

RESEARCH ARTICLE

Plant Community Responses to Prescribed Burning in Wisconsin Sedge Meadows

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ABSTRACT: In northern temperate regions, sedge meadows dominated by the tussock-sedge *Carex stricta* Lam. (Cyperaceae) were historically a fire-maintained community type. In two Wisconsin natural areas (Lulu Lake and Summerton), we assessed the effects of time since prescribed spring burning on plant composition and aboveground biomass in eight sedge meadows representing a partial chronosequence of zero to seven years since burning, plus no burning. We recorded plant species cover in line-intercept transects and measured live biomass and litter in sample plots along transects. Responses were prominent during the first two years after burning. In the Lulu Lake meadows, live biomass and annual forb cover reached their highest values during the first growing season after burning, whereas cover and frequency of perennial forbs were elevated for two seasons. Plant litter was removed by burning but returned to preburn levels in one to two years. In the Summerton meadows, where seven years had elapsed since the last fire, burned and unburned meadows did not differ in live biomass, litter, or relative cover of plant life-forms. It appears that periodic burns do not cause major shifts in the relative dominance of sedges and grasses, which are long-lived clonal perennials. However, because litter removal promotes recruitment of shorter-lived forbs, prescribed fire can enhance sedge meadow diversity by allowing plant species with different life histories to temporarily share dominance with the more abundant graminoids. Periodic seed inputs by forbs to the wetland seed bank may be a desirable fire management objective for maintaining sedge meadow diversity.

Index terms: prescribed burning, natural areas management, seed banks, sedge meadows

INTRODUCTION

Wildfires played a critical role in shaping the presettlement vegetation of the Upper Midwest region of the United States (Curtis 1959, Davis 1979, Kline and Cottam 1979, Grimm 1984). With the reduction or elimination of fires in recent history, many plant communities have undergone substantial changes in composition (Curtis 1959, McCune and Cottam 1985, McClain et al. 1993). Consequently, prescribed fire has been reintroduced to many natural areas as a management tool to preserve and restore presettlement vegetation. In Wisconsin, 4,800 to 9,000 ha (12,000 to 22,000 acres) are burned annually by public and private agencies (Henderson and Statz 1995). Prescribed fire is a flexible management practice that can achieve multiple objectives depending on its frequency, intensity, and seasonal timing. Fires can alter community properties such as biomass production and plant flowering, and they can also cause selective changes in community composition, such as elimination of woody plants, shifts in the relative dominance of cool- and warm-season species, and increased presence of annual species (Daubenmire 1968, Hulbert 1969, Vogl

1974, White 1983, Abrams and Hulbert 1987, Tester 1989, Glenn-Lewin et al. 1990, Anderson and Schwegman 1991, Laubhan 1995). Whereas these fire effects have been well documented for many up-land community types, the literature on fire in wetland communities of the Mid-west is sparse (Kirby et al. 1988, Henderson and Statz 1995).

Sedge meadow is an herbaceous wetland community dominated by *Carex* species, particularly the tussock-sedge *Carex stricta*, and by bluejoint grass, *Calamagrostis canadensis* (Stout 1914, Costello 1936, Curtis 1959; nomenclature follows Gleason and Cronquist 1991). Sedge meadows are found throughout the midwestern and northeastern United States in glacial lake beds and on the shores of lakes and streams. Similar communities also occur in Europe and Asia. Typically, the ground surface lies just above the permanent water table, and the soils are peats and/or mucks. On drier sites, this community type intergrades to wet prairie with high dominance of *Calamagrostis canadensis* and other grasses (Curtis 1959). Evidence from peat cores and from reconstructions of presettlement vegetation suggests that surface

fires were historically important in maintaining sedge meadows as open wetlands (Curtis 1959, Davis 1979). Where fire has been suppressed, many sedge meadows have been invaded by shrubs, an apparent successional process that has been hastened by artificial drainage and by declines in the farming practice of mowing for marsh hay (Costello 1936, White 1965, Vogl 1969). The resulting shrub-carr community is less easily burned, thus its presence may reduce the potential for natural fires and accelerate succession to lowland forest (White 1965, Davis 1979). Only the wettest sedge meadows may resist shrub colonization and thus not require fire for their persistence (Curtis 1959).

There are few studies of fire effects in sedge meadow communities. Experiments by Warners (1989, 1997) suggest that single or infrequent burns do not significantly alter the relative cover of the dominant perennial sedges and grasses, but instead influence meadow composition by promoting seedling recruitment of shorter-lived forbs. However, in prairie fens, a related community type, there is evidence that yearly dormant-season burning leads to greater dominance by graminoids and a cumulative loss of forb diversity (Bowles et al. 1996). These results suggest the hypothesis that periodic fire with a recovery interval may best maintain plant diversity. Here we report on plant community response to a program of prescribed fires that is being used to manage some Wisconsin sedge meadows. In a study of eight sedge meadows that comprised a partial chronosequence of time-since-burning, we addressed two general questions: (1) What are the apparent effects of prescribed spring fires on plant species composition, above-ground biomass, and litter accumulation? and (2) How long after burning do these effects persist? Our findings suggest several strategies that might guide future management procedures for this under-studied wetland type.

STUDY SITES AND PRESCRIBED BURNS CHRONOLOGY

Research was conducted in 1994–95 (Kost 1996) at two natural area reserves managed by the Wisconsin Chapter of The

Nature Conservancy (TNC). The Lulu Lake reserve is located in Walworth County in southeastern Wisconsin (42°50'N, 88°27'W). This 195-ha reserve contains ridges of glacial till supporting prairie and savanna species, as well as glacial kettle holes and extensive floodplains with a mosaic of bog, fen, marsh, and sedge meadow communities. The Summerton reserve is located in Marquette County in central Wisconsin (43°45'N, 89°30'W) and includes fen, sedge meadow, shrub-carr, tamarack swamp, old-field, and oak island communities within its 172-ha area. Geographically, both reserves occur south of Wisconsin's floristic "tension zone" and thus support a "southern sedge meadow" community type (see Curtis 1959).

Each reserve includes sedge meadows that have been managed with recent prescribed burns, as well as meadows that have not burned for many years. Because there was little comprehensive data on preburn plant composition, it was necessary to assess fire effects using postburn comparisons among these meadows. This approach represents a problematic "space-for-time" substitution (Pickett 1989) that assumes that all sites were similar prior to burning and that the postburn recovery trajectories are similar. However, the configuration of the study sites at each location, as described below, makes these assumptions plausible in the case of our study.

Lulu Lake Meadows

At Lulu Lake, we studied six sedge meadow sites that are partially separated by natural features, which allows them to be treated as individual management units. The meadows comprise two groups ("north" and "south") based on their locations within the reserve. The "north" group (n) consists of four adjacent 1- to 3-ha meadows that are partially separated from one another by a low glacial ridge and by a stream that bisects the ridge. The "south" (s) group consists of two adjacent meadows (2.5 and 3.4 ha) that are not physically separated but have a narrowed area of connection between them. The two south meadows are separated from the four north meadows by another glacial ridge.

The Wisconsin TNC initiated a program of spring burning for these sedge meadows in 1990. The initial purpose of the fires was to restore an ecological process characteristic of the community and to provide a presumed benefit in managing any shrub encroachment (N. Braker, The Nature Conservancy, Wisconsin chapter, Madison, pers. com). Individual meadows were burned in different years to leave refuge habitat for animals that might be affected by the fires. One of the south meadows (here designated Os) was first burned in the spring of 1994, the year of this study. Three of the four north meadows (1n, 2n, and 3n) were last burned one, two, and three years, respectively, prior to 1994. This "last" burn represented the second of two consecutive years of spring burning in each of the three meadows. The fourth north meadow (Un) and the other south meadow (Us) were not burned. Prior to these recent management activities, none of the six meadows had any known history of burning since the report of a wildfire in part of the north area in the 1940s or 1950s (Wisconsin TNC, unpublished records). Data on preburn composition were not available. However, given the close proximity and partial hydrologic continuity of the meadows, it is likely that the meadows were similar in composition prior to the burns.

Summerton Meadows

At Summerton, there are two adjacent 2-ha sedge meadow areas separated by a small channelized stream. Management objectives are similar to those for Lulu Lake. One meadow area (7b) had received an initial spring burn in 1980 and later received spring burns in 1985 and in 1987, seven years prior to the year of our study. The other meadow area (Ub) had no known record of past burning. At Summerton, postfire vegetation response was documented by Warners (1989) in the years immediately before and following the 1987 burn. This provided some prior data for comparison to 1994 meadow composition, although different measures of plant abundance were used in the two studies. Again, because the two meadows are contiguous, it is likely that their compositions were similar prior to the burns.

METHODS

Sampling

Vegetation composition was sampled at Lulu Lake from July 18 to August 5, 1994, and at Summerton from August 6 to September 4, 1994. These times were chosen as a compromise to facilitate identifications of earlier-flowering grasses and sedges versus later-flowering forbs. Vegetation was sampled with a modified line-intercept method. At Lulu Lake, three equally spaced, 100-m transects were laid out in each meadow, whereas at Summerton, six equally spaced 50-m transects were used in each meadow because of the shape of the meadows. All transects were oriented parallel to the direction of meadow drain-age. To estimate vegetative cover, we measured all plant species and their lengths of interception (in cm) within 1-m segments spaced at 10-m intervals along each transect (total = 30 segments, or 3,000 cm per meadow). In addition, in order to obtain more comprehensive estimates of community composition, we recorded as present all other plant species observed within 12.5 cm on either side of each 1-m segment (i.e., a 1-m x 0.25-m = 0.25-m² plot) and assigned these a cover value = 0.

To assess the possible impact of past burning on aboveground biomass, we collected five samples of live plant material and litter from each Lulu Lake meadow on August 26–27, and at each Summerton meadow on August 31, 1994. Along a 100-m transect through each meadow, in evenly spaced strips 1 m x 0.1 m (as in Gleeson and Tilman 1990), all live biomass was clipped at ground level and all dead plant litter was gathered from the bases of sedge tussocks and from between them when possible. The separate samples of living and dead material were dried at 110 °C for 48 hours before weighing.

Detailed hydrologic monitoring was not feasible for this study, but we collected simultaneous measurements of water depth in spring 1995 as an indicator of relative differences in water levels among meadows at each site. Measurements were taken at Lulu Lake on May 19 and at Summerton on May 26; in each meadow,

standing water depth above the soil surface (i.e., between sedge tussocks) was measured with a meter stick every 10 m along the sampling transect lines from the previous year (n=30 measurements per meadow).

Data Analyses

Species presence within the thirty 0.25-m² plots in each meadow was used to calculate pairwise similarities among all meadows, based on the Sorenson coefficient of community (Barbour et al. 1980). The line-intercept data were used to generate estimates of percentage cover for each species. Absolute cover of each species was first calculated as the sum of lengths of interception in the 1-m (100-cm) segments; species sums were calculated for individual transects within meadows and also for each meadow as a whole. To analyze plant life-form composition, each species was assigned to one of six categories: annual forbs, perennial forbs, grasses, sedges/rushes, ferns, and shrubs (see Appendix). Total vegetation cover (all species combined) was also summed for each transect and meadow. Using the following equation, percent cover was then computed for each individual species, for species life-forms, and for total vegetation as: $C_{i,ifs} / L \times 100$, where $C_{i,ifs}$ is the sum of lengths of either a single species (i), a life-form (if), or all species combined (S), and L is the total length sampled (for transects within each meadow, $L = 1,000$ cm at Lulu Lake and 500 cm at Summerton; for an entire meadow, $L = 3,000$ cm at both sites).

Because of differences in location and history, the two research sites (Lulu Lake and Summerton) were treated separately for statistical analyses. Within each site, differences among meadows in water depth, percent vegetation cover, aboveground biomass, and water depths were analyzed with a conservative univariate analysis of variance (ANOVA) model, in which transects within meadows were used as replicates. Where an ANOVA indicated an overall significant difference among meadows, we performed post-hoc tests to determine the source of significance. For vegetation cover and biomass, the tests were planned single degree-of-freedom contrasts

comparing the most recently burned meadows (0, 1 year) to the meadows with longer times since burning. For other data such as water depths, a Tukey's HSD test (all pairwise comparisons) was used because no specific a priori differences were expected. All analyses were performed using SYSTAT L (Wilkinson 1993).

RESULTS

Community Composition

There were significant floristic differences between the Lulu Lake and Summerton sites. Based on species presence-absence data (Kost 1996), the average pairwise similarity between the Lulu Lake meadows and the Summerton meadows was only 49% (± 2 SE), whereas similarity among meadows within a site was relatively high. Lulu Lake meadows had an average pair-wise similarity of 75% (± 1.0), and the two Summerton meadows were also 75% similar. The Lulu Lake meadows contained more total species than Summerton (57 vs. 36 species) and, in particular, had a greater variety of perennial forbs (30 vs. 20 species), sedges and rushes (10 vs. 5 species), and annual forbs (4 vs. 1 species) (Kost 1996).

Sedges (*Carex* spp.), perennial forbs, and grasses generally dominated the plant cover of all meadows (Appendix). Abundant species common to both Lulu Lake and Summerton included the tussock-sedge *Carex stricta*, the grass *Calamagrostis canadensis*, and the characteristic forbs *Eupatorium maculatum* and *Lycopus uniflorus*. Coverage of grasses (particularly *Calamagrostis canadensis*) was much higher at Summerton (54–68%) than at Lulu Lake (4–14%). Individual forb species generally had low cover values (Appendix); however, the perennial species *Cicuta bulbifera*, *Epilobium leptophyllum*, *Lysimachia thyrsoflora*, and *Scutellaria galericulata* occurred in greater frequencies at Lulu Lake, whereas Summerton had much higher incidences of the forbs *Solidago gigantea*, *Aster firmus*, and the fern *Thelypteris palustris* (Kost 1996). The higher dominance of grasses and wet-prairie forbs at Summerton may reflect drier conditions resulting from a history of stream chan-

nelizing and grazing disturbance at this site (TNC records). In 1994 the Summer-ton meadows dried by late summer, where-as the Lulu Lake meadows remained flooded or saturated (M. Kost, pers. observ.). Mean standing water depths measured in spring 1995 (Table 1) indicated shallow water depths at Summerton, whereas at Lulu Lake the two south meadows were wetter than the north meadows, and mead-ow In had deeper water than the other north meadows.

Vegetation Responses to Burning

The high percent similarities among meadows within a site did not suggest a large burn effect on species composition, nor did total species counts (= species richness) per meadow show any trend of in-increase or decrease in relation to time since

burn (Table 1). However, prescribed burning did appear to affect both plant biomass and patterns of species abundance.

Lulu Lake

At Lulu Lake, fire management effects were most apparent during the first growing season following burning. In the most recently burned meadow (Os), plant litter was removed by the spring burn, and live aboveground biomass was significantly higher (91 g/plot) than in the other five meadows (33–59 g/plot) (Table 1; post-hoc contrast: $F = 10.0$; $df = 1, 24$; $P < 0.01$). Cover of plant life-forms also differed significantly among meadows (Table 2, Figure 1). Similar to the pattern for biomass, percent cover of annual forbs was significantly higher in the newly burned meadow Os (55%) than in the other

five meadows (0–25%) (Figure 1; post-hoc contrast: $F = 67.5$; $df = 1, 12$; $P < 0.001$). The annual forb group consisted principally of clearweed (*Pilea pumila*), which occurred in all meadows but which reached >50% cover in meadow Os (Appendix).

Perennial forbs showed increased cover for two growing seasons following burning (Figure 1), based on significantly higher cover in the two most recently burned meadows (Os = 45% and 1n = 47%) compared to the other four meadows (17–26%) (post-hoc contrast: $F = 23.3$; $df = 1, 12$; $P < 0.001$). This pattern was most evident for *Lycopus uniflorus*, a small forb that grows on the tussocks of *Carex stricta*. Average cover of *L. uniflorus* in meadows Os and 1n was more than threefold higher than in the other four meadows (Appendix). Several other perennials that did not necessarily vary in percent cover nonetheless occurred at a higher frequency in either or both of the two most recently burned meadows (Kost 1996); these species included the forbs *Epilobium leptophyllum*, *Cicuta bulbifera*, and *Eupatorium maculatum*, as well as the perennial spike-rush *Eleocharis palustris*. The two most recently burned meadows also differed from the other four in having reduced amounts of plant litter. The absence of litter in mead-ow Os accounted for the significant overall ANOVA (Table 1); in meadow 1n, litter amounts were nonsignificantly lower (46 g/plot) than in the other four meadows (56–86 g/plot).

Percent covers of the other life-forms (sedges/rushes, grasses, ferns, and shrubs) also differed significantly among Lulu Lake meadows (Table 2), but these differences did not show consistent trends in relation to time since burning. These life-forms are longer-lived clonal species that are less reliant on seedling recruitment, thus differences may simply reflect individual meadow variation rather than any outcome of prescribed burning (Figure 1). For example, sedge/rush cover reached both its highest and lowest values in the two unburned meadows (Us = 152% and Un = 74%), while the other four burned meadows had comparable levels of sedge cover (98–118%) (Appendix). Total grass

Table 1. Characteristics of eight sedge meadows at Lulu Lake and Summerton, Wisconsin. Meadow codes indicate years since burn (0–7 years, and U = unburned) and site (Lulu: n = north, s = south; Summerton: b). Species totals are estimated from presence in thirty 0.25-m² sample plots (see Methods).

| | Water Depth (cm) (mean ± s.e.) | Aboveground Biomass (g) (mean ± s.e.) | | Number of Species |
|--------------------------|-----------------------------------|--|----------|----------------------|
| | | Live | Litter | |
| Lulu Lake Meadows | | | | |
| Os | 15.2 ± 0.6 | 91 ± 18 | 0 ± 0 | 29 |
| in | 9.5 ± 0.2 | 54 ± 7 | 46 ± 10 | 30 |
| 2n | 3.4±0.2 | 51 ± 19 | 86 ± 12 | 27 |
| 3n | 3.1 ± 0.2 | 36 ± 2 | 64 ± 8 | 42 |
| Un | 4.7 ± 0.2 | 33 ± 8 | 60 ± 8 | 39 |
| Us | 12.1 ± 0.6 | 59 ± 14 | 56 ± 24 | 32 |
| ANOVA: | F 164.1 | 2.6 | 5.0 | |
| | df 5, 174 | 5, 24 | 5, 24 | |
| | p ** | * | ** | |
| Summerton Meadows | | | | |
| 7b | 4.1 ± 0.2 | 78 ± 8 | 105 ± 15 | 32 |
| Ub | 3.3±0.3 | 114±25 | 143±21 | 26 |
| ANOVA: | F 4.1 | 2.0 | 2.1 | |
| | df 1, 58 | 1, 8 | 1, 8 | |
| | P * | ns | ns | |

* $P < 0.05$; ** $P < 0.01$; ns = not significant

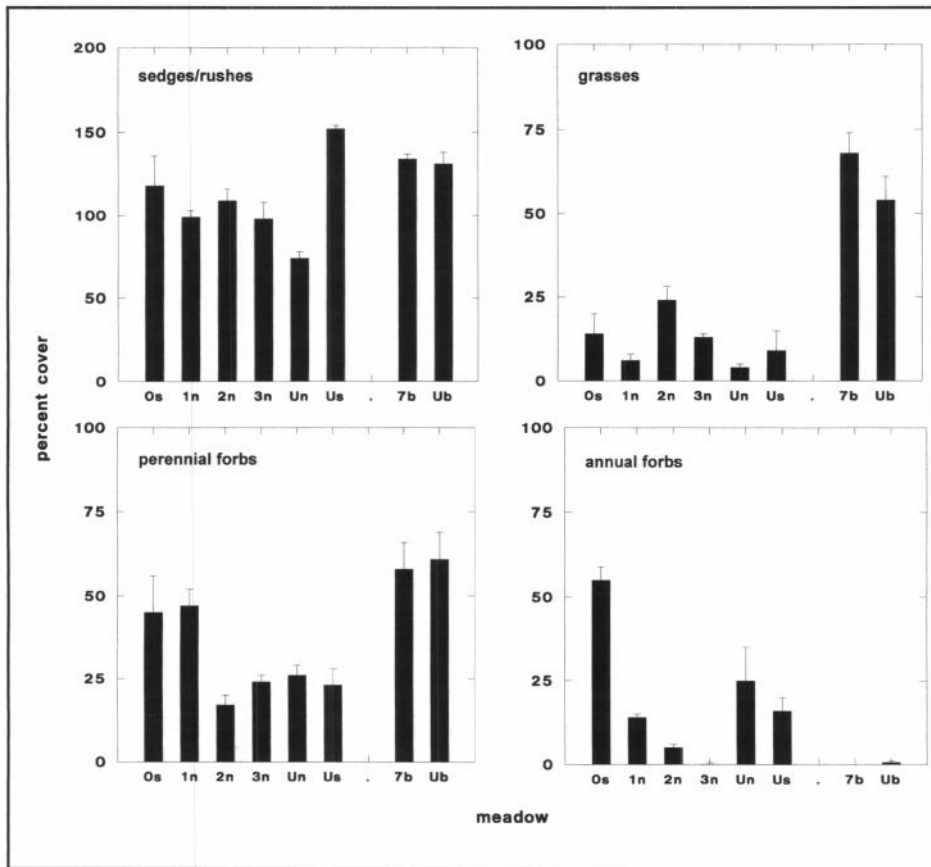


Figure 1. Mean percent cover \pm SE ($n = 3$ transects) of four major plant life forms in six sedge meadows at Lulu Lake and two sedge meadows at Summerton, Wisconsin. Meadows are arrayed according to years since the last burn (0–7 years and U = unburned) and by research site (Lulu Lake: n = north, s = south; Summerton: 7b = 7 years postburn, Ub = unburned).

Table 2. Results of ANOVAs for among-meadow differences in percent cover for six plant life form groups at Lulu Lake ($n=6$) and at Summerton ($n=2$), Wisconsin.

| Life Form | Lulu Lake | | Summerton | |
|-----------------|-----------|-----|-----------|----|
| | F | P | F | P |
| sedges/rushes | 7.8 | ** | 0.1 | ns |
| grasses | 3.1 | * | 2.3 | ns |
| perennial forbs | 5.0 | * | 0.1 | ns |
| annual forbs | 16.9 | *** | 1.8 | ns |
| shrubs | 13.9 | *** | 4.1 | ns |
| ferns | 3.7 | * | 0.4 | ns |
| ANOVA df | 5, 12 | | 1, 10 | |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant

cover was highest (24%) in the meadow burned two years previously (2n), but no other consistent trend of response to burning was apparent. Ferns (principally *Thelypteris palustris*) and shrubs (principally *Salix* spp. and *Potentilla* , *fruticosa*) were more abundant in meadow 3n, but were rare in the other meadows (Appendix). Shrubs showed no obvious trend toward increased cover with longer time since burning.

Summerton

In 1994 the two Summerton meadows 7b (last burned seven years previously) and Ub (unburned) did not differ significantly in either total vegetation cover (ANOVA, $F=1.4$; $df = 1, 10$; n.s.) or in the cover of any of the six life-form groups (Table 2; Figure 1). Considered separately, live biomass and litter did not differ significantly between the two meadows (Table 1), but total biomass was higher in the unburned meadow (ANOVA, $F= 8.1$; $df = 1, 8$; $P < 0.05$).

Warner's (1989) study allowed us to compare postburning composition with composition seven years later. In the growing season following the 1987 spring burn, Warners (1989) had observed increased abundances of five common perennial species: *Carex sartwellii*, *C. stricta*, *Calamagrostis canadensis*, *Ghreria striata*, and *Thelypteris palustris*. We assessed whether these postburning responses had persisted by testing whether the percent covers of these species still differed between the two meadows in 1994. Of the five species, only the sedge *Carex stricta* was significantly more abundant in the burned meadow (7b) in 1994 ($F = 5.6$; $df = 1, 10$; $P < 0.05$). However, the difference was relatively small (100% cover in 7b vs. 93% cover in Ub), and this species occurred with equal frequency (100%) in both meadows (Kost 1996). In 1994 we observed several forbs (e.g., *Aster firmus*, *Campanula aparinoides*, *Lycopus* spp., *Mentha arvensis*, *Scutellaria galericulata*) in greater frequency in the burned meadow (Kost 1996), and these were species that Warners (1989) had recorded as increasing in "commonness" following the 1987 burn. Finally, we compared the 1987

Table 3. Changes in relative frequency of species life forms (as a percent of total species) in Summerton meadows 7b (burned) and Ub (unburned) from the last year of burning to seven years later. Data for 1987 are from Warners (1989).

| Life Form | % of Total Species | | | |
|----------------------|-----------------------|------|-----------------------|------|
| | Meadow 7b | | Meadow Ub | |
| | 1987 | 1994 | 1987 | 1994 |
| sedges/rushes | 10 | 16 | 14 | 19 |
| grasses | 10 | 16 | 11 | 12 |
| perennial forbs | 60 | 56 | 62 | 58 |
| annual forbs | 8 | 0 | 5 | 4 |
| shrubs | 8 | 9 | 5 | 0 |
| ferns | 3 | 3 | 3 | 8 |
| | $\chi' = 3.34$ (n.s.) | | $\chi' = 2.65$ (n.s.) | |
| total species | 38 | 37 | 32 | 26 |

and 1994 data with respect to the relative numbers of species within each life-form, as a percentage of the total species in each meadow (Table 3). This comparison suggested that the presence of annual forb species may have declined over the seven years since the last prescribed burn, from 8% of all species in 1987 to essentially none in 1994.

DISCUSSION

Based on this burning chronosequence, it appeared that effects of prescribed fire on these Wisconsin sedge meadows were most evident during the first growing season following a burn and decreased thereafter. Live biomass was higher in the season after spring burning but then declined to lower levels. Plant litter was initially removed by burning but returned to preburn levels in one to two years. The principal effects on plant community composition were increased cover of the annual forb *Pilea pumila* and increased cover or frequency of various perennial forbs in recently burned meadows. The duration of these increases appeared to be one growing season for the annual forbs and at least two seasons for the perennial forbs.

Although the study design was restricted to comparisons across an unreplicated chronosequence, the patterns we observed are supported by results from experimen-

tal studies of fire effects. The dominant graminoids that form the sedge meadow matrix are long-lived perennials that re-produce vegetatively, and intermittent fires are unlikely to greatly alter their relative dominance (Warners 1989, 1997). In contrast, shorter-lived forb species may require periodic fires for recruitment from seed. Notably, Warners (1997) documented increased perennial forb seedling densities following prescribed burning of sedge meadows in Michigan. Studies in other graminoid communities have also recorded higher seedling densities following burning (Hulbert 1969, Tester 1989, Glenn-Lewin et al. 1990, Anderson and Schwegman 1991). These responses are consistent with the higher abundances of annual forbs and increased presence of perennial forbs that we observed in our study.

These fire-induced plant recruitment responses are mediated by changes in microsite conditions following the removal of plant litter (Warners 1997). In prairies, for example, it has been estimated that 60% more light reaches the soil surface in burned areas than in unburned areas (Knapp 1984). The blackened plant residues and soil surface promote warmer soil temperatures during the day, but night soil temperatures fall to lower levels in the absence of an insulating litter layer (Daubenmire 1968, Hulbert 1969, Viro

1974, Peet et al. 1975, Warners 1997). Burning of accumulated litter releases plant nutrients that can increase biomass growth and stimulate flowering and seed production (Daubenmire 1968, Vogl 1974, Collins and Gibson 1990, Laubhan 1995). Because the seeds of many species require high light or alternating temperature cycles to break dormancy (Thompson and Grime 1983, van der Valk 1986), the increased light levels and wider daily temperature fluctuations can enhance germination and establishment from the seed bank.

Litter removal also promotes earlier spring growth and thus a longer growing season for many species (Daubenmire 1968, Hulbert 1969, Vogl 1974). This effect may be important in sedge meadows because of the growth dynamics of the dominant plants. Many sedges overwinter as young shoots and thus have a temporal advantage for light and space capture in the spring, when other species are just beginning to emerge (Gorham and Somers 1973, Bernard and Gorham 1978). Spring burns can temporarily delay sedge regrowth to later in the growing season (Warners 1997) and thus enhance the recruitment of less-dominant species. At Lulu Lake, it appeared that the opportunities for earlier growth associated with both reduced litter and reduced competition with the sedges particularly benefited herbaceous species with small stature (e.g., *Eleocharis palustris*, *Epilobium leptophyllum*, *Lycopus uniflorus*, and *Pilea pumila*).

In summary, the results from the Lulu Lake sedge meadows suggest that prescribed burning provides a one- to two-year window of recruitment opportunity for forb species. At Lulu Lake, the balance of live biomass and litter levels approached that of unburned sites by the second growing season following burning. Redevelopment of the litter layer may account for the sharp decline in annual forb cover by the second growing season, with slower declines in the perennial forbs owing to their differing life histories. At Summerton, few differences were found between the unburned meadow and the meadow burned seven years previously, and declines in annual species since the burn may also be

attributed to lowered recruitment opportunities after return of litter to preburn levels.

Management Implications and Future Research

With appropriate season and/or frequency of burning, prescribed fire can be used to maintain and enhance sedge meadow plant diversity. However, practical considerations (e.g., weather or local regulations) may limit the timing of burns to the dormant or early spring seasons, even though growing-season burns may control woody plants more effectively (e.g., Anderson 1990) and may have different effects on vegetation (e.g., Howe 1994). Frequency of burning is more readily manipulated and can also influence diversity. In savannas and tall-grass prairies, a cycle allowing several years between burns was found to maximize species richness (Tester 1989, Collins et al. 1995). In contrast, in some annually burned prairies and prairie fens, dormant-season or spring burning caused increases in graminoid dominance and decreases in forb diversity (Collins et al. 1995, Bowles et al. 1996). In sedge meadows, periodic fire may not greatly alter species richness, but it can allow annual forbs to temporarily share dominance with the sedges and may bolster perennial forb abundance (Warners 1997, this study).

The responses of short-lived forbs in our sedge meadows also suggest that maintenance of seed banks can be an explicit goal of prescribed fire management. Burning can enhance flowering and seed production, but fires conducted too frequently (e.g., annually) might deplete the local seed bank for some species. For example, perennial forbs may require more than one growing season to begin producing seed, and seeds generated in a previous growing season may be insufficiently incorporated into the substrate and could be consumed along with the surface litter in the next fire. Thus, we suggest that a rotation that allows several years to elapse between fires could serve to replenish the seed banks of more transient sedge meadow species. An implication, deserving of further research, is that plant diversity in depauperate or disturbed meadows might be enhanced by artificial seeding of desired species in con-

cert with this burning rotation.

In practice, burning intervals can be varied flexibly in response to other management concerns (e.g., the need for control of shrub invasion). In the meadows we studied, shrubs formed only a minor component of plant cover. Where shrub encroachment is a greater problem, it may indicate a lack of favorable hydrology for self-maintaining sedge meadows. More frequent burning might be utilized for control in such cases; however, this creates a potential management conflict, because the fire frequency needed to manage shrub cover may compromise diversity management objectives. In studies of shrub-can vegetation at Summerton, Reuter (1985) observed temporary reduction in shrub cover following a burn, but the shrubs were able to resprout to preburn levels within one to two years. Thus, if very frequent (i.e., annual or biennial) fires are used to reduce shrubs in sedge meadows, the benefits of enhancing seed banks and recruitment of short-lived forbs could be lessened, particularly if frequent burning also leads to higher graminoid dominance (e.g., Collins et al. 1995, Bowles et al. 1996). An alternative approach to shrub control could be winter-season cutting accompanied by herbicide application to stumps (see Reinartz 1997).

An important issue for future research is how fire frequency affects the dominant sedge *Carex stricta*, which shapes this community's overall physiognomy (Stout 1914, Costello 1936). The culms of this sedge grow from large, persistent tussocks formed by the roots. Tussocks can occupy >40% of the meadow area, with densities ranging from one to four tussocks per square meter (Costello 1936). Areas between tussocks are shaded by the *Carex* canopy and covered by a thick litter layer. In wetter (flooded) meadows, these areas contain standing water, which restricts many meadow forbs (e.g., *Epilohium leptophyllum*, *Galium* spp., *Lycopus uniflorus*, *Pilea pumila*, *Scutellaria galericulata*, and *Viola* spp.) to growing almost exclusively on the sides or tops of the tussocks. Therefore, fire impacts on *C. stricta* could influence the abundance and distribution of other sedge meadow species. If, similar to prairie grasses, *C. stric-*

ta responds to frequent burning by increasing in dominance, then sedge meadow species richness could decline as colonizable areas between tussocks are reduced in extent. Conversely, it is possible that frequent and high-intensity fires could gradually reduce the size and vigor of the tussocks (M. Kost, pers. observ.) and this would negatively impact the abundances of those species that grow upon the tussocks. A greater understanding of how this very dominant species responds both to burning frequency (and perhaps to burn season) may be useful in shaping the long-term management strategy that best maintains sedge meadow communities.

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Appendix. Percent cover (mean per transect) of plant life forms and of individual species in eight sedge meadows at Lulu Lake and Summerton, Wisconsin, in 1994. Codes for individual meadows indicate years since burning (0-7 and U=unburned) and site (n, s = Lulu north, south; b = Summerton). Species nomenclature follows Gleason and Cronquist (1991).

| | Lulu Lake | | | | | | Summerton | |
|--|--------------|-------------|--------------|--------------|--------------|--------------|--------------|-------------|
| | Os | in | 2n | 3n | Un | Us | 7b | Ub |
| Total vegetation cover (%) | 233.3 | 171.9 | 156.2 | 162.9 | 131.9 | 209.2 | 273.6 | 257.7 |
| Sedges/Rushes | | | | | | | | |
| <i>Carex aquatilis</i> | | 0.1 | 13.2 | 7.4 | 13.0 | | | - |
| <i>C. lacustris</i> | 5.8 | 25.3 | 26.0 | 28.4 | 23.5 | | 8.9 | 25.6 |
| <i>C. lasiocarpa</i> | 31.3 | 8.5 | 6.2 | 6.8 | | 49.2 | 0.5 | |
| <i>C. prairea</i> | | | | | | - | 1.3 | 0.1 |
| <i>C. rostrata</i> | 19.1 | 0.7 | 22.2 | 1.9 | 5.4 | 35.3 | - | - |
| <i>C. sartwellii</i> | | | | | | | 23.1 | 12.2 |
| <i>Carex</i> spp. (<i>diandra</i> , <i>prairea</i> , <i>sartwellii</i>) | 1.2 | 0.8 | 1.0 | 14.8 | 0.6 | 3.8 | | |
| <i>C. stricta</i> | 52.1 | 63.9 | 40.8 | 37.6 | 30.2 | 61.0 | 100.0 | 93.2 |
| <i>Eleocharis palustris</i> | 7.6 | | 0.2 | 1.1 | 1.3 | 1.3 | | |
| <i>Scirpus validus</i> | 0.8 | - | - | - | - | 1.7 | - | - |
| All Species | 117.9 | 99.3 | 109.7 | 98.1 | 74.1 | 152.3 | 133.8 | 131.2 |
| Grasses | | | | | | | | |
| <i>Bromus ciliatus</i> | - | - | - | 0.3 | - | - | 0.4 | - |
| <i>Calamagrostis canadensis</i> | 13.8 | 4.3 | 23.5 | 8.3 | 4.4 | 9.0 | 60.7 | 48.6 |
| <i>Glyceria striata</i> | - | - | | | | | 1.3 | - |
| <i>Muhlenbergia glomerata</i> | | 1.4 | | 2.5 | | | 5.2 | 5.1 |
| Poaceae spp. | | | | 1.5 | - | 0.2 | 0.5 | 0.1 |
| All Species | 13.8 | 5.7 | 23.5 | 12.6 | 4.4 | 9.2 | 68.1 | 53.7 |
| Annual Forbs | | | | | | | | |
| <i>Bidens coronata</i> | 0.5 | - | - | | | | - | - |
| <i>Impatiens capensis</i> | | 0.4 | - | - | 1.4 | - | - | 0.7 |
| <i>Pilea pumila</i> | 54.2 | 13.1 | 4.9 | 0.1 | 23.6 | 16.4 | - | - |
| <i>Polygonum hydropiper</i> | 0.2 | | | - | - | | | |
| All Species | 54.8 | 13.5 | 4.9 | 0.1 | 25.0 | 16.4 | 0.0 | 0.7 |
| Perennial Forbs | | | | | | | | |
| <i>Angelica atropurpurea</i> | | | - | - | | 0.2 | - | - |
| <i>Aster firmus</i> | | 0.2 | 0.2 | 0.3 | 0.1 | 0.2 | 19.3 | 13.1 |
| <i>A. lanceolatus</i> | - | 0.1 | | 3.5 | - | 0.7 | | |
| <i>Calystegia sepium</i> | | | | | - | - | 2.3 | 7.3 |
| <i>Campanula aparinoides</i> | 1.7 | 1.7 | 2.1 | 1.5 | 1.2 | 0.2 | 1.9 | 1.0 |
| <i>Chelone glabra</i> | | | | | | - | 0.2 | - |
| <i>Cicuta bulbifera</i> | 1.0 | 0.4 | | | | - | - | - |
| <i>Epilobium leptophyllum</i> | 5.0 | 2.4 | 1.7 | 0.5 | 2.8 | 3.4 | | |
| <i>Eupatorium maculatum</i> | - | 9.7 | 0.1 | 3.6 | 0.5 | 1.5 | 21.0 | 29.0 |

continued

Appendix, continued.

| | Os | in | Lulu Lake | | | | Summerton | |
|-----------------------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | | | 2n | 3n | Un | Us | 7b | Ub |
| Perennial Forbs, continued | | | | | | | | |
| <i>E. perfoliatum</i> | | 0.4 | 0.2 | 0.2 | - | - | - | 0.6 |
| <i>Galium asprellum</i> | - | - | - | - | - | - | 0.4 | 0.6 |
| <i>Galium</i> spp. | 2.2 | 0.5 | 0.5 | 2.2 | 1.2 | 1.0 | | - |
| <i>Helenium autumnale</i> | - | - | - | - | - | - | 0.3 | |
| <i>Lathyrus palustris</i> | - | - | - | - | - | - | 0.1 | 2.4 |
| <i>Lycopus americanus</i> | - | - | - | - | - | - | 1.1 | - |
| <i>L. uniflorus</i> | 14.0 | 17.9 | 1.3 | 0.9 | 1.3 | 4.2 | 0.7 | 1.3 |
| <i>Lysimachia thyrsoiflora</i> | 1.7 | 4.2 | 3.8 | 1.5 | 3.3 | 5.8 | 0.1 | 0.3 |
| <i>Mentha arvensis</i> | - | - | - | - | - | - | 0.3 | |
| <i>Polygonum amphibium</i> | 0.3 | 0.9 | 1.2 | 0.8 | 3.1 | 1.2 | - | - |
| <i>Potentilla palustris</i> | 4.0 | 0.7 | - | - | - | - | - | |
| <i>Rubus pubescens</i> | - | - | - | - | - | - | 2.1 | |
| <i>Rumex orbiculatus</i> | 0.5 | 0.1 | 1.6 | | 2.7 | - | - | - |
| <i>Sagittaria latifolia</i> | 10.1 | 5.8 | 3.7 | 5.7 | 6.2 | 1.7 | - | |
| <i>Scutellaria galericulata</i> | 2.8 | 1.4 | 0.3 | 0.2 | 1.0 | 2.7 | 0.4 | - |
| <i>Solidago altissima</i> | - | - | - | - | - | - | | 1.3 |
| <i>S. gigantea</i> | | 0.4 | - | 0.6 | 0.2 | | 6.7 | 3.7 |
| <i>S. patula</i> | - | - | - | | 0.5 | - | | |
| <i>Solidago</i> sp. | - | - | - | 0.4 | | | - | |
| <i>Thalictrum dasycarpum</i> | - | - | - | | - | | 0.3 | 0.6 |
| <i>Triadenum fraseri</i> | | 0.1 | 0.5 | 0.4 | 0.1 | 0.2 | | - |
| <i>Typha angustifolia</i> | 0.2 | -- | - | 0.4 | 0.7 | | - | |
| <i>T. latifolia</i> | 1.3 | -- | - | 0.7 | 1.2 | 0.2 | | |
| <i>Viola</i> spp. | - | -- | - | 0.7 | - | 0.2 | 0.2 | |
| All Species | 44.7 | 46.7 | 16.9 | 24.2 | 26.0 | 23.2 | 57.5 | 61.0 |
| Ferns | | | | | | | | |
| <i>Onoclea sensibilis</i> | - | -- | - | - | 0.2 | | | 1.5 |
| <i>Thelypteris palustris</i> | 2.0 | 3.5 | - | 13.5 | 0.8 | 8.2 | 13.2 | 9.7 |
| All Species | 2.0 | 3.5 | - | 13.5 | 1.0 | 8.2 | 13.2 | 11.2 |
| Shrubs | | | | | | | | |
| <i>Betula pumila</i> | - | -- | - | 0.7 | - | - | - | - |
| <i>Cornus sericea</i> | - | 2.4 | - | - | - | - | 0.4 | - |
| <i>Potentilla fruticosa</i> | - | -- | 1.2 | 2.3 | 1.5 | - | - | - |
| <i>Ribes hirtellum</i> | - | -- | - | 0.9 | - | - | - | - |
| <i>Salix</i> spp. | - | 0.7 | - | 10.5 | - | - | 0.2 | - |
| <i>Spiraea alba</i> | | | | - | | | 0.4 | - |
| All Species | - | 3.1 | 1.2 | 14.4 | 1.5 | - | 1.0 | - |