed fire management units (1-30 ha each) within an area of ca. 240 ha of upland oak woodlands, savannas, and old-field grasslands, using natural firebreaks and existing roads as unit boundaries. They randomly assigned management units to prescribed fire treatments with frequencies ranging from zero to ten fires per decade. In the 1980s, they added four additional management units to the program. Burn crews ignited scheduled fires in spring (April-May) under weather and fuel conditions prescribed to produce low fire intensity (Peterson & Reich 2001). Because most trees and understorey species initiate above-ground shoot growth in mid-May or later, the fires consumed mostly dead leaves and herbaceous litter.

Under this program, individual management units burned 0-26 times during the period 1962-1995, producing a fire frequency gradient of zero to eight fires per decade. We defined and calculated fire frequency as the total number of fires divided by the number of years since the year preceding the first prescribed fire. This fire frequency measure approximates the inverse of the mean fire return interval and emphasizes time between fires over the total number of fires.

Methods

Data collection

We established 26 permanent plots within 23 pre-scribed fire management units to monitor changes in ecosystem structure and function in response to the prescribed fire frequency treatments. Three units contained two plots, with each representing areas with different initial structural conditions. Plots consisted of four parallel 50-m sampling transects spaced 25 m apart, with sample points placed at 10-m intervals along each transect (24 sample points per plot).

To obtain plant functional group cover estimates, we surveyed understorey vegetation at each sample point in 1995 using quadrat sampling methods (0.5 m^2 area, 624 total sample points). We attempted to survey plots at times when understorey plant cover was near maximum, and most species could be detected and accurately identified. As a result, we surveyed woodland and forest plots in late June and July and savanna plots in August. We estimated cover visually for each plant species using a modified Braun-Blanquet scale (1 = 1%, 2 = 2-5%, 3 = 6-25%, 4 = 26-50%, 5 = 51-75%, and 6 = 76-100%; Kent & Coker 1992).

We measured tree canopy cover, an indirect measure of understorey light availability, at each sample point on all plots under diffuse light conditions using a LICOR LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, Nebraska). We took tree canopy cover readings using a 270-degree lens cap (90° occluded to exclude operator), with the sensor positioned above the shrub layer (up to 2.5 m). Tree canopy cover measured with the LAI-2000 is strongly correlated with leaf area index ($r^2 = 0.86$) and tree basal area ($r^2 = 0.95$) in oak ecosystems at Cedar Creek (Reich et al. 2001), and is a good surrogate for light reaching the understorey.

Data analysis

To examine plant functional group responses to fire frequency and tree canopy cover, we assigned species to one of three functional groups: woody plants (including shrubs, vines, and regenerating trees), forbs, and grasses (all graminoids, including sedges). We further subdivided grasses into C$_3$- and C$_4$-grasses to test for differences in responses among species with similar morphologies but different photosynthetic pathways. We also subdivided forbs into two groups – N-fixing forbs and other forbs – to see if nitrogen-fixing ability altered forb responses to fire frequency and tree canopy cover. N-fixing forbs were of particular interest because previous studies have demonstrated important linkages between N-cycling and vegetation dynamics at Cedar Creek (Tilman 1987;

Reich et al. 2001). We calculated plant functional group cover for each group at each sample point by summing observed cover values for member species, where cover was estimated from the cover class midpoints (1 = 0.5%, 2 = 3.5%, etc.). Prior to statistical analysis, we transformed plant functional group cover values using a square-root transformation ($y' = \sqrt{y}$) to better meet assumptions of normally distributed residual error terms.

We used hierarchical linear modeling to assess the effects of fire frequency and tree canopy cover on plant functional group cover (Singer 1998; Raudenbush & Bryk 2002). We fit a series of models with the goals of (1) partitioning variance in plant functional group cover into within- and between-plot components; (2) assessing the amount of between-plot variance that could be accounted for by fire frequency and mean tree canopy cover; (3) assessing the amount of within-plot variance that could be accounted for by local tree canopy cover; (4) developing a multi-level model of plant functional group cover responses to fire frequency (plot level) and local tree canopy cover (sample point level); and (5) testing to see if fire frequency altered local tree canopy cover effects on plant functional group cover (interactive effect).

We used mixed model procedures in the SAS statistical package to estimate model parameters (Singer 1998). In selecting models, we sought to minimize the adjusted Akaike Information Coefficient (AIC), subject to the constraint that model parameters for highest-order polynomial and interaction terms had to be significantly different from zero ($\alpha = 0.10$).

For each plant functional group, we hypothesized that variability in cover at the sample point level (within plots) was controlled by local tree canopy and other unknown factors. We therefore modeled cover at the sample point level as

$$Y_{ij} = \beta_0 + \beta_1 \cdot (CC_{ij})^a + \beta_2 \cdot (CC_{ij})^{a+1} + \varepsilon_{ij}, \qquad (1)$$

where Y_{ij} was functional group cover at sample point j on plot i, CC_{ij} was tree canopy cover at a sample point (j) on a plot (i), β_n ($n = 0, 1, 2$) were estimated model parameters, and ε_{ij} was a residual ($\varepsilon_{ij} \sim N(0,\sigma^2)$). To account for non-linear responses and the inherent lower bound on percent cover, we tested three competing models for describing plant functional group responses to tree canopy cover: (1) a simple linear model ($a = 1$, $\beta_2 = 0$), (2) a quadratic model ($a = 1$), and (3) a cubic model ($a = 2$).

At the plot level, we hypothesized that mean plant functional group cover was controlled by fire frequency, mean tree canopy cover, and other random plot-level factors. Furthermore, we hypothesized that fire frequency modified the relationship between plant functional group cover and tree canopy cover at the sample point

level (within plots). To assess plot-level (between-plot) effects of fire frequency and tree canopy cover on mean plant functional group cover, we modeled the intercept parameter as

$$\beta_0 = \gamma_{00} + \gamma_{01} \cdot FF_i^a + \gamma_{02} \cdot FF_i^{a+1} + \gamma_{03} \cdot CC_{i\cdot}^a + \gamma_{04} \cdot CC_{i\cdot}^{a+1} + \gamma_{05} \cdot FF_i^a \cdot CC_{i\cdot}^a + u_{0i} \qquad (2)$$

where FF_i was the fire frequency for plot i, $CC_{i\cdot}$ was the mean tree canopy cover on plot i, γ_{0n} terms were plot level model parameters, u_{0i} terms were random plot-level effects, and the exponent ($a = 1, 2$) varied as for the sample point model. To test for potential cross-level interactions, we modeled slope parameters as

$$\beta_1 = \gamma_{10} + \gamma_{11} \cdot FF_i + \gamma_{13} \cdot CC_{i\cdot} + u_{1i} \qquad (3a)$$

$$\beta_2 = \gamma_{20} + \gamma_{21} \cdot FF_i + \gamma_{23} \cdot CC_{i\cdot} + u_{2i} \qquad (3b)$$

The full multilevel model combined the plot and sample point models to simultaneously assess sample point effects, plot-level effects, and cross-level interactions.
To quantify the relative magnitudes of fire frequency and tree canopy effects on plant functional group cover, we first partitioned the random variance in plant functional group cover into within- and between-plot components by fitting a simple, unconditional means model ($Y_{ij} = \gamma_{00} + u_{0i} + \gamma_{ij}$) with a global mean ($\gamma_{00}$), a random variable for plot means (u_{0i}), and a residual error term (γ_{ij}). The variance of u_{0i} estimated the potentially explainable variance in plot means (between-plot variance) and the error variance estimated the potentially explainable variance within plots (Singer 1998; Raudenbush & Bryk 2002). We computed the variance explained by tree canopy cover at the sample point level as the proportional reduction in the within-plot (error) variance for a random coefficients model with tree canopy cover as the only fixed effect, compared to the unconditional means model (Singer 1998). We computed the variance explained by plot-level variables (fire frequency and mean tree canopy cover) as the proportional reduction in variance of plot-level mean cover for a model with plot-level predictor variables compared to the same basic model (unconditional means or random coefficients model) without plot-level predictor variables (Singer 1998; Raudenbush & Bryk 2002).

Results

Fire frequency and tree canopy cover

Fire frequency and tree canopy cover were negatively correlated at the plot and sample point levels. Fire frequencies within the study area ranged from complete fire exclusion to near-annual fires (8 fires per decade). Within this fire frequency gradient, mean tree canopy cover (plot-level means) ranged from a low of 18% cover on a plot with biennial fire frequency (5 fires per decade) to a high of 97% cover on a plot with no fires, with a study area mean of 57%. Tree canopy cover was negatively correlated with fire frequency at both the plot level ($r = -0.70$, $p < 0.001$) and sample point level ($r = -0.54$, $p < 0.001$, Fig. 1). Despite these correlations between fire frequency and tree canopy cover, there was still considerable variability in tree canopy cover between plots (presumably due to different original stand structural conditions) and within plots, so it was still possible to assess fire frequency effects standardized for tree canopy cover and *vice versa*.

Variance partitioning

The proportion of cover variance explainable by plot-level variables varied among plant functional groups (Fig. 2a). Plot-level variables, like fire frequency and mean tree canopy cover, could explain roughly 50% of the total variance in cover for the woody plants and grasses groups, 40% of the variance for the C_3- and C_4-grasses groups, and 30% of the variance for the three forbs groups (Fig. 2a). This suggests that within-plot effects are more important for forbs than for the other groups and, likewise, that plot-level effects are more important for grasses and woody plants than for forbs.
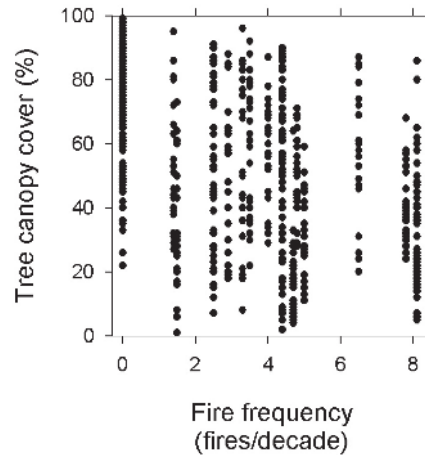

Fig. 1. Distribution of sample point across the fire frequency and tree canopy cover gradients.
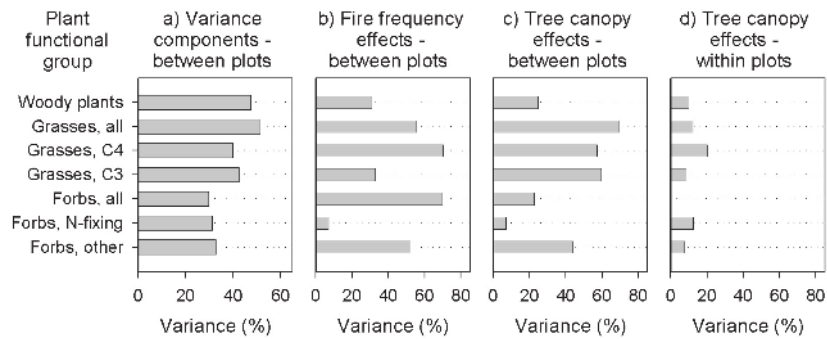
Fig. 2. Variance partitioning and percentages of cover variance 'explained' by fire frequency and tree canopy cover for plant functional groups based on hierarchical linear modeling. Graphs indicate (**a**) percentages of total variance potentially explained by plot-level predictor variables; (**b**) percentage of between-plot variance explained by fire frequency; (**c**) percentage of between-plot variance explained by mean tree canopy cover; and (**d**) percentage of within-plot variance explained by local variability in tree canopy cover.

Woody plant cover

Woody plant cover averaged 41% across all plots, with plot means ranging from 5% to 81%. Mean woody plant cover declined with increasing fire frequency, from over 45% on fire exclusion plots to about 10% on frequently burned plots (Fig. 3a), and increased with mean tree canopy cover, from less than 10% in open savannas (< 25% tree cover) to more than 40% in woodlands with 60-90% tree canopy cover (Fig. 4a). The full mixed model analysis indicated that fire frequency and tree canopy cover effects were additive, with no significant fire-canopy interactions. The final model predicted maximum woody plant cover in unburned areas with 50-80% tree canopy cover, with cover declining with increasing fire frequency and decreasing tree canopy cover (Fig. 5a). Fire frequency was able to explain 31% of between-plot variability, while tree canopy cover was able to explain up to 25% of between-plot and 10% of within-plot variability in woody plant cover (Fig. 2b-d).

Grass cover

Grass cover averaged 21% overall, with plot means ranging from less than 1% to 50%. At the plot level, mean grass cover increased with fire frequency (Fig. 3b), from less than 10% on unburned plots to over 30% on plots burned annually to biennially. Mean grass cover declined with increasing mean tree canopy cover, from over 30% in open savannas to less than 5% in closed-canopy forest (Fig. 4b) and was negatively correlated with tree canopy cover within plots as well. The full mixed model analysis indicated that grass cover was maximized in frequently burned savannas with 20-40% tree canopy cover, and declined at lower fire frequen-

cies and with increasing tree canopy cover (Fig. 5b). Fire frequency did not alter tree canopy effects on total grass cover.

Within the grasses group, the C_4- and C_3-grasses subgroups responded differently to fire frequency and tree canopy cover. C_4-grass cover was positively correlated with fire frequency (Fig. 3c), but negatively correlated with mean tree canopy cover (Fig. 4c) and tree canopy cover within plots. Cover of C_3-grasses was maximized at approximately biennial fire frequencies (Fig. 3d) and 40-50% mean tree canopy cover (Fig. 4d). Within plots, C_3-grass cover was maximized at 40-60% tree canopy cover, with the optimum level depending on fire frequency (Fig. 5d). However, fire frequency had very little effect on mean C_3-grass cover after accounting for tree canopy effects. For C_4-grasses, mean cover (plot level) was positively correlated with fire frequency and negatively correlated with mean tree canopy cover (Fig. 5c), and was also negatively correlated with tree canopy cover within plots. There was some evidence to suggest that tree canopy effects on C_4-grass cover were stronger on frequently burned plots than on unburned or infrequently burned plots (interaction term $p = 0.107$).

Fire frequency was able to explain 55% of between-plot variability, while tree canopy cover was able to explain up to 70% of between-plot and 12% of within-plot variability in total grass cover (Fig. 2b-d). Fire frequency effects were stronger for C_4-grasses (70% of between-plot variance explained) than for C_3-grasses (33%, Fig. 2b). Between-plot variance explained by mean tree canopy cover was similar for both groups (57-59%), but local variability in tree canopy cover accounted for more within-plot variance for C_4-grasses (20%) than for C_3-grasses (9%, Fig. 2d).
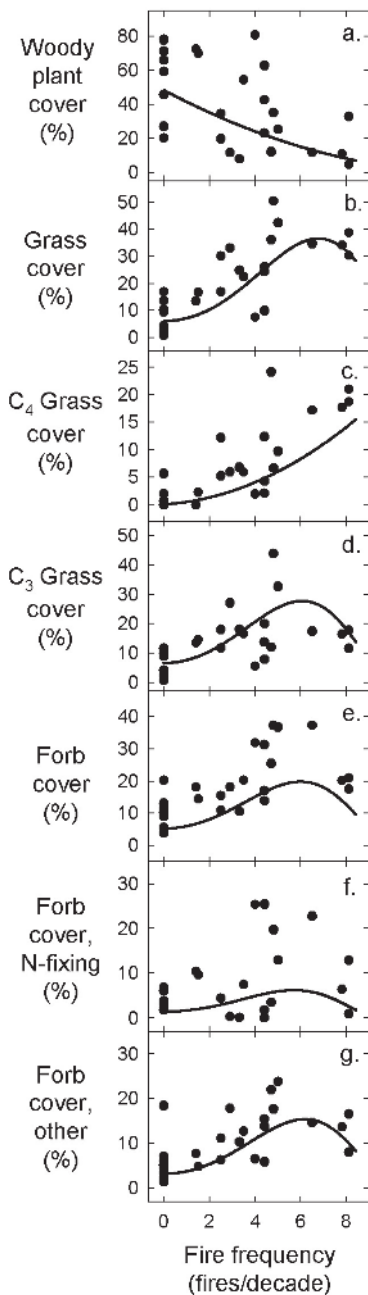
Fig. 3. Fire frequency effects on cover for the woody plants, grass, and forb functional groups. Symbols indicate observed mean cover for each group at each plot. Regression lines indicate expected cover values at the sample point level, based on modeling of square-root transformed cover data.

Fig. 4. Tree canopy cover effects on cover for the woody plants, grass, and forb functional groups. Symbols indicate observed mean cover for each group at each plot. Regression lines indicate expected cover values at the sample point level, based on modeling of square-root transformed cover data.

Forb cover

Forb cover averaged 19% overall, and ranged from 4% to 37%. Mean forb cover peaked at fire frequencies of 4-7 fires per decade (Fig. 3e), and was negatively correlated with mean tree canopy cover (Fig. 4e). Rela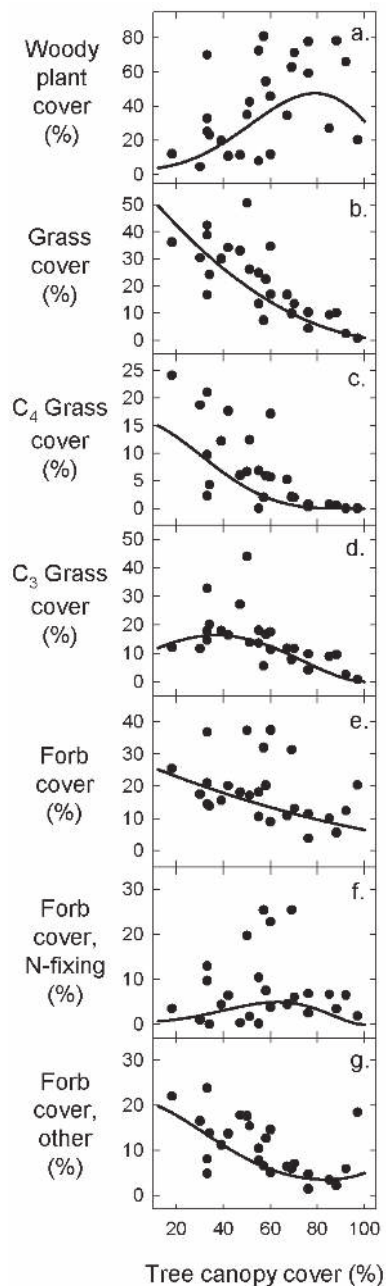tionships between forb cover and tree canopy cover were highly variable among plots. In the full mixed model analysis, fire frequency was the only significant predictor of total forb cover, explaining 70% of the between-plot variance in forb cover (Fig. 2b).

The two forb subgroups responded similarly to fire frequency, but differed in their responses to tree canopy cover. Fire frequency and mean tree canopy cover had
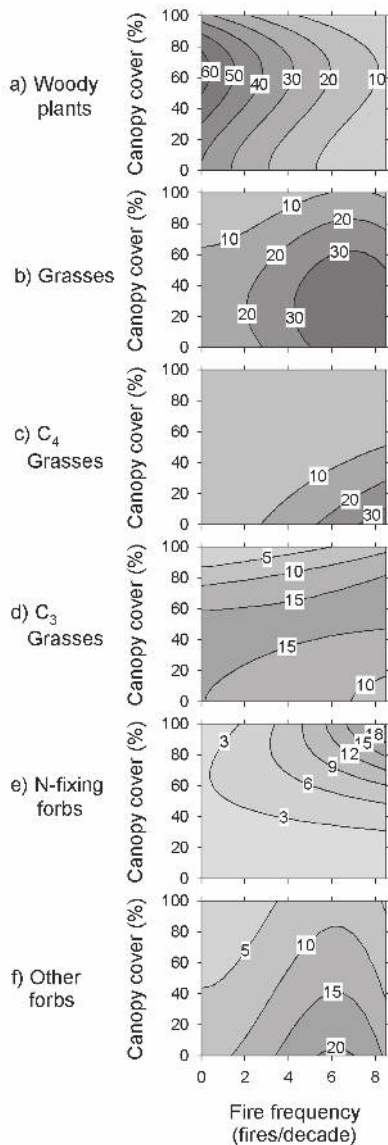
Fig. 5. Modeled effects of fire frequency and tree canopy cover on expected plant functional group cover at the sample point level based on full mixed model analysis. Contour labels indicate percent cover, with darker shading indicating higher predicted cover.

only weak effects on cover of N-fixing forbs at the plot level (Figs. 3f, 4f). The full mixed model analysis identified a significant interaction between fire frequency and tree canopy cover effects on cover of N-fixing forbs. Cover was greatest on partially to fully shaded sites on plots with occasional to frequent fires and was generally low (< 5%) on open sites (Fig. 5e). Cover of 'other' forbs was maximized at fire frequencies of 4-8 fires per decade (Fig. 3f) and was negatively correlated with tree canopy cover (Fig. 4f, 5f). Fire frequency and tree canopy cover were much better predictors of cover for 'other' forbs than for N-fixing forbs (Fig. 2b-d).

Discussion

Results from this study are consistent with previous findings that high frequency fire regimes favor grasses and forbs (Kucera & Koelling 1964; Vogl 1974; Lewis & Harshbarger 1976; Tester 1989; Waldrop et al. 1992) and low fire frequencies favor increased woody plant dominance (Curtis 1959; Vogl 1974; Lewis & Harshbarger 1976) in savannas and grasslands. Previous work, however, could not determine whether fire frequency effects were primarily due to fire effects on plant mortality and regeneration, indirect fire effects caused by changes in (or maintenance of) overstorey structure, or some combination of both. Our results indicate that tree canopy cover significantly influences cover of grasses, forbs, and shrubs independent of fire frequency, and that fire frequency and tree canopy effects vary among plant functional groups.

Woody plants

Fire frequency was important for controlling cover of understorey shrubs, trees, and vines. Prescribed fires kill almost all above-ground woody stems less than 2-3 cm basal diameter (White 1983; Peterson 1998). Most shrub and tree species at Cedar Creek resprout after fire; however, recovery of lost biomass and vertical structure can take 2-4 years (or more) and repeated burning may reduce sprouting vigor (Peterson 1998). Sexual reproduction and associated population expansion may also be delayed until new stems have reached maturity.

At all fire frequencies, understorey woody plant cover was highest at 50-80% tree canopy cover, probably due to reduced competition during establishment and greater soil water and nutrient availability. Davis et al. (1999) found that oak seedling photosynthesis, growth, and mortality were significantly influenced by competition with herbaceous plants for soil water. Mortality was lowest on moist, shaded sites, without competing herbaceous vegetation. Woody plant cover also increases in response to elevated nitrogen supply rates on these soils (Tilman 1987). We suggest that woody plant cover increases with tree canopy cover (up to a point), despite reduced light availability, because shading reduces herbaceous competition for soil water during establishment and because tree-induced higher N availability (Reich et al. 2001; Dijkstra et al. 2006) increases productivity of understorey shrubs and trees. Reductions in N availability at high fire frequencies (Reich et al. 2001) may also produce slower growth and recovery after fire, thereby contributing to the decline in woody plant cover with increasing fire frequency.

Grasses

Fire frequency and tree canopy effects on C_4-grass cover can probably be best explained by shading (light availability) and fire effects on reproduction. The C_4 photosynthetic pathway produces high water- and nitrogen-use efficiency; however, lower canopy N concentrations and higher energetic requirements reduce light use efficiency, so C_4-grasses may be at a competitive disadvantage in shaded environments (Pearcy & Ehlringer 1984; Lee et al. 2001). In tall-grass prairie, increased productivity of C_4-grasses following fire has been attributed to reduced energy limitation following litter removal that allows productivity to increase until soil water or nutrients become limiting (Blair 1997). In savannas, C_4-grasses contend with multiple layers of shading. At high fire frequencies, shading from herbaceous litter and understorey woody plants is minimized, so C_4-grass cover and overall above-ground herbaceous production are strongly correlated with tree canopy cover (Reich et al. 2001). Where tree canopy cover is low, litter and understorey woody plants are the primary sources of shade and C_4-grass cover is strongly correlated with fire frequency. Besides reducing shading, fires may promote added cover of C_4-grasses by stimulating flowering and seed production (Glenn-Lewin et al. 1990). Fire-induced mortality and biomass loss rates are low for C_4-grasses because meristem tissues are well protected and fires are scheduled before the onset of active shoot growth.

Cover of C_3-grasses and sedges was highest in partially shaded savanna environments, as has been found in other Midwestern oak savannas (Leach & Givnish 1999). Despite reducing light availability, partial shading may provide some benefits for C_3 grasses and sedges by reducing evaporative demand, improving water use efficiency (Pearcy & Ehleringer 1984), and reducing competition for soil resources from C_4-grasses (Davis et al. 1999). Some C_3 grasses and sedges (e.g. *Carex pensylvanica* and *Poa pratensis*) commence shoot growth in early spring and may therefore be more susceptible to biomass loss during spring fires (Towne & Owensby 1984); however, we found no evidence of significant negative fire effects on C_3-grass cover. It may be that where C_3-grasses are abundant, higher fuel moisture levels reduce local fire intensity and severity during spring prescribed fires.

Forbs

Moderate to high fire frequency was clearly important for promoting high total cover of forbs. Kucera & Koelling (1964) reported that biennial fires produced higher density of forbs than annual fires in tall-grass prairie in Missouri, but the reasons were unclear. It may be that near-biennial fire frequencies are sufficient to minimize competition from shrubs, but not so frequent as to allow C_4-grasses to dominate competition for below-ground resources.

This study found no significant, common responses of total forb cover to variations in tree canopy cover within and between plots, but did find significant tree canopy effects for the two forb subgroups. Controlling for fire frequency, N-fixing forb cover was positively correlated with tree canopy cover, while other forb cover was negatively correlated with tree canopy cover. In this case, 'forbs' is probably an overly broad and diverse functional group, particularly with respect to tree canopy cover responses. Leach & Givnish (1999) noted that mean leaf width, leaf height, and leaf angle all varied to some degree across a light gradient in Wisconsin savannas, and these factors should influence responses to shading. Further investigation at the species level would probably be helpful for identifying empirical functional groupings based on fire and tree canopy responses.

Across much of the fire frequency gradient, tree canopy cover was positively correlated with cover of N-fixing forbs. In open patches, herbivory by deer (*Odocoileus virginiana*) and insects appears to be suppressing cover of N-fixing legumes (Ritchie et al. 1998). Higher cover of N-fixing forbs in shaded areas is driven in large part by high cover of *Amphicarpa bracteata*, which may be less palatable. Whether the correlation with tree canopy cover is caused by herbivore effects or an environmental gradient, higher cover of N-fixing forbs in shaded areas may help to explain positive correlations between tree canopy cover and N availability in these systems (Reich et al. 2001). The negative correlation between tree canopy cover and cover of the other forbs species was not surprising, given that most of the forb species encountered were native to tall-grass prairie ecosystems (Tester 1989) and can therefore be expected to thrive in high light environments.

Restoration and management of temperate oak savannas

This study showed that tree canopy cover does significantly influence the functional group composition of understorey vegetation, independent of fire frequency effects. If the goal of savanna restoration is an understorey vegetation layer in which grasses and forbs are dominant, mean tree canopy cover should probably be reduced to 30% or less. Higher canopy cover levels may also support C_4-grasses and prairie forbs under a high frequency fire regime, however, particularly if tree spatial patterns produce high variability in tree canopy cover and large open patches. Achieving these goals using prescribed fire alone is possible but may be unacceptably slow (White 1983; Peterson & Reich 2001). Killing overstorey trees

with mechanical thinning, girdling, and/or herbicides can reduce overstorey canopy cover and modify understorey environments quickly, but cannot completely substitute for prescribed fire.

Control of established understorey shrubs and trees and modification of soil resource availability are two important fire effects that are not addressed by mechanical reductions in tree canopy cover. In woodlands with high soil nitrogen availability (Reich et al. 2001), rapid reductions in tree canopy cover will initially produce an understorey environment with high light and nitrogen availability that is likely to initially favor established plant populations, particularly woody species. Subsequent high frequency prescribed fires may be both useful and necessary to suppress shrub and understorey tree dominance, facilitate the establishment and growth of C_4-grasses and prairie forbs, and reduce N-availability through repeated volatilization and changes in plant litter quality (Dijkstra et al. 2006). High frequency fire regimes may be particularly important for controlling shrubs and trees on sites with sandy soils, where competition from grasses for soil water is less effective at limiting woody plant establishment and survival (Knoop & Walker 1985).

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