

SUCCESSION AND FIRE SEASON IN EXPERIMENTAL PRAIRIE PLANTINGS¹

HENRY F. HOWE

*Biological Sciences (M/C 066), University of Illinois at Chicago,
845 W. Taylor Street, Chicago, Illinois 60607 USA*

Abstract. Fire season influenced the cover of species and flowering guilds of plants in replicated grass and forb plantings of tallgrass prairie species in Wisconsin. Over two burn cycles at 3-yr intervals, cover increased in the rhizomatous perennials *Andropogon gerardii*, *Aster simplex* and *Solidago altissima* in plots burned in spring, or summer, or left unburned, but cover showed dramatic positive or negative responses to spring or summer burns in *Agropyron repens*, *Erigeron annuus*, *Panicum virgatum*, *Phalaris arundinacea*, and *Rudbeckia hirta*. Aggregate response of flowering guilds was stronger. By the last (1993) census, the phenological guild flowering before mid-July (summed cover values for nine species) accounted for 4% cover in unburned plots and <2% cover in plots burned in early spring, but 32% cover in plots burned in midsummer. The late-flowering guild (summed values for 21 species) accounted for 93% cover in unburned plots and 97% cover in plots burned in early spring, but 66% cover in plots burned in midsummer. Remaining space was taken by a mid-season guild (11 species), only one of which (*E. annuus*) was common enough for individual statistical analysis.

These results have implications for succession of prairie vegetation under different seasonal fire regimes. Over 8 yr, summer fires that simulated the timing of lightning fires retarded progression to dominance of large, late-flowering C₄ grasses, allowing early-flowering species eliminated in other treatments to persist or even prosper. Primaeval lightning fires in midsummer may have produced quite different communities than anthropogenic fires, which are rarely set during the middle of the growing season.

Key words: fire ecology; grassland; guild; phenology; prairie; restoration; succession.

INTRODUCTION

Fire maintains tallgrass prairies by suppressing woody vegetation and stimulating grasses and forbs (Hulbert 1986, Anderson 1990). The season of burning is of interest because tallgrass remnants, now <1% of grasslands that once covered 570,000 km² of central North America, are maintained by anthropogenic burns set in fall, winter, or spring (e.g., Ehrenreich and Aikman 1963, Rock 1981, McClain 1986). As a consequence, most scientific insights concerning ungrazed American tallgrass vegetation are derived from communities maintained by burns outside of the growing season (e.g., Hulbert 1969, 1986, 1988, Risser et al. 1981, Collins and Wallace 1990). It is becoming clear, however, that midsummer burns caused by lightning fires are possible (Bragg 1982, Ewing and Engle 1988) and common on large prairie tracts when not suppressed (Komarek 1968, Vogl 1974, Higgins 1984). Most prairie fires ignited by lightning occur in July and August (Higgins 1984). Moreover, prescribed summer burns that simulate the timing of midsummer lightning fires may influence flowering, recruitment, and species composition in prairies (Steuter 1987, Biondini et al. 1989, Glenn-Lewin et al. 1990, Steuter et al. 1990,

Howe 1994a, b). This paper explores the impact of spring and summer burns, compared with unburned replicates, on cover of species and flowering guilds in 21 tallgrass plots planted in 1986.

Most studies of prescribed burning consider fire itself "the treatment." Here, I test alternative hypotheses concerning fire season in the context of succession of prairie restorations. First, I test the hypothesis that conventional early spring fires favor late-flowering grasses and forbs. Second, I test the hypothesis that midsummer fires simulating the timing of lightning ignition favor early-flowering grasses and forbs. Changes in species and guild cover after two cycles of spring and summer fire at 3-yr intervals are compared with each other and with replicated unburned plots that offer a standard of early successional change without fire.

Extending a detailed evaluation of before and after effects of one burn cycle (Howe 1994a), I focus on succession of species and flowering guilds under different seasonal burn regimes over 8 yr. The key assumption of this study is that fires in the spring and summer impact early and late species differently by killing aboveground plant parts at different phenological stages. More subtle effects of clearing 10–40 cm of litter are alluded to in general terms, but detailed analysis of the causes of idiosyncratic responses by particular species to such effects is outside the scope

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of this study. Species incidence, richness, and turnover will be discussed elsewhere.

METHODS

Site

Twenty-one 12 × 15 m plots were planted in an abandoned cornfield in the Driftless (unglaciated) Region of southwestern Wisconsin (Webster Township, 43°32' N, 90°20' W) in 1986, using standard restoration techniques (Rock 1981; see Howe 1994a for details). In southwestern Wisconsin, mean annual precipitation from 1983–1992 ranged from 57.7 to 103.1 cm, overall (mean ± 1 SE) 84.6 ± 4.4 cm/yr (NOAA 1983–1992). Precipitation in the planting year (1986) and subsequent year was close to the overall mean. In Viroqua, 20 km from the site, July precipitation in burn years 1989 and 1992 was within 0.5 cm of the 30-yr mean (missing data for some months in some years preclude use of Viroqua data for summaries). Precipitation in 1993 was the heaviest on record, but NOAA data were not yet compiled at the time of writing.

Plantings are in sandy loam on a floodplain of Elk Run; water puddles after heavy rains throughout the growing season, making this a "wet-mesic" prairie restoration (Rock 1981). History of the site, specifics of field preparation and planting, surrounding vegetation, and other details are discussed in Howe (1994a).

Plants

Plant species discussed here include native prairie species planted in 1986, in a roughly lognormal abundance distribution, and volunteer species that appeared over the course of the study (Howe 1994a: Appendices 1–3). Of the 73 native species planted, 28 were abundant enough to be sampled (100 cm², contiguous), and 21 were still present in 1993 following the second burn cycle in 1992. Fifteen of the 35 "volunteer" species disappeared by the 1993 census.

I avoid the difficulty of quantitative community studies in which most species are too uncommon for individual analysis (e.g., see Magurran 1988, Howe 1990) by summing cover values for species into phenological guilds that indicate whether they are likely to flower before, during, or after the July and August peak of lightning-caused grassland fires in central North America (see Higgins 1984). Those that complete flowering and most seeding before mid-July are termed "early-season," those that flower from June to August, "mid-season," and those that flower and seed after mid-July, "late-season."

Common early species included *Agropyron repens**, *Phalaris arundinacea**, and *Rudbeckia hirta*, with species too infrequent for individual analysis: *Bromus inermis**, *Carex* spp.*, *Penstemon digitalis*, *Poa pratensis**, *Stellaria media**, and *Tradescantia ohiensis* (* volunteers). Most were invaders in plantings that, as is usual in tallgrass restorations, overrepresented mid-

season and late-season species. Only one mid-season species, *Erigeron annuus**, remained common enough for individual statistical analysis; its guild included *Achillea millefolium**, *Asclepias incarnata*, *Asclepias syriaca**, *Echinacea purpurea*, *Lactuca* spp.*, *Monarda fistulosa*, *Oenothera biennis*, *Potentilla arguta*, *Trifolium* spp.*, and *Verbascum thapsis**. Common late-season species included *Andropogon gerardii*, *Aster simplex**, *Panicum virgatum*, and *Solidago altissima**, with less common species too infrequent for individual ANOVA analysis: *Aster novae-angliae*, *A. ercoides*, *A. laevis*, *A. pilosus*, *A. prenanthoides**, *A. puniceus**, *Bouteloua curtipendula*, *Elymus canadensis*, *Heliopsis helianthoides*, *Napea dioecia*, *Ratibidia pinnata*, *Rudbeckia subtomentosa*, *Schizachyrium scoparium*, *Silphium integrifolium*, *Solidago rigida*, *Sorghastrum nutans*, and *Verbena hastata*. In older literature, six of the eight common species discussed in depth here are routinely associated with wet-mesic prairies in Illinois and Wisconsin (Sampson 1921, Curtis 1959). *A. repens* and *E. annuus* are clearly weedy opportunists. Nomenclature follows Mohlenbrock (1986).

Burns

Burns in early spring were accomplished as the earliest species emerged; summer burns in mid-July were at the height of the growing season of late-season species. The first spring burns on 31 March 1989 reduced all aboveground plant biomass to ash in seven plots; fire engulfed each 15 × 18 m plot in 3–5 min, with flames 1.5 m high. The first summer burn on 15 July 1989 killed 85–100% (96 ± 2%, mean ± 1 SE) of aboveground shoots, reducing 10–60% (34 ± 8%) to ash. The rapidly moving fire, with flames 0.8 m high, consumed each plot within 15–30 min. Remaining aboveground shoots (66%) were left standing dead. The second set of spring burns on 2 April 1992 reduced 20–70% (45 ± 7%) of the dry vegetation to ash in the same plots burned in early 1989; fires engulfed plots in 10–15 min with flames 0.5 m high, leaving patches of moist litter 1–5 cm deep. The second summer burn on 19 July 1992 killed 87–100% (97 ± 2%) of the aboveground vegetation in the seven summer burn plots; a fire with flames 0.1 m high crept through litter among the standing plants for 30–60 min in each 15 × 18 m plot. These July 1992 fires consumed virtually all ground litter, but left upright vegetation standing dead. In both 1989 and 1992, the same seven plots left unburned in 1989 remained unburned in 1992, with an accumulation of 10–40 cm litter by 1993.

No two burns are identical, and burns between years at the same season and between seasons in the same year are almost sure to differ in behavior and intensity. This is particularly true of seasonal differences: most aboveground plant biomass in early spring is dead and often dry, while in midsummer it is live, green, and moist. Converting Van Wagner's (1965) definition of fire intensity (*I*) to standard metric units,

$$I = \text{kW/m} = \text{J/kg} \times \text{kg/m}^2 \times \text{m/s},$$

where kW = kilowatts = kJ/s, J = joules, m = metres, and s = seconds. The actual energy transferred depends on the amount of fuel consumed per area, expressed as a rate. For present purposes, a more useful measure is the easily estimated approximation (reviewed by Johnson 1992):

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

where L is flame length in metres. This shorthand calculation permits estimates of intensity for March 1989, July 1989, April 1992, and July 1992 of 626 kW/m, 161 kW/m, 57 kW/m and 2 kW/m, respectively. In each year, early spring burns of almost entirely dead plant matter were much more intense than midsummer burns, when fire consumed litter around green stems that were killed and left standing dead. Even very low-intensity growing-season fires in 1992 killed almost all aboveground shoots. More precise estimates of intensity might permit ad hoc inferences about the idiosyncratic responses of particular species, but they probably would not improve on the basic observation that fires of very different intensities kill virtually all herbaceous shoots above ground.

Sampling

Cover was sampled in late September and early October from 1987 through 1993. In 1987, 10 randomly placed 1-m² quadrats were used in each plot, with a field map drawn to scale for species showing ≥ 100 cm² contiguous canopy cover in a plot. Thereafter, 12 quadrats were used per plot. In 1993, an additional 15 June sample was taken. Aboveground vegetation was also clipped within a 25 × 25 cm square in eight of the 12 cover sample quadrats in each plot in 1990 and 1993. Clippings were dried to constant mass and weighed. Dicot and monocot seedlings were counted within the 25 × 25 cm squares before clipping in 1993. No samples are presented for burn years.

Analyses

Cover values of 252 m² samples are partitioned by treatment (three), replicates per treatment (seven), and samples per replicate (12). Analyses of within- and between-plot variance were major foci of an earlier study (Howe 1994a), but here the mean of 10 or 12 samples for cover of species or guilds for each plot is used, yielding seven means per treatment per sampling period. Multivariate analyses of variance, repeated measures, and Tukey tests for individual species and guilds (summed mean cover values for species in functional groups) were accomplished on this database using SYSTAT 5.03 (Wilkinson 1991). Standard errors accompany means.

To avoid small cell sizes and peculiar distributions, ANOVAs of individual species were limited to four grasses and four forbs that were common by 1990;

some of these virtually disappeared from many replicates and some treatments by 1993, complicating statistical analyses. Cover summed as flowering groups (phenological guilds) met ANOVA requirements throughout the study.

RESULTS

Background natural history

Common species differed in height and aboveground productivity. Early-season *Agropyron repens* and *Rudbeckia hirta* and mid-flowering *Erigeron annuus* were shorter (generally ≤ 1 m tall) than early-flowering *Phalaris arundinacea* (1.5–2.0 m). Late-season *Aster simplex*, *Panicum virgatum*, and *Solidago altissima* were of intermediate height (1.5–2.0 m), while late-season *Andropogon gerardii* could be tall (2.0–3.5 m). In September 1993, monocultures of early-season *Phalaris arundinacea* averaged aboveground biomass of 598.4 ± 64.0 g/m² ($n = 25$), and *Agropyron repens* 510.4 ± 64.0 g/m² ($n = 24$). In contrast, monocultures of late-season *Andropogon gerardii* averaged 1384 ± 129.6 g/m² ($n = 62$), *Panicum virgatum* 836.8 ± 100.8 g/m² ($n = 37$), and *Solidago altissima* 838.4 ± 92.8 g/m² ($n = 23$). *Andropogon* was more productive than the other species, with Tukey tests of $P < 0.025$ for comparisons with *Panicum* and *Solidago*, $P < 0.001$ for *Phalaris* and *Agropyron*. No significant differences in biomass between monocultures of conspecifics could be demonstrated between treatments and years.

Aboveground productivity largely determines fuel load, and contributions of different guilds to biomass accumulation should influence fuel build-up between burns. Aboveground biomass of growth 1 yr after the 1989 and 1992 burns was higher after spring than summer burns (Tukey tests $P < 0.025$), with biomass in unburned plots intermediate. Productivity per square metre for 1990 and 1993, respectively, was 1110.4 ± 87.1 g and 980.0 ± 104 g 1 yr after spring burns; 667.2 ± 59.0 g and 544.6 ± 14.1 g after summer burns; and 942.2 ± 135.2 g and 686.4 ± 85.4 g in unburned plots. Lower values across treatments in 1993 were probably due to a cool, wet summer. Differences in aboveground biomass between treatments within a year were significant (univariate ANOVAs: $P < 0.025$ for 1990, $P < 0.001$ for 1993), and were probably due to the much smaller size of early-season species common after summer burns.

Counts of seedlings in 25 × 25 cm (0.0625 m²) plots in 1993 confirmed earlier impressions that summer fires promoted seedling recruitment. In plots burned in summer 1992, numbers of dicot seedlings were higher (equivalent to 76.0 ± 24.0 /m²) than in plots burned in spring 1992 (17.0 ± 8.7 /m²; Tukey test: $P < 0.05$), or than in unburned plots (3.4 ± 1.4 /m²; Tukey test: $P < 0.01$). Grass recruitment was indistinguishable across treatments (overall mean 4.0 ± 0.7 seedlings/m²).

Accumulated litter probably suppressed seedling re-

cruitment. In summer-burned plots, much of the ground not covered by emerging shoots was bare in late June a year after a burn season, while in the other plots, it was covered with emerging shoots or dead thatch 2–10 cm deep (spring-burned plots) to 10–40 cm deep (unburned plots). On 26 June 1993, litter covered $29.0 \pm 6.0\%$ of the ground in plots burned in April 1992, $2.1 \pm 1.1\%$ of the ground in plots burned in July 1992, and $40.0 \pm 9.4\%$ in unburned plots. Litter cover of plots burned in summer is less than that of plots burned in spring (Tukey test: $P < 0.005$) or left unburned (Tukey test: $P < 0.001$). Few seedlings were detected under thick thatch in September counts, but were often present on bare ground.

In 1987, annuals accounted for 4% of the cover, biennials 12%, and perennials 84% (99% of the species planted in 1986 were perennials). Proportions changed to 3%, 4%, and 92%, respectively, by 1990, and to <1%, 3%, and 96%, respectively, by 1993. Univariate ANOVAs in 1990 show strong responses of all three categories to burn treatment (all $P \leq 0.001$), with annual and biennial species more common after summer burns. The same general pattern held in 1993, with almost vanished annuals showing a marginal response ($P = 0.06$), and biennials and perennials a stronger response ($P < 0.001$ and $P < 0.01$, respectively,) to burn treatment.

Other functional indicators showed a progression over time without significant differences among treatments. The experimental plots were 77% grass-covered 1 yr after planting in 1987, 75% in 1990, and 62% in 1993, mostly due to increasing cover of *Solidago altissima* and *Aster simplex*. Non-experimental volunteers contributed 52% of the cover in 1987, 41% in 1990, and 43% in 1993. Most weeds were natives; in 1987 and 1990, 98% of the total cover consisted of species indigenous to North America, becoming 100% in 1993.

In October 1992, soil samples 10 cm deep from each plot indicated a loam with $33.1 \pm 0.6\%$ sand, $60.2 \pm 0.6\%$ silt, and $6.8 \pm 0.2\%$ clay, with no significant variations among plots exposed to different burn treatments. Within this loam, organic matter ($3.40 \pm 0.08\%$), total nitrogen ($0.19 \pm 0.01\%$), phosphorus (145 ± 12 mg/kg), and pH (7.01 ± 0.03) did not vary with treatment. Potassium in unburned plots (289 ± 8 mg/kg) was less than that in summer-burned plots (329 ± 10 mg/kg; Tukey test: $P < 0.05$), but indistinguishable from spring-burned plots (316 ± 11 mg/kg). Potassium may have been sequestered in standing dead vegetation and litter, which had accumulated for one to eight seasons, depending on treatment.

Species cover

Long-term patterns.—Eight common species had different fortunes over time, and in some cases, gross changes suggested that fortunes differed among treatments (Fig. 1, Table 1). Among grasses, late-season

Andropogon gerardii was the dominant in most plots, increasing in abundance in all treatments over time; early-season *Phalaris arundinacea* increased only in plots burned in midsummer. Late-season *Panicum virgatum* and early-season *Agropyron repens* were most prevalent in 1988 before the first burn cycle and decreased thereafter; *Panicum* best held its own in plots burned in early spring, whereas *Agropyron* persisted only in plots burned in midsummer. Among forbs, late-season *Solidago altissima* and *Aster simplex* increased throughout. Within 4 yr of planting, the early-season biennial *Rudbeckia hirta* was evident only after summer burns, while the mid-season annual *Erigeron annuus* all but disappeared over time, except after summer burns. Not shown is *Aster ericoides*, which increased to 2% cover in some unburned plots, but was negligible elsewhere.

Cumulative responses to burn regimes.—Cumulative differences in cover for eight common species were evident 1 yr after the second burn (Table 2). Low mean values, high and uneven variances among species, and a number of empty cells made MANOVA unwieldy for several individual species. MANOVA and Tukey tests did show that mean cover did not vary significantly among treatments for *Andropogon gerardii*, *Aster simplex*, and *Solidago altissima*. As a group, however, these three late species clearly responded. When the 1993 cover values of these species were summed into one variable, exclusive of 18 other late-season species, Tukey tests showed that the mean cover of plots burned in summer ($58.2 \pm 0.14\%$) was lower than that of plots burned in spring ($82.5 \pm 3.7\%$; $P < 0.001$) or left unburned ($81.8 \pm 7.9\%$; $P < 0.001$). The collective response of these three species was far more obvious than the individual response of each alone. This aggregate effect was due to strong increases in *Andropogon gerardii* after spring burns, and substantive, but lesser, increases in *Aster simplex* and *Solidago altissima*. The latter two, which begin spring growth well before *Andropogon* and therefore could be affected by spring fires, actually had higher numerical scores in unburned plots than in spring-burn plots.

Despite a general decline, late-season *Panicum virgatum* cover was clearly higher after spring burns than in other treatments, while early-season *Phalaris arundinacea* fared better after summer burns than in other treatments. After two burn cycles, uneven presence (resulting in high variance and low mean cover) precluded statistical demonstration of responses by *Agropyron repens*, *Erigeron annuus*, and *Rudbeckia hirta* that were evident after one burn cycle (Howe 1994a), when mean cover was higher and each species was present in most plots. These three species all but disappeared by 1993, except in plots burned in midsummer.

Tests of between-species abundance in 1993 show clear dominance of two or three species in each treatment, with indistinct rankings of other species (listed

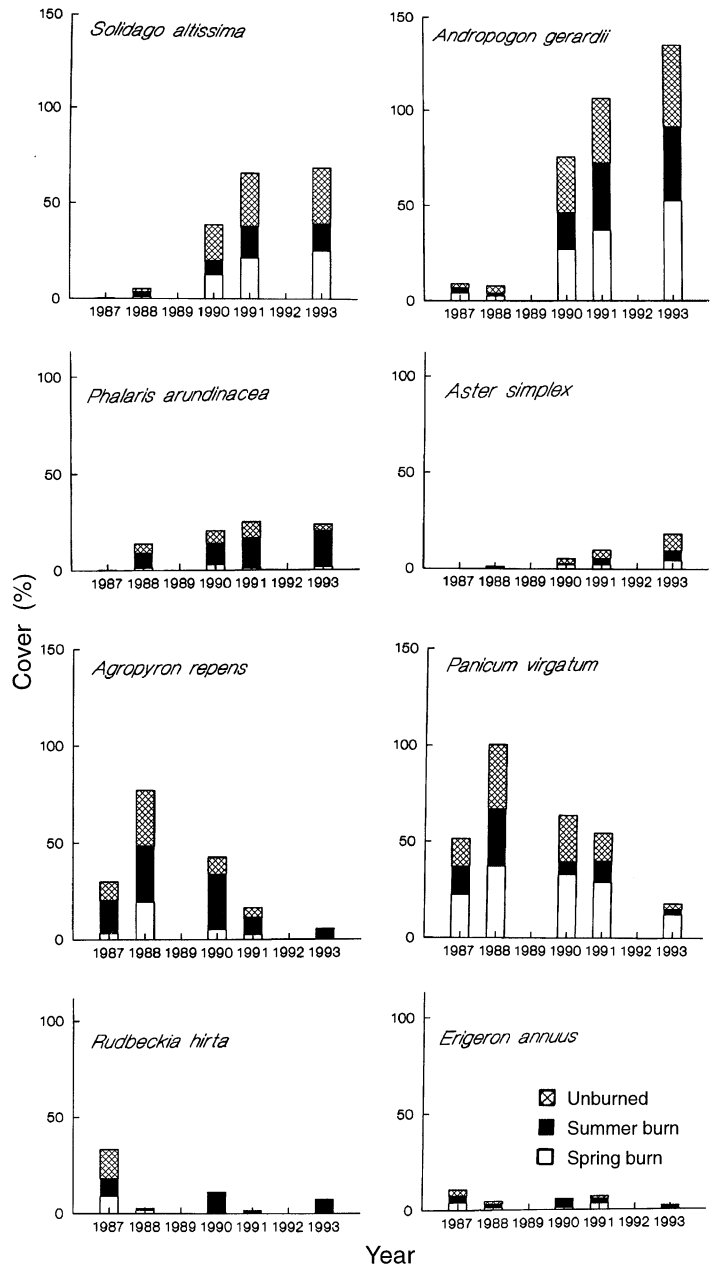


FIG. 1. Change in the mean percentage cover of eight common species on 21 planted prairie plots in Wisconsin. Seven plots were burned in early spring and seven in midsummer in 1989 and 1992. *Agropyron repens* and *Phalaris arundinacea* (both grasses) and *Rudbeckia hirta* (a forb) flower and seed before mid-July; *Erigeron annuus* (a forb) flowers in midsummer; *Andropogon gerardii* and *Panicum virgatum* (both grasses) and *Aster simplex* and *Solidago altissima* (both forbs) flower and seed after mid-July.

in descending numerical order of cover: differences significant at $P < 0.05$ as shown by Tukey tests are indicated by “>”, while means that cannot be so distinguished are indicated by “=”). After spring burns, rankings of dominants ranged in mean cover from 25 to 53%, with *Andropogon gerardii* > *Solidago altissima* > *Aster simplex* = *Phalaris arundinacea* = *Panicum virgatum* = *Agropyron repens* > *Erigeron annuus* (trace) > *Rudbeckia hirta* (absent). After summer burns, dominant cover ranged from 19 to 39%, with *Andropogon gerardii* > *Phalaris arundinacea* > *Solidago altissima* = *Rudbeckia hirta* = *Agropyron repens* = *Aster simplex* = *Panicum virgatum* = *Erigeron an-*

nuus. In unburned plots, dominant cover ranged from 29–44%, with *Andropogon gerardii* = *Solidago altissima* > *Aster simplex* = *Phalaris arundinacea* = *Panicum virgatum* = *Agropyron repens* > *Erigeron annuus* (trace) > *Rudbeckia hirta* (absent).

Cover of flowering guilds

Long-term patterns.—Flowering guilds clearly responded to different burn regimes, reflecting and amplifying the responses of common species (Fig. 2, Table 3). The late-flowering guild, overrepresented at planting, came to dominate all treatments, but less after summer burns than in the spring burn or unburned treat-

TABLE 1. Univariate ANOVAs from a repeated measures ANOVA by burn treatment (spring burn, summer burn, no burn) for each of eight species in experimental prairie plots in Wisconsin. *F*-statistics indicate the degree to which each flowering guild responded to treatment.†

| Year | Grasses | | | | Forbs | | | |
|------|-------------------------------------|---|--|-------------------------------------|------------------------------------|------------------------------------|----------------------------------|---------------------------------------|
| | Early or mid-season | | Late season | | Early or mid-season | | Late-season | |
| | <i>Agropyron repens</i> <i>F</i> | <i>Phalaris arundinacea</i> <i>F</i> | <i>Andropogon gerardii</i> <i>F</i> | <i>Panicum virgatum</i> <i>F</i> | <i>Erigeron annuus</i> <i>F</i> | <i>Rudbeckia hirta</i> <i>F</i> | <i>Aster simplex</i> <i>F</i> | <i>Solidago altissima</i> <i>F</i> |
| 1987 | 1.41 | 1.00 | 0.80 | 1.24 | 0.14 | 5.52** | absent | 1.01 |
| 1988 | 0.79 | 1.30 | 0.60 | 0.89 | 0.04 | 1.92 | 0.05 | 0.42 |
| 1989 | | | | | Burn year | | | |
| 1990 | 6.72** | 1.41 | 1.63 | 8.59** | 5.16* | 25.71*** | 1.16 | 2.28 |
| 1991 | 0.56 | 2.46 | 0.06 | 7.80** | 1.14 | 1.84 | 0.27 | 1.11 |
| 1992 | | | | | Burn year | | | |
| 1993 | summer only‡ | 4.21* | 0.95 | 17.96** | summer only‡ | summer only‡ | 0.54 | 0.20 |

† Each test had 2 df for treatment, 18 df for error. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

‡ Early *Agropyron repens* and *Rudbeckia hirta* were all but absent in 1993 except in plots burned in midsummer; ANOVAs with all or most cells empty from other treatments are inappropriate. In 1987, *Rudbeckia hirta* cover was higher in plots later left unburned than in those later burned, making the above effect all the more decisive for that species. Mid-season *Erigeron annuus* almost disappeared by 1993, mostly persisting after summer fires.

ments. The early-season guild persisted in low cover values in unburned plots, reflecting succession without human intervention, and declined drastically in spring burn plots. The early-flowering guild persisted at high values only in plots burned in midsummer. Univariate ANOVAs from repeated measures MANOVA showed that cover of early and late species responded to burn treatments, but that differences among scarce mid-season species were not obvious. For the MANOVA itself, *F*-statistics for the Wilks' lambda ($F = 21.79$, $df = 30, 8$), Pillai trace ($F = 7.386$, $df = 30, 10$), and Hotelling-Lawley trace ($F = 58.88$, $df = 30, 6$) were all highly significant ($P \leq 0.001$), indicating that differences in cover among years and treatments were real.

Cumulative responses to burn regimes.—One year after the second burn cycle, the late-flowering guild heavily dominated spring-burned and unburned treatments, with lesser dominance after summer burns (see 1993 in Fig. 2). Tukey tests showed that, for the early

guild, mean cover for spring-burned (2%) and unburned (4%) treatments did not differ, but that cover of the early guild was higher after summer burns (32%) than in either of the other treatments ($P \leq 0.001$). Conversely, cover values of the late-flowering guild in spring-burned (97%) and unburned (93%) treatments were not distinguishable, but were higher than in summer-burned treatments (66%; $P \leq 0.001$). No pattern was obvious for the mid-season guild, which all but disappeared by 1993.

DISCUSSION

Spring and summer fires had important effects on succession of tallgrass prairie. First, fire season influenced species dominance and persistence. The fact that most species were not common or distributed evenly enough for individual analyses illustrates the general limitations of a species-by-species approach. Second, burn season influenced the prevalence of functional

TABLE 2. Mean (± 1 SE) percentage cover of eight common grasses and forbs in plots burned in the early spring, midsummer, or left unburned 1 yr after the second-burn cycle in 1992.

| Species | Burn treatment | | |
|-----------------------------|-----------------|------------------|-----------------|
| | Spring | Summer | Unburned |
| | Grasses | | |
| <i>Andropogon gerardii</i> | 52.7 \pm 19.6 | 38.9 \pm 15.1 | 43.6 \pm 22.0 |
| <i>Panicum virgatum</i> | 12.3 \pm 3.5* | 2.6 \pm 2.0 | 2.9 \pm 4.4 |
| <i>Phalaris arundinacea</i> | 1.5 \pm 3.5 | 18.6 \pm 20.2* | 3.5 \pm 4.3 |
| <i>Agropyron repens</i> ‡ | 0.1 \pm 0.2 | 4.9 \pm 10.3† | 0.4 \pm 1.0 |
| | Forbs | | |
| <i>Solidago altissima</i> | 25.1 \pm 17.2 | 14.2 \pm 12.6 | 29.3 \pm 16.0 |
| <i>Aster simplex</i> | 4.6 \pm 5.6 | 5.1 \pm 9.7 | 8.9 \pm 9.5 |
| <i>Rudbeckia hirta</i> ‡ | absent | 7.5 \pm 6.1† | absent |
| <i>Erigeron annuus</i> ‡ | 0.7 \pm 0.7 | 1.2 \pm 1.4 | 0.1 \pm 0.2 |

* Values are significantly different than those for conspecifics in other treatments not so indicated (Tukey tests: $P < 0.05$).

† Values are different from those of conspecifics by inspection (statistical tests are not applicable).

‡ See footnote ‡ for Table 1.

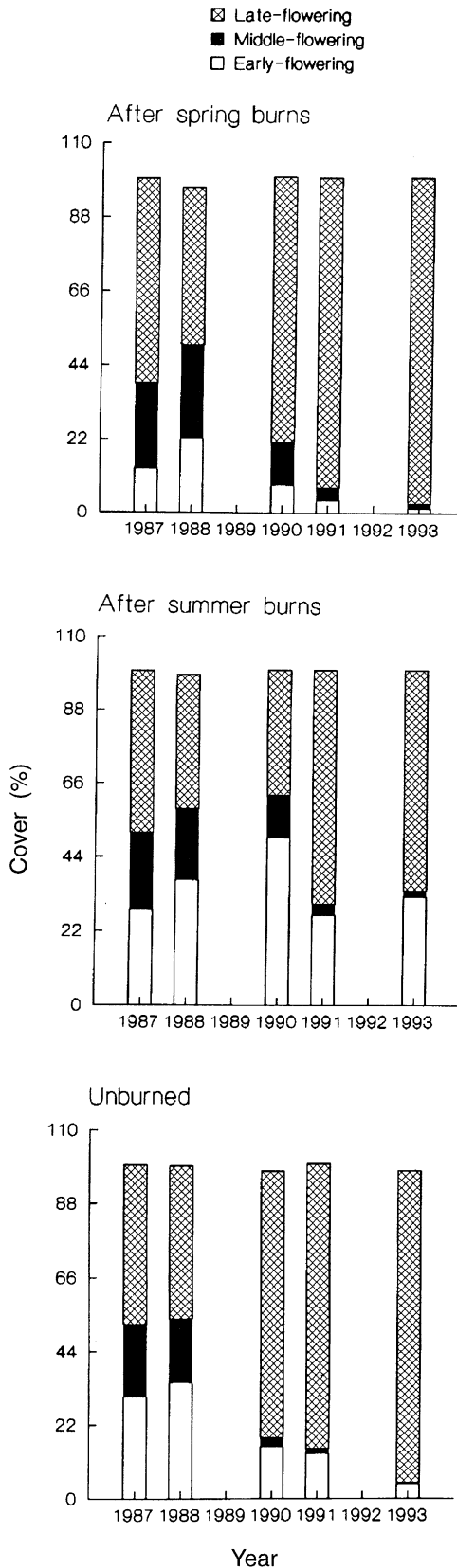


TABLE 3. Univariate ANOVAs from a repeated measures ANOVA by burn treatment (spring burn, summer burn, no burn) for each of three flowering guilds in experimental prairie plots. *F*-statistics indicate the degree to which each flowering guild responded to treatments. †

| Year | Flowering guild‡ | | |
|-------|-----------------------|---------------------|----------------------|
| | Early-season <i>F</i> | Mid-season <i>F</i> | Late-season <i>F</i> |
| 1987§ | 7.78** | 0.43 | 2.22 |
| 1988 | 2.02 | 1.80 | 0.56 |
| 1989 | | Burn year | |
| 1990 | 28.84*** | 2.98 | 31.33*** |
| 1991 | 3.65* | 1.59 | 3.78* |
| 1992 | | Burn year | |
| 1993 | 14.12*** | 1.44 | 14.41*** |

† Each test had 2 df for treatment, 18 df for error. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

‡ Summed mean cover values for the early-season guild included nine species, for the mid-season guild 11 species, and for the late season guild 21 species.

§ Significant effects due to *Rudbeckia hirta* in plots later left unburned; see footnote ‡ for Table 1.

flowering guilds, thereby affecting community character as well as species composition. As aggregate variables, cover values of different flowering guilds, each summing responses of 9–21 species, responded to burn season more predictably than did individual species. Early spring and midsummer fires shaped identical replicated plantings into very different plant communities.

Responses of common species

Abundant species and their interactions often bias ecological interpretation (Brown and Heske 1990). Such a bias favors overinterpretation of effects of common species in a community, while potentially overlooking the importance of uncommon “strong interactors” (Paine 1992) or the aggregate influence of the majority of species, which are uncommon or rare (Magurran 1988, Howe 1994b).

A priori, fire at different times during the growing season should suppress shoot and root elaboration and reproduction of some competitors more than others (Neiland and Curtis 1956, Howe 1994b). For instance, early-season species burned during the period of emergence and early growth should suffer a disadvantage compared with late-season species, which, in March or April in Wisconsin, have not yet invested much in growth or reproduction. Alternatively, late-season species should be disadvantaged by midsummer fire which

FIG. 2. Change in the mean percentage cover of phenological guilds on 21 planted prairie plots in Wisconsin. Seven plots were burned in early spring and seven in midsummer in 1989 and 1992. Members of the early-flowering guild (nine species, open) flower and seed before mid-July; members of the middle-flowering guild (11 species, black) flower and seed from June to August; and members of the late-flowering guild (21 species, hatched) flower and seed after mid-July.

destroys aboveground organs during maximal growth, thereby favoring early-season plants that have already finished annual growth and reproduction.

Five of eight common species were affected by fire season (Fig. 1, Tables 1 and 2). Unburned plots showed initial increases of the early-season grass *Agropyron repens* and late-season grass *Panicum virgatum* to peaks in 1988, 2 yr after planting, followed by declines. *Agropyron* decline was precipitous except in plots burned in midsummer; *Panicum* decline was precipitous except in plots burned in early spring. The early-season grass *Phalaris arundinacea* declined in cover in unburned plots, almost disappeared in plots burned in early spring, but increased steadily in plots burned in July. The annual *Erigeron annuus* all but disappeared, except in plots burned in July, where it barely persisted. *Rudbeckia hirta* disappeared everywhere except in plots burned in July, where it thrived.

In these plantings, three species were not significantly influenced by burn treatments. A dominant grass (*Andropogon gerardii*), a dominant forb (*Solidago altissima*), and a less common forb (*Aster simplex*) increased steadily in cover in all treatments. Each showed numerically lower cover in plots burned in midsummer than in others; over time and further burning iterations, they might, as expected, show significant species responses. All three are vigorous cloners, which may mute response to fire season. As noted earlier, the summed cover values of these three species showed a dramatic collective response to seasonal burn treatments.

Responses of flowering guilds

Collective responses of flowering guilds to burn season were clear. The late-flowering guild (21 species) dominated all treatments within 8 yr, but less after summer burns than in the spring burn or unburned treatments. Early-season (nine species) and mid-season (11 species) guilds virtually disappeared in plots burned in spring or left unburned. The early guild flourished after summer burns. These results are consistent with the prediction by Higgins (1984) that a prevalence of summer burns set by people or lightning would favor shorter and earlier-flowering species that would otherwise be eliminated by competition from large, late-flowering competitors. Reduction of productivity by summer burns, not explicitly predicted, is plausible in light of size differences in species that flower and seed early in the season as compared with species that grow through the summer and flower and seed in late summer or autumn.

Pooling data into functional guilds assumes that, under particular ecological conditions, species of quite different taxonomic affinities respond in similar ways as "ecological equivalents." Ecological equivalents in a flowering guild need not be similar in other ways, nor should they necessarily respond similarly under quite different conditions (Fowler 1981a, b, Simberloff

and Dayan 1991). For instance, rhizomatous and non-rhizomatous grasses with similar flowering phenologies might respond similarly to seasonal burn regimes, but not necessarily to grazing or to competition from forbs. Moreover, species responses cannot be assumed to be strictly additive; members of a functional guild may respond in different degrees to the same conditions, and the degree of response among different species may not vary in parallel. Nonetheless, analysis by guild can be instructive if, as in this study, aggregate responses are substantially more predictable and informative than responses of individual species.

Fire season and succession

Most tallgrass communities in central North America require fire to impede forest encroachment (Sauer 1950, Platt 1975, Pyne 1986, Anderson 1990). The "unburned" treatment in this study is not as much a control as a comparison with alternative burn regimes, since without burning, cutting woody vegetation, or browsing by ungulates, unburned plots ultimately revert to forest.

Ungrazed tallgrass prairies in North America are deliberately burned in fall, winter, or spring, when dry vegetation burns easily (see Risser et al. 1981, Collins and Wallace 1990). Quantitative understanding of the effects of fire is usually derived from such managed prairie communities (e.g., Hulbert 1969, 1986, 1988, Collins and Wallace 1990). Such evidence shows that fall, winter, and spring burn regimes strongly favor large C₄ grasses. If heavy dominance of C₄ grasses is viewed as the end point for tallgrass succession, summer burns may be viewed as disruptive setbacks to the norm, favoring species that would otherwise be eliminated.

As discussed by Huston (1979), however, disruptions of forest succession by large-scale disturbances such as fires, shifting agriculture, mudslides, or climatic change, or even small-scale changes in patterns of tree-fall disturbance, often maintain different communities than would otherwise exist. Similar principles should apply to succession of prairie grasses and forbs. At the moist, fertile Wisconsin site discussed here, summer burns every year or 2nd yr, rather than every 3rd yr, might favor a higher proportion of early-season species, while less frequent summer burns would probably speed the progression of late-season species. (Note partial recovery of the late-season guild 2 yr after a burn in Tables 1 and 3.) Inclusion of more early-season tallgrass species at planting would probably also allow a stronger response to summer burns. Different burn frequencies would undoubtedly yield different community-level consequences in sites with different soil and drainage characteristics and species pools. A logical extension of Huston's perspective suggests that any number of "end-points" of dominance and species composition, brought about by different fire seasons, fire frequencies, grazing intensities and frequencies,

and local edaphic conditions, would represent legitimate tallgrass habitats short of succession to hardwood forest.

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