

Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone

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Abstract Disturbances and environmental heterogeneity are two factors thought to influence plant species diversity, but their effects are still poorly understood in many ecosystems. We surveyed understory vegetation and measured tree canopy cover on permanent plots spanning an experimental fire frequency gradient to test fire frequency and tree canopy effects on plant species richness and community heterogeneity within a mosaic of grassland, oak savanna, oak woodland, and forest communities. Species richness was assessed for all vascular plant species and for three plant functional groups: grasses, forbs, and woody plants. Understory species richness and community heterogeneity were maximized at biennial fire frequencies, consistent with predictions of the intermediate disturbance hypothesis. However, overstory tree species richness was highest in unburned units and declined with increasing fire frequency. Maximum species richness was observed in unburned units for woody species, with biennial fires for forbs, and

with near-annual fires for grasses. Savannas and woodlands with intermediate and spatially variable tree canopy cover had greater species richness and community heterogeneity than old-field grasslands or closed-canopy forests. Functional group species richness was positively correlated with functional group cover. Our results suggest that annual to biennial fire frequencies prevent shrubs and trees from competitively excluding grasses and prairie forbs, while spatially variable shading from overstory trees reduces grass dominance and provides a wider range of habitat conditions. Hence, high species richness in savannas is due to both high sample point species richness and high community heterogeneity among sample points, which are maintained by intermediate fire frequencies and variable tree canopy cover.

Keywords Community heterogeneity · Intermediate disturbance hypothesis · Oak savanna · Oak woodland · Prescribed fire · Species richness

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Introduction

Competitive exclusion, disturbance processes, and environmental heterogeneity are three key determinants of plant species diversity in terrestrial ecosystems (Whittaker 1975; Connell 1978;

Huston 1994). Competitive exclusion reduces species diversity as strong competitors first suppress lesser competitors and later drive them to local extinction. Environmental heterogeneity can promote high species diversity by promoting spatial niche partitioning and heterogeneity in plant community composition across environmental gradients (β diversity; Whittaker 1975). Disturbances can reduce plant species diversity by eliminating disturbance-sensitive species, increase species diversity by opening up growing space and resources for use by colonizing species, maintain species richness by slowing or preventing competitive exclusion, and alter spatial heterogeneity in plant community composition (Huston 1994).

Ecological theory predicts important linkages between disturbance frequency and species diversity (Grime 1973; Connell 1978; Huston 1979). The intermediate disturbance hypothesis (IDH, Connell 1978; Huston 1979) predicts that species diversity will be maximized at intermediate disturbance frequencies and severities that minimize species losses due to competitive exclusion and direct disturbance effects, while maintaining opportunities for establishment of new species. Although the IDH is well studied (Roxburgh et al. 2004), species diversity responses to fire frequency often do not follow predicted patterns. In tallgrass prairie, species richness declines with increasing fire frequency as higher fire frequencies favor the dominant C_4 grasses and reduce community heterogeneity (Collins 1992; Collins et al. 1995; Collins and Steinauer 1998). In savannas and woodlands, species richness often increases with increasing fire frequency up to biennial (Tester 1989; Brockway and Lewis 1997) or annual (Walker and Peet 1983) fires. However, rigorous tests of the IDH have been few in savannas and woodlands, in part due to the scarcity of long-term studies using a wide range of fire frequency treatments applied to large plots. Without sufficient replication of treatments in time and space, tests of the IDH may produce ambiguous results (Beckage and Stout 2000).

Fire frequency may also influence understory species richness indirectly in savanna, woodland, and forest ecosystems through its influence on

overstory tree density and canopy cover. Huston (1994) proposed that high fire frequencies promote high species richness in savannas by preventing competitive exclusion of grasses and forbs by woody plants. Furthermore, understory plant community composition and diversity in savannas often varies across gradients in understory light and soil resources associated with spatial variability in overstory tree cover (Bray 1958; Belsky et al. 1989; Vetaas 1992; Scholes and Archer 1997; McPherson 1997; Brewer 1998). Thus, high plant community heterogeneity and overall species richness may be observed in savannas with intermediate and spatially variable tree canopy cover (Leach and Givnish 1999) due to high plant resource heterogeneity. High species richness in fire-maintained savannas (compared to neighboring forests and grasslands) may also be the result of intermediate resource availability that reduces dominance and competitive exclusion by both woody plants and grasses and allows greater forb species richness (Leach and Givnish 1999). Although fire frequency and tree canopy (or understory light) effects on species diversity have each been investigated separately, we are aware of only one previous study that explicitly examined the potential influence of tree canopy structure (basal area) on the relationship between fire frequency and plant species diversity (Mehlman 1992).

Prior to modern settlement, fires annually burned large areas of the tallgrass prairie biome of North America (Gleason 1913). At the forest-prairie biome transition zone, topographic barriers to the spread of wildfire created spatial heterogeneity in fire frequency and vegetation structure (Gleason 1913; Grimm 1984; Leitner et al. 1991). Grasslands and oak savannas occupied areas with high and medium fire frequencies, while oak woodlands and deciduous forests occupied areas with low fire frequencies (Gleason 1913; Grimm 1984; Leitner et al. 1991). Decades of land-use change, landscape fragmentation, and active fire suppression have largely excluded wildfires and produced dramatic losses of intact oak savannas to the point where they are now rare (Nuzzo 1986). Management with prescribed fire (or fire surrogates) may be necessary if restoration of oak savanna ecosystems is

a priority. Yet, long-term effects of different prescribed fire regimes on oak savanna vegetation, and particularly plant species diversity, are not well understood.

The purpose of this study was to assess the combined effects of fire frequency and overstory canopy structure on plant species diversity within an area of the prairie-forest biome transition zone in central North America. Plant species diversity was assessed in terms of species richness and community heterogeneity (a measure of β diversity). Fire frequency and tree canopy cover effects on species richness were assessed at both the plant functional group (grasses, forbs, and woody plants) and whole plant community levels. We tested the following hypotheses related to fire frequency and canopy cover effects on plant species diversity:

- (1) Species richness will be greatest at an intermediate fire frequency that minimizes species losses due to fire and competition while promoting new species establishment (intermediate disturbance hypothesis).
- (2) The fire frequency at which species losses to fire and competition are minimized will vary among plant functional groups due to mean differences in fire adaptations, ability to colonize following disturbance, and competitive ability (vital attributes corollary to IDH).
- (3) Species richness will be higher in savannas than in grasslands or woodlands due to intermediate resource availability that limits dominance by grasses and woody plants and promotes high forb diversity (intermediate resource hypothesis).
- (4) Community heterogeneity will be higher in savannas than in grasslands or forests due to spatial variability in overstory canopy structure and associated plant resources (resource heterogeneity hypothesis).

While the focus of this paper is on plant species diversity, related papers from this study provide information about overstory tree structure and dynamics (Peterson and Reich 2001), factors influencing plant functional group cover (Peterson et al. 2007), and carbon and nitrogen dynamics (Reich et al. 2001).

Methods

Study area

The study was conducted at Cedar Creek Natural History Area (CCNHA), a 2,300 ha reserve located on the Anoka Sand Plain in east-central Minnesota (45°25' N, 93°10' W). The climate is humid continental, with cold winters and warm summers. Mean daily temperature ranges from -11°C in January to 22°C in July. Mean annual precipitation is 790 mm, more than half of which falls during the growing season (May–September). Soils are well-drained sands of the Sartell and Zimmerman series (Grigal et al. 1974), terrain is relatively flat, and erosion after prescribed fires is minimal.

CCNHA lies within the transition zone between the tallgrass prairie and temperate deciduous forest biomes in central North America. Upland areas currently support a mosaic of forests, woodlands, savannas, and old fields, which are floristically similar to the southern dry forest, oak barren, and dry-mesic prairie types described by Curtis (1959). Northern pin oak (*Quercus ellipsoidalis* E.J. Hill) and bur oak (*Quercus macrocarpa* Michx.) are the dominant tree species.

Prescribed burning experiment

Prescribed fire programs were initiated at CCNHA and the adjacent Helen Allison Savanna (a 20-ha oak savanna reserve owned by the Nature Conservancy) in the early 1960s within more than 200 ha of mixed oak woodlands, oak savannas, and old-field grasslands. Treatments were designed to test fire frequency effects on the structure and species composition of oak savannas and woodlands and to restore and maintain the historically important oak savanna ecosystems (Irving 1970; Faber-Langendoen and Davis 1995). Management units (1–30 ha each) originally containing savanna and/or woodland structure were randomly assigned fire frequency treatments ranging from annual and biennial fires to complete fire exclusion. Additional management units were added to the prescribed fire programs in the 1980s. Canopy cover has

increased with continued fire exclusion in some unburned units (Faber-Langendoen and Davis (1995), adding closed-canopy forest conditions to the structural gradient. Old-fields were embedded within some management units and have remained relatively stable structurally. Management units are protected from livestock grazing, but herbivory by white-tailed deer (*Odocoileus virginianus*), pocket gophers (*Geomys bursarius*), and insects does influence plant and nutrient dynamics in these systems (Inouye et al. 1987; Ritchie et al 1998).

Prescribed fires were conducted mostly between mid-April and mid-May, prior to leaf expansion in overstory trees (Peterson and Reich 2001). Most understory plants (except for some cool-season grasses and spring forbs) do not initiate aboveground growth until mid-May, so the fires generally consumed dead plant material. Fires were usually ignited using the strip headfire technique with prescribed weather conditions of 15–25°C air temperature, 25–45% relative humidity, and winds less than 20 kph. Fire behavior varied with weather conditions and fuel loads, but fire prescriptions were written to produce fires of low intensity, and mean flame lengths were typically less than 1 m (personal observation). Management units were burned 0–26 times during 1962–1995. We defined realized fire frequency as the total number of prescribed fires divided by the number of years the unit was part of the prescribed fire experiment. We defined the starting year as the year prior to the first fire. Realized fire frequencies ranged from complete fire exclusion to about eight fires per decade for the near-annual fire treatment.

Field sampling

We sampled vegetation on 26 permanent plots established in savanna, woodland, and forest stands within the prescribed fire management units. Each plot consisted of four parallel 50-m long sampling transects placed 25 m apart, encompassing a total area of 0.375 ha. We placed understory vegetation sampling points at 10-m intervals along each transect (24 sample points per plot). Management units contained one or two plots each; where management units

contained two plots, the plots represented areas with different initial overstory structural conditions. In three prescribed fire management units, we also sampled vegetation on temporary plots in old-field grassland areas to expand the range of overstory structural conditions studied (total = 29 plots).

In summer 1995, we surveyed understory vegetation at each of the 696 sample points using quadrat sampling methods adjusted for herbaceous and woody plants. We assessed herbaceous species richness (and cover) at each sample point based on visual cover estimates within a rectangular frame (0.5 m²). We assessed woody plant species richness (shrubs, trees, and vines) based on stem count surveys within a 1-m radius circular quadrat (3.14 m²), but estimated total woody plant cover using the 0.5-m² rectangular frames (Peterson et al. 2007). We used larger sampling areas for woody plant species richness to compensate for larger mean plant sizes and generally lower plant densities. We obtained overstory tree species richness for each plot from a complete survey of living trees (diameter ≥5 cm). Most of the units receiving prescribed fire treatments had been burned within 2 years of sampling. We attempted to survey plots at times when understory 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 measured tree canopy cover, the fraction of sky obscured by overstory trees, at each sample point (24 per plot) during the summer growing season using a Plant Canopy Analyzer (LAI-2000, LI-COR, Lincoln, Nebraska, USA). To measure tree canopy cover, we positioned the sensor at the top of the shrub layer at each sample point (up to a maximum height of about 2 m), using a 270° lens cap (90° occluded), and matched readings with simultaneous readings from a paired sensor in a nearby old-field grassland. Canopy cover values are closely related to understory light levels (Machado and Reich 1999) and local stand basal area (Peterson 1998). Averaged over a plot, canopy cover is also a good indicator of aboveground net primary productivity and nitrogen cycling rates (Reich et al. 2001).

Data analysis

We calculated species richness, the number of unique species in a sample or group of samples, for individual sample points (quadrat species richness) and for all samples pooled within a plot (plot species richness). We calculated quadrat species richness as the sum of herb species richness (grasses and forbs) from the herbaceous survey (0.5 m² quadrat) and woody plant species richness from the understory shrub and tree survey (3.1 m² quadrat). Plot species richness was the number of unique plant species in the pooled sample from all 24 sample points in a plot. We also calculated species richness for three plant functional groups: woody plants (understory trees, shrubs, and vines), forbs, and grasses (grasses and sedges).

We calculated community heterogeneity as the mean dissimilarity of species lists for all pairwise combinations of sample points within a plot. We used the Sorensen similarity index, $C_s = 2j / (SR_a + SR_b)$, to calculate similarity between pairs of sample points, where SR_a and SR_b are quadrat species richness values for quadrats a and b, and j is the number of species common to both quadrat samples. We calculated dissimilarity as the complement of similarity, $1 - C_s$. To quantify community heterogeneity among plots, we used Whittaker's beta statistic, $\beta_w = TSR / PSR_{avg}$, where TSR is the number of unique plant species in the pooled sample from all 29 plots in the study and PSR_{avg} is the mean plot species richness (Magurran 1988).

We used hierarchical linear modeling (Raudenbush and Bryk 2002) with SAS PROC MIXED (Littell et al. 1996) to model combined fire frequency and tree canopy cover effects on total and plant functional group species richness at the sample point level. To reduce heteroscedasticity in model residuals, we transformed sample point species richness values with a square root function prior to analysis. The level-1 model was $SR_{ij} = \beta_0 + \beta_1 \cdot CC_{ij} + \beta_2 \cdot CC_{ij}^2 + r_{ij}$, where SR_{ij} is species richness, CC_{ij} is local tree canopy cover, and r_{ij} is a random error for sample point j on plot i . We modeled the β_0 coefficient as a function of fire frequency (linear and quadratic) and a plot-level random variable, and modeled

the β_1 and β_2 coefficients as functions of fire frequency (linear term only) and plot-level random variables.

Results

We encountered 190 vascular plant species. Of this total, 38 were grass and sedge species, 39 were shrubs and trees, and 113 were forbs. Plot species richness varied between 32 and 71 species (mean = 55) and mean quadrat species richness varied between 8.8 and 16.6 species. Beta diversity among plots was 2.6 for woody species, 3.0 for grasses, 4.2 for forbs, and 3.5 for all plants. About half of the plant species were relatively rare, being recorded at fewer than 10 sample points.

Overstory tree species richness was highest on plots protected from fire and declined with increasing fire frequency (Fig. 1). Only two tree species, bur oak (*Quercus macrocarpa*) and northern pin oak (*Q. ellipsoidalis*), were present on plots with the highest fire frequencies. Plots protected from fire typically contained shade-tolerant, fire-sensitive species (e.g., *Acer*

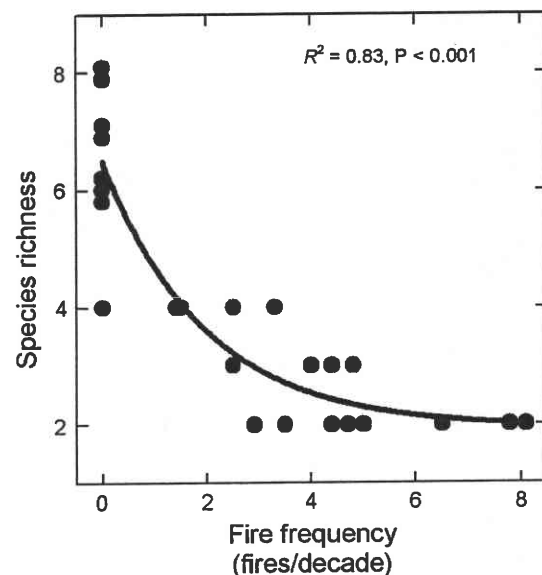


Fig. 1 Fire frequency effects on overstory tree species richness. Regression line is based on a negative exponential function. Old-field plots were omitted from this analysis because the absence of overstory trees ($SR = 0$) on these plots was caused primarily by human removal prior to cultivation rather than by fire effects

rubrum, *Prunus serotina*) in addition to the oaks. Old-field grassland plots contained no overstory trees.

Total understory plant species richness (plot level) was maximized at an intermediate fire frequency of about five fires per decade, consistent with the predictions of the intermediate disturbance hypothesis (Fig. 2a). The fire frequency at which plot-level species richness was maximized varied among plant functional groups, however, consistent with the predictions of our

vital attributes corollary to the IDH. Woody plant species richness was highest in plots protected from fire and declined with increasing fire frequency (Fig. 2b). Forb species richness increased with fire frequency to a maximum at about five fires per decade, but declined somewhat at higher fire frequencies (Fig. 2c). Grass species richness was lowest in plots protected from fire and generally increased with fire frequency, although grass richness tended to level off at fire frequencies greater than five fires per decade (Fig. 2d).

Fig. 2 Fire frequency and tree canopy cover effects on plant species richness at the plot level. Species richness values are for all plants (a, e), woody plants (b, f), forbs (c, g), and grasses (d, h). Open circles indicate old-field grassland plots. Solid lines indicate significant linear or quadratic relationships based on regression analysis. Vertical dotted lines indicate fire frequency or mean tree canopy cover values with maximum predicted species richness

