

---

# Fire Season and Dominance in an Illinois Tallgrass Prairie Restoration

Tanya E. Copeland<sup>1</sup>

William Sluis<sup>2</sup>

Henry F. Howe<sup>3,4</sup>

## Abstract

North American prairie remnants and restorations are normally managed with dormant-season prescribed fires. Growing-season fire is of interest because it suppresses dominant late-flowering grasses and forbs, thereby making available light and other resources used by subdominant grasses and forbs that comprise most prairie diversity. Here we report a twofold increase in mean frequency and richness of subdominant species after late-summer fire. Stimulation of subdominants was indiscriminate; richness of prairie and volunteer species increased in species that flowered in early, mid-, or late season. Early spring fire, the management tool used on this site until this experiment, had no effect on subdominant richness or frequency. Neither burn treatment affected reproductive tillering of the tallgrasses *Sorghastrum nutans* or *Panicum virgatum*. Flowering of *Andropogon gerardii* increased 4-fold after early-spring fires and 11-fold after late-summer fires. These preliminary results suggest that frequency and species richness of subdominants can be improved by late growing-season fire without compromising vigor of warm-season tallgrasses.

**Key words:** biodiversity, dominance, ecological restoration, fire season, species richness, tallgrass prairie.

---

<sup>1</sup>TAMS Consultants, an Earth Tech Company, One East Wacker Drive, Suite 1200, Chicago, IL 60601, U.S.A.

<sup>2</sup>Department of Biology, Lewis University, Route 53, Romeoville, IL 60446, U.S.A.

<sup>3</sup>Department of Biological Sciences (M/C 066), University of Illinois at Chicago, 845 W. Taylor Street, Chicago, IL 60607, U.S.A.

<sup>4</sup>Address correspondence to H. F. Howe, Tel.: 312-996-0666; Fax 312-413-2435; E-mail: hfhowe@uic.edu

## Introduction

Periodic fire maintains Midwestern tallgrass prairies by slowing woody succession and stimulating native grasses (Anderson 1982, 1990; Leach & Givnish 1996). The beneficial effects of fire for tallgrass productivity, tillering, and area cover are well documented (Curtis & Partch 1948; Kucera & Ehrenreich 1962; Ehrenreich & Aikman 1963; Hulbert 1969; Old 1969). Recognition that fire improves tallgrass vigor while suppressing woody vegetation has led to widespread management of prairie restorations and remnants with prescribed burns, almost always set for convenience and aesthetics in early or late spring (e.g., Rock 1981; McCain 1986). Management practices that strongly favor dominant tallgrasses, however, can have negative consequences for competitively inferior subdominants and hence raise concern that such practices may undermine the long-term maintenance of prairie biodiversity (Howe 1994a, 1999a, 1999b). A challenge is to create or maintain communities that hold enough common prairie dominants to have the appearance of tallgrass prairies, without eliminating most biodiversity by favoring these aggressive species too much.

Ecological communities are frequently dominated by a few common species (Preston 1948, 1962; Magurran 1988), which in grasslands may monopolize up to 95% of the available space (see Howe 1994a). Most subdominant species are restricted to small patches not occupied by dominants or are sparsely co-mingled with dominants. Distinguishing between fire effects on dominants and on infrequent or rare subdominants is important for predicting effects of management practices on prairie biodiversity (e.g. Howe 1994a, 1994b, 1999a). In general, practices that encourage dominance suppress or exclude interstitial species, causing a decline in species diversity (see Cornell & Lawton 1992; Huston 1994). Conversely, practices that suppress dominants increase diversity through competitive release of subdominants (see Collins & Gibson 1990; Howe 1994a, 1999b; Engle et al. 2000). Management for uncommon and rare plant species may amount to intentional suppression of dominants to varying degrees.

Timing of fire directly alters competitive abilities of plants by damaging plants at different developmental stages and indirectly by altering the physical environment and favoring or suppressing competitors. Direct responses are possible, for instance, if the timing of fire interacts with growth phenology (Lovell et al. 1982; Steuter 1987; Howe 1994a). By damaging aboveground plant parts at critical times in their growth cycle, such as during periods of rapid growth, fire can impact overall vigor and reproduction of herbaceous prairie plants. Post-fire performance in growth, reproduction, and competitive

ability may depend on the stage at which aboveground parts are destroyed.

Indirect fire effects may be equally important, with quite different community impacts of fires early and late in a season. Litter inhibits early growth of prairie plants by reducing light penetration to the soil surface (Knapp 1984a; Knapp & Seastedt 1986; Hulbert 1988). Litter removal by fire in the spring contributes to short-term increases in productivity and flowering, especially of late-flowering dominants, first by removing inhibition and second by allowing increased solar warming of bare soils, which are moist at that time of year (Curtis & Partch 1950; Hulbert 1969; Old 1969). Increased solar radiation after summer fires may result in desiccation and inhibition of regrowth during dry years and increased germination and regrowth from rhizomes or rootstalks for plants capable of rapid response in wetter years. Fire *extends* the growing season and may or may not increase the rate of photosynthesis *during* the growing season, with the particular influences depending on the timing of the fire during the season, the assemblage of plants affected, and the weather. Both dominants and subdominants potentially benefit from litter and canopy removal, but timing of that removal is likely to affect their competitive abilities differently.

Spring fires damage early grasses and forbs as they initiate growth, with late-spring fires causing the most damage (Lovell et al 1982; Hulbert 1988). Early-flowering forb species especially may show reduced vigor for the duration of the season after spring burns. Forbs that sustain direct fire damage are unable to respond to improved growing conditions associated with litter and canopy removal the year of the burn; by the next growing season, a year of tallgrass growth has already created a new layer of detritus. Late C<sub>4</sub> tallgrasses quickly recover from spring fires and by the end of the season often show evidence of stimulation.

Mid- and late-summer fires have the potential to suppress warm-season tallgrasses by causing direct fire damage to aboveground plant parts during a period of maximum growth and reproduction (Howe 1994a, 2000; Engle et al. 1998). Direct fire damage to warm-season grasses during the growing season may reduce their vigor the following year and may reduce the intensity of competition experienced by subdominants. Even if summer fire does not compromise tallgrass vigor, forbs still benefit the following year by a reduction in shade concomitant with canopy removal. In wet-mesic Wisconsin restorations, Howe (1994b, 1995, 1999a) found that tallgrass canopies recovered from spring fires within 3 to 4 weeks, but following late-summer fires much of the ground remained exposed to sun for 12 to 24 growing-season weeks.

Here we test the hypothesis that late growing-season fire causes a short-term increase in frequency and species richness of subdominants. If direct fire effects on late-

flowering species drive this response, differential flowering phenology as a response to summer fire should be apparent and dominants should be suppressed; growing-season fire should suppress late-growing and flowering subdominant species and favor early-growing and flowering subdominants (Howe 1994b). If indirect effects of tallgrass canopy and litter removal are more important, growing-season fire should stimulate interstitial species indiscriminately; dominants may or may not be adversely affected (see Howe 1999b, 2000). Early-spring fire should stimulate dominant warm-season grasses and reduce subdominant species richness.

## Materials and Methods

To evaluate the effect of fire season on dominant and subdominant species, prescribed burns were applied to six replicate plots in early spring or late summer. Presence or absence of data on subdominant species and counts of reproductive tillers of dominant grasses were collected one year before and one year after burn treatments in 1997. This allowed for both within-year and between-year comparisons of spring and summer burn plots.

## Study Site

The research site, Goose Lake Prairie State Natural Area, is located in Grundy County in the Grand Prairie Division of northeastern Illinois. The area is characterized by level topography, varied soils, and poor natural drainage (Mohlenbrock 1986). The site used in this experiment is approximately equally divided between two soils, the Bryce-Calamine silty loam overlying silty clay and High-Gap loam, which is a mixture of clay and silty loam. Before European settlement, wet and mesic prairie, marsh, and prairie pothole communities were widespread. Most of Grundy County has since been converted to farmland. Goose Lake Prairie State Natural Area extends over 1,027 ha. Of this, 600 ha are classified as remnant wet prairie and prairie marsh and 225 ha are restored tallgrass prairie. Remnant wet prairie is dominated by *Calamagrostis canadensis* Michx. (blue joint grass) and *Spartina pectinata* Link (prairie cord grass). Restorations occupy land that was previously drained and cultivated. Dominant matrix-forming species include the warm-season grasses *Sorghastrum nutans* (L.) Nash (Indian grass), *Panicum virgatum* L. (switch grass), and *Andropogon gerardii* Vitm. (big bluestem) and an aggressive cloning goldenrod *Solidago altissima* L. (tall goldenrod). Soils vary greatly over the entire Goose Lake site, but change in vegetation is usually gradual unless there are major discontinuities in moisture (Nelson & Anderson 1983). There are no obvious vegetation discontinuities that could be attributed to soil among our study plots.

Sample plots were established in the 3-ha Prairie Grove, which was planted in autumn of 1976. Dominant grasses were well mixed and evenly distributed. Subdominants, or interstitial species, included more than 40 species of grasses, sedges, and forbs, most of which were mid- to late flowering (see Appendix, nomenclature follows Swink & Wilhelm 1994). Because there were no records of the identity or number of forb species planted, we distinguished native prairie from invasive species, some of which were early successional natives and many of which were exotics. This site was burned in early to mid-April in 1987, 1990, 1991, 1992, and 1996 (William Glass, personal communication).

### Burns

Spring and summer burns were accomplished on 23 April and 3 September 1997. On the day of spring burns the air temperature averaged 8°C, with relative humidity of 79% and a northeast wind at 16 km/hr. On the day of late-summer burns the temperature averaged 22°C, with a relative humidity of 63% and a south wind at 19 km/hr. All plots were backfired from edges opposite the prevailing wind direction and then completed with a wind-driven headfire. Weather and fire data were reported by the site assistant superintendent. A representative flame height and percent consumption of above-ground vegetation were recorded for each 10 × 10-m plot.

In this experiment burns were carried out in April and early September of the same year. Responses were evaluated in the subsequent year. This means that spring burns are evaluated about 1.75 growing seasons after the burn and September burns about 1.25 growing seasons after the burn. This had some impact on results, because invasive early successional natives and exotics are probably more prevalent after any burn than they are a year after dominant vegetation can close in. This difference may not be as great as it may seem because differences in response are largely due to inherent differences in species responding, which in any case are likely to persist for at least 2 to 3 years or longer (see Howe 2000). An alternative, to burn in August of one year, in May of the next, and to evaluate productivity in autumn of the second year, would leave a similar but reversed one-half season disparity in growing time (for August burns, evaluation after 1.25 growing seasons, for May burns after 0.75 season). The additional burden for interpretation of different year burns would be confounded differences in growing times with unshared winter effects and unshared growing-season effects in the critical early weeks of recovery from burns. Either burn regime could have consequences for conspecific comparisons, but neither would appear to make much difference in a system where differences in species present are due to interspecific responses, not subtle variations in intraspecific recovery.

### Sampling

Twelve 10 × 10-m plots were arranged in a 3 × 4 grid with plots separated by 10 m mowed fire lanes. Spring and summer burn treatments were systematically assigned to plots in a checkerboard pattern, resulting in six plots per burn treatment. Vegetation sampling was conducted in 1996 and 1998, one year before and one year after the 1997 burn treatments. Seven 1 × 1-m quadrats were randomly sampled for presence or absence of data on subdominant species and counts of reproductive tillers of dominant grasses from each of twelve 10 × 10-m plots. No samples were taken within 1 m of the plot border. Presence/absence sampling was conducted in late June and early July and counts of flowering stalks in early October.

### Species Richness and Frequency

Species richness was analyzed at the scale of 1-m<sup>2</sup> quadrats and 10 × 10-m plots. Subdominant species were designated as prairie or volunteer and as early, mid- or late flowering. Volunteer species include exotic and native species that do not commonly occur in prairies. Species flowering at the time of sampling (late June/early July) were designated as mid-season. Other flowering times follow Mohlenbrock (1986), with early season occurring until mid-June and late season from mid-July on. This allowed for examination of interaction effects between year, burn season, and species designation.

### Analyses

Species richness and counts of reproductive tillers were analyzed by two-way nested analysis of variance; treatment effects are indicated by significant year-by-burn season interactions. Main factors were year and burn season, each of which had two levels. Year was either 1996 or 1998, corresponding to pre- or post-burn sampling. Burn season was either spring or summer. Plots are nested within burn season. Overall treatment effects are evaluated by comparison of least square means of burn season-by-year interactions. Differences between means are determined using a post-hoc Bonferroni test. Counts of *A. gerardii* reproductive tillers were square root transformed to improve distribution and homogeneity of variances. For all other analyses, no transformations were necessary to meet analysis of variance assumptions. Mean values of plots were analyzed for *P. virgatum*. Results are expressed as means ( $\pm$  SE) unless noted otherwise.

Treatment effects on frequency of subdominant species were analyzed by Wilcoxon signed rank test. Frequency values were calculated as the proportion of total quadrats in spring- or summer-burn plots where a species was present. Seven quadrats were sampled in each of

six replicate plots per burn treatment for 1996 and 1998, so that a total of 42 quadrats were sampled for each burn season-by-year combination. Frequency measures for each species in 1996 and 1998 in each burn treatment were paired.

**Results**

**Burns**

Rates of spread were calculated from fire ignition and extinction times for each 10 × 10-m plot. Spring fires had higher flame heights (1.9 ± 0.4 m) compared with summer burn flame heights (0.7 ± 0.1 m, *t* = 3.291, *df* = 5.2, *p* < 0.025). Consumption of litter was total (100%, no variance) after spring fires and substantial but less (91% ± 2%, Mann-Whitney *U* = 36,  $\chi^2$  = 9.542, *df* = 1, *p* < 0.005) after summer fires. Following Johnson (1992), fire intensity (*I*) is approximated by

$$I = 259.83L^{2.174}$$

where *I* is fire intensity in kW/m and *L* is flame height in m, which corresponds to 1262.4 ± 519.4 and 118.3 ± 20.1 kW/m for April and September burns, respectively (Mann-Whitney *U* = 36,  $\chi^2$  = 8.609, *df* = 1, *p* < 0.005). Rates of spread were similar (1.3 ± 0.2 m/min).

**Subdominant Species Richness**

Each 10 × 10-m plot had a mean of eight species in 1996, with no pretreatment differences between plots assigned to spring (8.17 ± 1.08) or summer (8.17 ± 1.38, Bonferroni, *p* = 1.0) burn treatments (Table 1). There was a significant burn season-by-year interaction effect on species richness (*F*<sub>1,10</sub> = 21.75, *p* < 0.01). Species number increased between 1996 and 1998 in plots subjected to late-summer fire (8.17 ± 1.38 compared with 14.17 ± 1.85, Bonferroni, *p* < 0.01), whereas species number in plots burned in early spring was unchanged (8.17 ± 1.08 compared with 7.83 ± 1.11, Bonferroni, *p* = 1.0).

No pretreatment differences in richness were evident between plots assigned to spring and summer burn treatments for either prairie (3.17 ± 0.98 compared with 3.50 ± 0.76) or volunteer species (5.00 ± 0.37 compared with 4.83 ± 0.87, Bonferroni, *p* = 1.0 for both contrasts). After burns, the number of volunteer species (5.58 ± 0.44) exceeded that of prairie species (4.04 ± 0.50, *F*<sub>1,30</sub> = 14.47, *p* < 0.01). As with overall species richness, when prairie and volunteer species are considered separately, a significant year-by-burn season interaction is apparent (*F*<sub>1,30</sub> = 14.47, *p* < 0.01), indicating that each increased in richness in a treatment (here, summer burns). However, an interaction between year, burn season, and species designation was not observed (*F*<sub>1,30</sub> = 0.10, *p* = 0.76), indicating that neither prairie nor volunteer species increased more than the other. Species number increased in summer burn plots (4.17 ± 0.59 to 7.08 ± 0.68, Bonferroni, *p* < 0.01) but remained unchanged in spring burn plots (4.08 ± 0.57 to 3.92 ± 0.56, Bonferroni, *p* = 1.0). The absence of a significant interaction effect between year, burn season, and species designation indicates that prairie and volunteer species responded similarly to fire treatments. Similar results were obtained when species number was analyzed at the scale of 1 × 1-m quadrats (Fig. 1, year × burn, *F*<sub>1,30</sub> = 21.13, *p* < 0.01).

Flowering guilds of subdominant species also responded indiscriminately to summer fires. There were no pretreatment differences in richness between spring and summer burn plots for early-flowering (0.67 ± 0.33 compared with 0.33 ± 0.21), mid-flowering (4.00 ± 0.73 compared with 4.17 ± 1.11), or late-flowering species (3.50 ± 0.56 compared with 3.67 ± 0.49, Bonferroni, *p* = 1.0 for all). Early-season species (1.17 ± 0.21) are under-represented compared with mid- (4.42 ± 0.53) and late-season species (3.96 ± 0.32, Bonferroni, *p* < 0.01). A significant year-by-burn season interaction was observed (*F*<sub>1,50</sub> = 10.27, *p* < 0.01), but there was not a significant interaction between year, burn season, and flowering guild (*F*<sub>2,50</sub> = 0.18, *p* = 0.83). Species richness increased regardless of flowering guild in response to late-sum-

**Table 1.** Subdominant species richness by species designation and flowering guild.

	Subdominant Species Richness* ( mean /10 × 10 m plot ± SE )			
	Spring Burn		Late-Summer Burn	
	1996	1998	1996	1998
Overall	8.17 ± 1.08 <sup>a</sup>	7.83 ± 1.11 <sup>a</sup>	8.17 ± 1.38 <sup>a</sup>	14.17 ± 1.85 <sup>b</sup>
Native prairie	3.17 ± 0.98 <sup>a</sup>	3.17 ± 0.79 <sup>a</sup>	3.50 ± 0.76 <sup>a</sup>	6.33 ± 1.02 <sup>b</sup>
Volunteer	5.00 ± 0.37 <sup>a</sup>	4.67 ± 0.71 <sup>a</sup>	4.83 ± 0.87 <sup>a</sup>	7.83 ± 0.87 <sup>b</sup>
Early flowering	0.67 ± 0.33 <sup>a</sup>	1.17 ± 0.31 <sup>a</sup>	0.33 ± 0.21 <sup>a</sup>	2.50 ± 0.22 <sup>b</sup>
Mid flowering	4.00 ± 0.73 <sup>a</sup>	3.33 ± 0.71 <sup>a</sup>	4.17 ± 1.11 <sup>a</sup>	6.17 ± 1.40 <sup>b</sup>
Late flowering	3.50 ± 0.56 <sup>a</sup>	3.17 ± 0.54 <sup>a</sup>	3.67 ± 0.49 <sup>a</sup>	5.50 ± 0.56 <sup>b</sup>

\* Mean species numbers within a category that do not have a common superscript are significantly different to at least the level of *p* < 0.05 as determined by a Bonferroni post-hoc analysis.

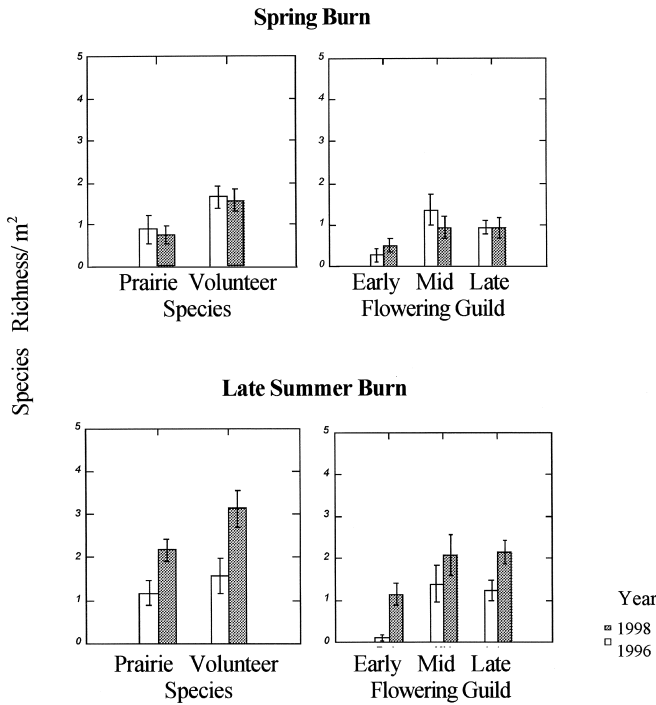


Figure 1. Species richness per square meter analyzed by flowering guild and species designation as prairie or volunteer. There is no evidence of an interaction between either species designation or flowering guild with fire season and year. Year-by-burn season interactions are significant in both analyses (species:  $F_{1,50} = 21.13$ ,  $p < 0.01$ ; flowering guild:  $F_{1,50} = 10.37$ ,  $p < 0.01$ ).

mer fire and remained unchanged in plots subjected to early spring fire. Analysis of flowering guilds at the scale of  $1 \times 1$ -m quadrats yielded similar results (Fig. 1, year  $\times$  burn,  $F_{1,50} = 10.37$ ,  $p < 0.01$ ).

### Subdominant Species Frequency

Frequency is defined as the proportion of total  $1 \times 1$ -m quadrats sampled in which a given species is present. The dominant *Sorghastrum nutans* was present in every  $m^2$  quadrat sampled in both 1996 and 1998, giving it a frequency of 1.0. Subdominant prairie species with the highest overall frequencies were *Polygala* sp. (0.56), *Helianthus mollis* (0.46), and *Liatris* sp. (0.33). Volunteer species with the highest frequencies included *Juncus* spp. (0.86), *Eragrostis* sp. (0.75), and *Eleocharis* spp. (0.48).

A graph of frequency versus species rank (Fig. 2) reveals a reduction in dominance and an increase in richness as a result of summer burn treatment. The degree of dominance is indicated by the initial slope of the curve. Steeper slopes indicate a greater concentration of dominance. The slope of the summer 1998 curve is initially less steep than the other three curves, indicating a lower degree of dominance in those plots.

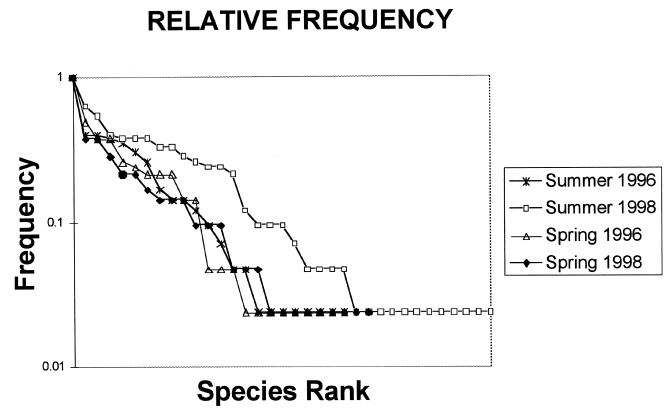


Figure 2. Relative frequency of species encountered in 1996 and 1998 in spring and summer burn plots plotted against rank order abundance. Slopes of frequencies plotted against ranks 1–24 are similar for plots burned in spring of 1997 ( $-0.024$ ) and plots yet unburned in 1996, but the slope is significantly less ( $-0.014$ ) for plots burned in the summer of 1997 ( $p < 0.001$ ), indicating reduced dominance after the summer burns.

Overall species richness and the mean frequency of subdominant species are highest in summer 1998 plots. Species richness increased from 23 to 35 between 1996 and 1998 in summer burn plots but remained virtually unchanged in spring burn plots. Frequency of subdominant species doubled in summer plots between 1996 and 1998, increasing from a mean of 0.08 in 1996 (on average a subdominant species present in 3 of 42 quadrats) to 0.15 in 1998 (species present in 6 of 42 quadrats). There was no change in frequencies in spring burn plots over the same time period (Wilcoxon sign rank test,  $Z = 3.32$ ,  $df = 33$ ,  $p < 0.01$  for summer burn treatment;  $Z = -0.40$ ,  $df = 23$ ,  $p = 0.69$  for spring burn treatment).

### Flowering Response of Dominant Grasses

Contrary to expectations, tillering of dominant late-season grasses was not reduced by summer burns (Table 2). There were no pretreatment differences in mean density of *Andropogon gerardii* reproductive tillers, but reproductive tillers increased in both spring and summer burn plots between 1996 and 1998, with a significant interaction between year and burn season ( $F_{1,154} = 9.69$ ,  $p < 0.01$ ). The increase in summer burn plots exceeded that of spring burn plots. No significant change in reproductive tillers, increase or decrease, was evident for *Panicum virgatum* or *S. nutans* that could be attributed to burn season.

### Discussion

Tallgrasses inhibit establishment of subdominants by forming a dense sod of rhizomes and roots, by shading

**Table 2.** Responses of dominant tallgrasses to spring and summer burns.

Species	Reproductive Tillers per m <sup>2</sup> *			
	Spring Burn		Late-Summer Burn	
	1996	1998	1996	1998
<i>Sorghastrum nutans</i> †	45.81 ± 3.21 <sup>a</sup>	37.71 ± 3.10 <sup>ab</sup>	32.81 ± 2.65 <sup>b</sup>	30.81 ± 2.59 <sup>b</sup>
<i>Andropogon gerardii</i> ‡	1.10 (0.42,2.10) <sup>a</sup>	4.93 (2.76,7.73) <sup>b</sup>	1.32 (0.61,2.34) <sup>a</sup>	14.90 (9.99,20.79) <sup>c</sup>
<i>Panicum virgatum</i> †	3.12 ± 1.67 <sup>a</sup>	1.78 ± 0.84 <sup>a</sup>	2.22 ± 1.26 <sup>a</sup>	1.38 ± 0.87 <sup>a</sup>

\* Mean flowering stalk densities within a species that do not have a common superscript are significantly different to at least the level of  $p < 0.05$  as determined by a Bonferroni post-hoc test.

† Values are means ± SE.

‡ Values are back-transformed means reported with lower and upper 95% confidence limits in parentheses.

shorter grasses and forbs, and by covering the ground with litter (Hulbert 1969, 1988; Knapp & Seastedt 1986). On general principles, management practices that suppress the competitive dominance of warm-season tallgrasses should favor numerous subdominants (Cornell & Lawton 1992; Howe 1999b, Maina & Howe 2000). Summer fire has the potential to suppress tallgrasses by causing direct fire to aboveground plant parts when they are at their peak productivity, which in this area occurs in late July or August. Such direct fire damage may result in competitive release of subdominants by altering the long-term competitive ability of affected tallgrasses or by simply removing tallgrass canopies and accumulated litter before the next growing season. By either mechanism, growing-season fire is expected to cause at least a short-term increase in number and frequency of subdominant species.

Here we report a twofold increase in subdominant species richness and mean frequency in plots subjected to late-summer fire. Richness and frequency are unchanged in plots subjected to early-spring fire. These results are consistent with other studies of forb response to dormant and growing-season burns. Biondini et al. (1989) reported species richness in summer burn plots to be higher than species richness in plots treated with either spring or fall prescribed burns. One year after fire treatment, summer and control plots had 51 species, whereas spring and fall burn plots averaged 38 species. Engle et al. (1998) did not have frequency measures but did demonstrate a 40 to 80% increase in forb productivity in plots treated with early September fire. As in our study, Abrams and Hulbert (1987) found no effect of spring burning on species richness.

Prairie and volunteer species responded similarly to fire treatment. This is an important result for managers concerned with whether fire prescriptions will make restorations more or less "weedy." In this study fire season did not affect one flowering guild more than another; all increased after summer fire. Temporary suppression of dominants evidently causes a general release of subdominant species, as suggested in simpler synthetic communities (Howe 2000), but was much more

clearly demonstrated here. This effect occurred even though dominant grasses were not significantly depressed in reproductive tillers by summer fire; evidently, shade of dominant grasses was reduced enough by summer fire to permit a surge in forb richness and frequency, even though the number of dominant plants was not reduced.

Other studies reported differential effects of fire season on individual forb species (Lovell et al. 1982; Biondini et al. 1989; Howe 1999a) and on flowering guilds (Howe 1994b, 1995). Species that flower early in the growing season were expected to be more likely damaged by spring fire, whereas late-flowering species were expected to be disproportionately damaged by summer fire. Howe (1995) observed an interaction between fire season and flowering guild when plots were burned in mid-July, a result that was not confirmed by the September fires used here. Ewing and Engle (1988) reported no effect of early September fire on either tallgrass productivity or tiller density one year after treatment of an *Andropogon-Sorghastrum-Panicum* tallgrass prairie. Engle et al. (1998) investigated effects of late-summer fire on productivity of mid-successional tallgrass prairie. Early August burns reduced productivity of warm-season perennial grasses and increased productivity of annual grasses.

Neither warm-season perennial grasses nor annual grasses were affected by our early September fire. It is possible that a six-week difference in timing of growing-season burns drastically alters the outcome or that something else, perhaps related to the site or availability of other plant resources, reduces the response of dominant grasses to growing-season fire at Goose Lake Prairie and some Missouri sites.

*Andropogon gerardii* may be more resilient than other warm-season grasses to growing-season fire, a possibility that has implications for the long-term consequences of management by growing-season fire (Peet et al. 1975). Reproduction is primarily vegetative, with new growth being initiated from a network of thick and extensively branched underground rhizomes (Weaver 1958). Because burns occurred in 6 of 10 previous years at Goose Lake, a profusion of tillering of this species af-

ter summer burns cannot be attributed to a response to infrequent burns. It may, as implied by treatment effects, be a response to late growing-season fire. By contrast, reproduction in *Panicum virgatum* occurs primarily through seedling establishment (Zhang & Maun 1991). *Panicum virgatum* growth is initiated from apical meristems, which by mid-June are elevated above the soil surface, making it especially susceptible to mid-summer fire (Branson 1953). *Andropogon gerardii*, *P. virgatum*, and *Sorghastrum nutans* all develop best on mesic sites. However, *A. gerardii* is most tolerant of the low soil moistures often encountered late in the growing season (Knapp 1984b). The clonal growth form of this species and its habit of dense sod formation, tall stature, and tolerance to drought and shade make it an aggressive competitor and may also enhance its resilience to disturbance by growing-season fire. The sharp increase in reproductive tillering in this species after infrequent late-summer fire may foretell future increases in cover and shade, perhaps at the expense of initially more common *P. virgatum* and *S. nutans*, or at the eventual expense of subdominants.

Flowering stalk density is positively correlated with tallgrass productivity (Kucera & Ehrenreich 1962; Ehrenreich & Aikman 1963; Old 1969; Knapp 1984a; Hulbert 1988) and resource availability (Old 1969; Knapp 1984a, 1984b) and reflects levels of carbohydrate reserves in underground plant organs (Henderson et al. 1982). Inflorescence production is also indicative of a species potential for regeneration and is a good indicator of long-term competitive ability. Suppression of tallgrasses should result in reduced inflorescence production. Contrary to expectations, September fire actually promoted flowering of *A. gerardii* in the next growing season, possibly as a consequence of improved growing conditions resulting from removal of accumulated litter (Knapp & Seastedt 1986).

Late-summer burning caused a short-term increase in species richness and frequency of subdominants. Species number increased indiscriminately, without regard to flowering guild. Vigor of *S. nutans* and *P. virgatum*, as indicated by flowering response, were unaffected, whereas *A. gerardii* showed evidence of stimulation. These results are what would be expected if indirect effects associated with litter and canopy removal are driving plant response to late-summer fire. No species among subdominants were widespread enough in their response to indicate a species-specific pattern. Dominants and subdominants both benefited from reduction in shade concomitant with removal of litter and senescent canopy before the next growing season.

This study is of too short a duration to permit clear recommendations of the effects of late-summer burns on diversity of native and invasive species (see Engle & Bidwell 2001; also Engle et al. 2000). Initial results indicate, however, that frequency and richness of interstitial species

might be improved by late-summer fire without compromising vigor of dominant warm-season grasses. If substantiated with further replicated experiments over time, increased diversity might be accomplished without disproportionately encouraging introduced or non-prairie species. This study does offer statistically strong results from sets of replicated burns in each season, which as Engle and Bidwell (2001) pointed out is absent from much of this literature. The possibility should be entertained that late growing-season fire offers a viable alternative to spring burning for maintenance of diversity in prairie restorations and remnants. This may be especially true where small prairie remnants are managed for conservation rather than for commercial purposes.

### Acknowledgments

This project would not have been possible without the enthusiastic assistance of J. Nyhoff and J. Settles of Goose Lake Prairie in coordinating burns. W. Glass reconstructed burn histories. M. Miriti helped establish the plots. N. Cordeiro, J. Klock, J. Lussenhop, C. Martinez-Garza, M. Miriti, D. Murray, M. Pacheco, S. Saha, and B. Zorn-Arnold offered constructive comments on the manuscript. Supported in part by the Goose Lake Prairie Natural Area, the University of Illinois, the National Science Foundation of the USA, and TAMS Consultants.

### LITERATURE CITED

- Abrams, M. D., and L. C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. *American Midland Naturalist* 117:442–445.
- Anderson, R. C. 1982. The eastern prairie-forest transition—an overview. Pages 86–92 in R. Brewer, editor. *Proceedings of the Eighth North American Prairie Conference*. Western Michigan University Press, Kalamazoo.
- Anderson, R. C. 1990. The historic role of fire in the North American grassland. Pages 81–97 in S. L. Collins and L. L. Wallace, editors. *Fire in North American tallgrass prairies*. University of Oklahoma Press, Norman.
- Biondini, M., A. A. Steuter, and G. E. Grygiel. 1989. Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in the Northern Mixed Prairie. *Vegetatio* 85:21–31.
- Branson, F. A. 1953. Two new factors affecting resistance of grasses to grazing. *Journal of Range Management* 6:167–171.
- Collins, S. L., and D. J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. Pages 81–97 in S. L. Collins and L. L. Wallace, editors. *Fire in North American Tallgrass Prairies*. University of Oklahoma Press, Norman.
- Cornell, H. V., and J. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61:1–12.
- Curtis, J. T., and M. L. Partch. 1948. Effects of fire on the competition between bluegrass and certain prairie plants. *American Midland Naturalist* 39:437–443.
- Curtis, J. T., and M. L. Partch. 1950. Some factors affecting flower production in *Andropogon gerardii*. *Ecology* 31:488–489.

- Ehrenreich, J. H., and J. M. Aikman. 1963. An ecological study of certain management practices on native plants in Iowa. *Ecological Monographs* **33**:113–130.
- Engle, D. M., and T. G. Bidwell. 2001. The response of central North American prairies to seasonal fire. *Journal of Range Management* **54**:2–10.
- Engle, D. M., R. L. Mitchell, and R. L. Stevens. 1998. Late growing-season fire effects in mid-successional tallgrass prairies. *Journal of Range Management* **51**:115–121.
- Engle, D. M., M. W. Palmer, J. S. Crockett, R. L. Mitchell, and R. Stevens. 2000. Influence of late-season fire on early successional vegetation of an Oklahoma prairie. *Journal of Vegetation Science* **11**:135–144.
- Ewing, A. L. and D. M. Engle. 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist* **120**:212–223.
- Henderson, R. A., D. L. Lovell, and E. A. Howell. 1982. The flowering responses of 7 grasses to seasonal timing of prescribed burns in remnant Wisconsin prairie. Pages 7–10 in R. Brewer, editor. *Proceedings of the Eighth North American Prairie Conference*. Western Michigan University Press, Kalamazoo.
- Howe, H. F. 1994a. Managing species diversity in tallgrass prairie: assumptions and implications. *Conservation Biology* **8**:691–704.
- Howe, H. F. 1994b. Response of early- and late-flowering plants to fire season in experimental prairies. *Ecological Applications* **4**:121–133.
- Howe, H. F. 1995. Succession and fire season in experimental prairie plantings. *Ecology* **76**:1917–1925.
- Howe, H. F. 1999a. Response of *Zizia aurea* to seasonal mowing and fire in a restored prairie. *American Midland Naturalist* **141**:373–380.
- Howe, H. F. 1999b. Dominance, diversity and grazing in tallgrass restoration. *Ecological Restoration, North America* **17**:59–66.
- Howe, H. F. 2000. Grass response to seasonal burns in experimental plantings. *Journal of Range Management* **53**:437–441.
- Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology*, **50**:874–877.
- Hulbert, L. C. 1988. Causes of fire effects in tallgrass prairie. *Ecology* **69**:46–58.
- Huston, M. A. 1994. *Biological diversity*. Cambridge University Press, Cambridge, United Kingdom.
- Johnson, E. A. 1992. *Fire and vegetation dynamics*. Cambridge University Press, Cambridge, United Kingdom.
- Knapp, A. K. 1984a. Post-burn differences in solar radiation, leaf temperature, and water stress influencing production in a lowland prairie. *American Journal of Botany* **71**:220–227.
- Knapp, A. K. 1984b. Water relations and growth of three grasses during wet and drought years in a tallgrass prairie. *Oecologia* **65**:35–43.
- Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* **36**:662–668.
- Kucera, C. L., and J. H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. *Ecology* **43**:334–336.
- Leach, M. K., and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* **273**:1555–1558.
- Lovell, D. L., R. A. Henderson, and E. A. Howell. 1982. The response of forb species to seasonal timing of prescribed burns in remnant Wisconsin prairie. Pages 11–15 in R. Brewer, editor. *Proceedings of the Eighth North American Prairie Conference*. Western Michigan University Press, Kalamazoo.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Jersey, Princeton, New Jersey.
- Maina, G., and H. F. Howe. 2000. Inherent rarity in community restoration. *Conservation Biology* **14**:1335–1340.
- McCain, W. E. 1986. *Illinois prairie: Past and future. A restoration guide*. Illinois Department of Conservation, Springfield, Illinois.
- Mohlenbrock, R. H. 1986. *Guide to the vascular flora of Illinois*. Southern Illinois University Press, Carbondale.
- Nelson, D. C., and R. C. Anderson. 1983. Factors influencing the distribution of prairie plants along a moisture gradient. *American Midland Naturalist* **109**:367–375.
- Old, S. M. 1969. Microclimate, fire and plant production in an Illinois prairie. *Ecological Monographs* **39**:355–384.
- Peet, M., R. Anderson, and M. S. Adams. 1975. Effect of fire on big bluestem production. *American Midland Naturalist* **94**:15–26.
- Preston, F. 1948. The commonness and rarity of species. *Ecology* **29**:254–283.
- Preston, F. 1962. The canonical distribution of commonness and rarity. Part I. *Ecology* **43**:185–215.
- Rock, H. 1981. *Prairie propagation handbook*. 6th Edition. Wehr Nature Center, Milwaukee.
- Steuter, A. A. 1987. C<sub>3</sub>/C<sub>4</sub> production shift on seasonal burns—northern mixed prairie. *Journal of Range Management* **40**:27–31.
- Swink, F., and G. Wilhelm. 1994. *Plants of the Chicago region*. 4th Edition. Indiana Academy of Sciences, Indianapolis.
- Weaver, J. E. 1958. Summary and interpretation of underground development in natural grassland communities. *Ecological Monographs* **28**:55–78.
- Zhang, J., and M. A. Maun. 1991. Establishment and growth of *Panicum virgatum* L. seedlings on a Lake Erie sand dune. *Bulletin of the Torrey Botanical Club* **188**:141–153.



**Appendix.** Species encountered during presence/absence sampling in 1996 and 1998.

Species <sup>a</sup>	Family	Life Form	Flowering Time	Guild <sup>b</sup>
<i>Prairie species</i>				
<i>Amorpha fruticosa</i> L.	Fabaceae	Shrub	May–June	Early season
<i>Antennaria plantaginifolia</i> L.	Asteraceae	Forb	April–May	Early season
<i>Apocynum</i> sp.	Apocynaceae	Forb	May–August	Mid season
<i>Aster ericoides</i> L.	Asteraceae	Forb	July–October	Late season
<i>Coreopsis tripteris</i> L.	Asteraceae	Forb	August–September	Late season
<i>Dodecatheon meadia</i> L.	Primulaceae	Forb	April–June	Early season
<i>Eryngium yuccifolium</i> Michx.	Apiaceae	Forb	July–August	Mid season
<i>Helianthus mollis</i> Lam.	Asteraceae	Forb	August–September	Late season
<i>Lespedeza capitata</i> Michx.	Fabaceae	Forb	August–September	Late season
<i>Liatris</i> sp.	Asteraceae	Forb	July–September	Late season
<i>Monarda fistulosa</i> L.	Lamiaceae	Forb	May–August	Mid season
<i>Oxalis violacea</i> L.	Oxalidaceae	Forb	April–June	Early season
<i>Parthenium integrifolium</i> L.	Asteraceae	Forb	July–September	Late season
<i>Polygala</i> sp.	Polygalaceae	Forb	May–September	Mid season*
<i>Potentilla arguta</i> Pursh	Rosaceae	Forb	June–July	Mid season
<i>Pycnanthemum virginianum</i> L.	Lamiaceae	Forb	July–September	Mid season*
<i>Rosa carolina</i> L.	Rosaceae	Shrub	June–July	Mid season
<i>Tradescantia ohiensis</i> Raf.	Commelinaceae	Forb	April–August	Mid season*
<i>Volunteer species<sup>a</sup></i>				
<i>Achillea millefolium</i> L.	Asteraceae	Forb	May–August	Mid season
<i>Ambrosia artemisiifolia</i> L.	Asteraceae	Forb	August–October	Late season
<i>Asclepias syriaca</i> L.	Asclepiadaceae	Forb	May–August	Mid season*
<i>Aster simplex</i> Willd.	Asteraceae	Forb	August–October	Late season
<i>Carex</i> spp.	Cyperaceae	Sedge	April–July	Mid season*
<i>Carex vulpinoidea</i> Michx.	Cyperaceae	Sedge	May–August	Mid season*
<i>Eleocharis</i> sp.	Cyperaceae	Sedge	May–October	Mid season*
<i>Epilobium</i> sp.	Onagraceae	Forb	July–September	Late season
<i>Eragrostis</i> sp.	Poaceae	Grass	July–October	Late season
<i>Erigeron canadensis</i> L.	Asteraceae	Forb	April–October	Mid season
<i>Eupatorium serotinum</i> Michx.	Asteraceae	Forb	August–October	Late season
<i>Galium</i> sp.	Rubiaceae	Forb	April–September	Mid season
<i>Hieracium</i> sp.	Asteraceae	Forb	June–September	Mid season
<i>Hypericum perforatum</i> L.	Hypericaceae	Forb	June–September	Mid season
<i>Juncus</i> spp.	Juncaceae	Rush	May–October	Mid season*
<i>Lactuca</i> sp.	Asteraceae	Forb	June–September	Mid season
<i>Oenothera biennis</i> L.	Onagraceae	Forb	June–October	Mid season
<i>Physalis</i> sp.	Solanaceae	Forb	May–October	Mid season
<i>Poa pratensis</i> L.	Poaceae	Grass	March–July	Early season
<i>Polygonum</i> sp.	Polygonaceae	Forb	June–October	Late season
<i>Rumex crispus</i> L.	Polygonaceae	Forb	April–May	Early season
<i>Stachys</i> sp.	Lamiaceae	Forb	June–September	Mid season
<i>Taraxacum officinale</i> Weber	Asteraceae	Forb	March–November	Mid season

<sup>a</sup> Volunteer species include exotic species and native species that do not commonly occur in prairies. Nomenclature and habitat designation follow Swink and Wilhelm (1994).

<sup>b</sup> Species marked with an asterisk were flowering at the time of sampling (late June/early July) and were designated as mid-season. Other flowering times follow Mohlenbrock (1986).