The Role of Fire in *Spartina pectinata*-Dominated Tallgrass Prairie Wetlands

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ABSTRACT

Seasonal and diurnal patterns in gas exchange, leaf and soil nitrogen, and aboveground biomass production of *Spartina pectinata* were compared in annually and long-term unburned wetlands in a northeastern Kansas tallgrass prairie. CO_2 uptake was consistently higher in burned *Spartina pectinata* plants early in the growing season, but differences between treatments disappeared by mid-season. Plants in annually burned wetlands reached a peak CO_2 uptake of 43.2 ± 1.6 μmol m^{-2} s^{-1} in late June, while peak photosynthesis in unburned sites was 39.1 ± 1.2 μmol m^{-2} s^{-1} in mid-July. Leaf width, specific leaf mass, aboveground biomass production, plant height at anthesis, and flowering culm density were all greater in burned wetlands. There were no differences in culm density, % leaf nitrogen content, or soil N between burned or unburned sites. There were also microsite differences in CO_2 uptake and biomass accumulation in burned wetlands which corresponded to the amount of litter remaining after the fire. We conclude that the removal of accumulated litter by fire appears to be critical for maximizing annual production and reproductive effort of *Spartina pectinata* in these wetlands.

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INTRODUCTION

Studies of the several North American coastal *Spartina* species have focused on productivity, ecological interactions, responses to grazing, and salt inundation (Odum and Fanning 1973; Kirby and Gosselink 1976; Cain and Harvey 1983; Pearcy and Ustin 1984; Seneca and Blum 1984; Turner 1987; Davison and Bratton 1988; Morris and Haskin 1990; Bertness 1991; Schmalzer et al. 1991). In contrast, responses within this genus to discrete fire events and frequencies have received relatively little attention (Turner 1987; Schmalzer et al. 1991).

Spartina pectinata (prairie cordgrass) is a dominant midwestern North American wetland species commonly found in marshes, along stream banks, and below seeps throughout much of the tallgrass prairie from Mexico to northwestern Canada (Wali et al. 1973; Beetle 1978; Brotherson 1983; Schwarz and Redmann 1988). This species also occurs in small rocky margins of freshwater tidal marshes in Massachusetts (Caldwell and Crow 1992). Prairie wetlands, dominated by *Spartina pectinata, Typha* spp. and *Salix interior,* provide critical habitat for migratory birds moving through the Great Plains (Zimmerman 1990). Small *S. pectinata* wetlands in prairie lowlands may serve as prime nesting sites for red-wing blackbirds (*Agelaius phoeniceus*)and Le Conte's Sparrows (*Ammodramus leconteii*) (Zimmerman 1993) as well as cover and resting sites for deer (*Odocoileus* sp.), and foraging sites for gray tree frogs (S. Johnson, pers. obs.). *Spartina pectinata* may also be an important component of wetland sites favored by the rare crayfish frog, *Rana areolata* (Platt et al. 1974; Collins 1993). In addition to associations with wildlife, *Spartina* wetlands have been frequently used as forage for cattle (Teal and Teal 1969; McAtee et al. 1979; Angell et al. 1986; Kirby et al. 1989).

Natural fires were once common throughout the Great Plains (Pyne 1982; Collins and Gibson 1990), and today are used for tallgrass prairie management (Anderson 1972; Hulbert and Wilson 1983; Towne and Owensby 1984; Blankespoor 1987; Whisenant and Uresk 1989). Therefore, it is important to understand wetland responses to fire. The objectives of this study were to 1) quantify growth and reproductive responses to fire in *S. pectinata* dominated wetlands, 2) compare seasonal and diurnal dynamics of leaf-level gas exchange in *S. pectinata* shoots between annually burned and unburned wetlands, 3) identify and quantify variability in litter depth and available inorganic soil nitrogen between burned and unburned sites and 4) quantify microsite differences in gas exchange relative to the amount of litter remaining after fire and available soil nitrogen.

METHODS

Study Sites

Research was conducted at the Konza Prairie Research Natural Area (KPRNA), a native tallgrass prairie in northeastern Kansas (39° 05′N, 96° 35′W). Individual wetlands within KPRNA were selected on the basis of fire history and the size of the local stands of *Spartina pectinata.* Typical stand size was > 30 m^2. All prescribed fires occurred on KPRNA in the spring (late March–April).

Two annually burned and two long-term unburned sites (burned only once in the last 10 to 20 years), were selected as principal sites for assessing seasonal (1993) patterns of gas exchange [CO_2 uptake (A) and stomatal conductance (g_{wv})] in *S. pectinata* wetlands. Two additional burned and two unburned sites were used as replicates for quantifying end-of-season differences in flowering culm density and aboveground biomass production. All sites were located in different watersheds on KPRNA.

Seasonal Measurements

The seasonal dynamics of midday A and g_{wv} were measured using a portable gas exchange system (Li-Cor LI 6200, LICOR, Inc., Lincoln, NE) at two week intervals beginning in mid-May and ending in mid-September, 1993. Two mature leaves from each of 10 plants were selected from the top of the canopy and independently measured (n=20 leaves from 10 plants). In conjunction with seasonal A and g_{wv} measurements, monthly pre-dawn and midday leaf xylem pressure potential (ψ^{leaf}) estimates were made for burned and unburned *S. pectinata* plants. A pressure chamber (model 1000, PMS Inc., Corvallis, OR) was used to estimate ψ^{leaf} on 10 leaves from each site.

In addition to the biweekly measurements of midday gas exchange, diurnal comparisons of burned and unburned *S. pectinata* A and g_{wv} were made in mid-June and mid-August. Leaves from 5–10 plants from adjacent burned and unburned wetlands were used for these more intensive gas exchange measurements. During all measurements, leaves were exposed to full sunlight (>1500 μmol m^{-2} s^{-1}, photosynthetic photon flux density (PPFD) 0.4–0.7 μm). Ambient humidity was maintained in the gas exchange cuvette by routing a portion of the sample flow through desiccant. Vapor pressure deficits from the leaf to the air within the cuvette during measurements were similar at all measurement dates (3.5 to 3.6 kPa).

To quantify differences in seasonal biomass dynamics, specific leaf mass (gram dry mass/cm^2 leaf area), leaf tissue nitrogen (%) and extractable soil nitrogen (ppm) were measured in the burned and unburned sites. Leaf samples for nitrogen analysis (n=20 from each of two burned and two unburned sites) were oven-dried at 60° C for 72 hrs and analyzed with a Carlo-Erba series 1500 automated C-N analyzer. Soil samples were collected at 0–5 cm and 6–25 cm depths (approximately 20 cores at each depth) from soils beneath three burned and three unburned *S. pectinata* stands. Soils were air-dried and analyzed for extractable NO_3-N and NH_4-N using standard procedures (Dahnke 1980) at the soil testing lab at Kansas State University.

Microhabitat, Biomass, and Reproduction

Spartina wetlands on Konza Prairie occur along stream banks and in the lower reaches of ravines, and thus, most wetlands span small-scale topographic gradients. Moreover, fires are not always of similar intensity or equally effective at removing biomass from all locations along these gradients. To investigate the effect of small microhabitat differences in burned *S. pectinata* wetlands, additional measurements of A and g_{wv}, leaf tissue nitrogen and soil N were made in June. These data were collected at three locations along a linear transect located parallel to a stream bed through an annually burned wetland (elevational gradient < 1.5 m). In addition to the early season data (mid-June), gas exchange was also measured in mid-July, mid-August, and mid-September. In September, 20 leaf samples from each site were collected to quantify specific leaf mass. At the same time, litter and aboveground biomass samples were collected within 10 0.1 m^{-2} quadrats for each site.

Portions of *Spartina pectinata* wetlands in standing water at the time of burning were easily identified by the presence of significant amounts of previous year's litter that did not burn. These locations were also intensively investigated to determine if aboveground biomass production differed in these wetlands between the completely burned edges and partially burned central zones. Completely burned edges, two intermediate locations and partially burned central zones (approximately 5 m^2) were sampled for aboveground biomass (and litter) with 10 0.1 m^{-2} quadrats. These estimates were repeated in two other unevenly burned wetlands. Litter depth to the nearest 0.1 cm was also measured (n=20). Finally, measurements were made of previous year's litter depth and litter mass in three long-term unburned *S. pectinata* wetlands to quantify litter remaining on unburned sites from all years prior to 1993. Litter mass was estimated by harvesting all biomass in 0.1 m^{-2} quadrats (n=30), oven-dried at 80° C for 72 hrs and weighed.

At the KPRNA, *S. pectinata* emerges soon after fire in mid- to late April. Plants achieve a three leaf stage at a height of ca. 14 to 20 cm by mid-May. By mid-June plants are approximately 1–1.5 m tall with 6 to 8 functional leaves and by mid-August, plants are approximately 2 to 2.5 m tall with 10 to 12 functional leaves. *Spartina pectinata* flowers in late July through late August in KPRNA.

In late May, stem diameters and leaf widths in *S. pectinata* were measured to quantify differences in early season shoot size that may contribute to differences in late season biomass and flowering (McAtee et al. 1978). Changes in total vegetative culm densities were measured in burned wetlands beginning in mid-March (Day of Year (DOY) = 66) and in unburned wetlands beginning in mid-May (DOY = 135) and continued until late August. In mid-August, we measured heights of flowering culms, flowering culm density, and aboveground biomass in burned and unburned wetlands. Densities were quantified within 0.1 m^2 quadrats (three burned and three unburned sites, n=10 per site) and heights of plants within each quadrat were measured to the nearest 0.1 cm. All aboveground biomass was harvested from 10 0.1 m^2 quadrats and oven dried at 80° C for 72 hrs prior to weighing.

While belowground processes in *S. pectinata* wetlands are probably also directly and indirectly affected by fire through increased soil microbial activity or rapid influx of mineralized ash leachates (Vásquez et al. 1993; Soto and Diaz-Ferros 1993), measurements of these parameters were beyond the scope of this study.

Statistical Analyses

Corresponding measurements of seasonal dynamics of A, g_{wv}, specific leaf mass, litter mass, aboveground biomass, and soil nitrogen for burned and unburned *S. pectinata* plants and wetlands represent independent data by wetland and were therefore placed into a between-subjects experimental design (Maxwell and Delany 1990) and were analyzed by standard ANOVA procedures at the $\alpha = 0.05$ level (Zar 1984). Individual points for more intensive gas exchange measurements (diurnal data), and ψ_{leaf} data were also analyzed by repeated measures ANOVA. All values presented herein represent a mean ± one standard error of the mean.

RESULTS

Seasonal Measurements

Midday CO_2 uptake (A) was significantly higher ($p<0.011$) in *S. pectinata* plants in burned watersheds during all measurements taken early in the growing season (Figure 1). At both sites, A was relatively low in mid-May. However, plants in annually burned wetlands had significantly higher A (32.7 ± 1.6 μmol CO_2 m^{-2} s^{-1}; n=20, $p<0.021$) than plants in unburned wetlands (27.6 ± 1.6 μmol CO_2 m^{-2} s^{-1}; n=20). Seasonal maximum A in burned sites (43.2 ± 1.6 μmol CO_2 m^{-2} s^{-1}; n=20) occurred in late June (DOY = 181) while seasonal CO_2 uptake in unburned sites gradually decreased to a significantly lower ($p<0.05$) maximum A (39.1 ± 1.2 μmol CO_2 m^{-2} s^{-1}; n=20) in mid-July (DOY = 198; Figure 1). Following these peak periods, A was not significantly different between treatments. From late July to mid-August, both burned and unburned wetlands showed a significant and synchronized reduction in A and g_{wv} to 33.2 ± 4.3 μmol m^{-2} s^{-1} and 345 ± 20 mmol m^{-2} s^{-1}, respectively. In late August (DOY = 243), both burned and unburned sites showed a secondary peak in A that were not significantly different.

Seasonal patterns in stomatal conductance (g_{wv}) closely followed A and only differed significantly ($p<0.001$) between burned and unburned plants early in the growing season (Figure 1). At the period of highest A, g_{wv} wAs 545 ± 18 mmol m^{-2} s^{-1} in burned plants and 351 ± 20 mmol m^{-2} s^{-1} in unburned plants (Figure 1). There were no significant differences in burned vs. unburned wetlands in ψ_{leaf} (Figure 1). Seasonal minimum ψ_{leaf} was measured in late May (DOY = 150; −0.58 ± 0.14 MPa, pre-dawn and −0.98 ± 0.24 MPa, midday).

In June and August, diurnal patterns of gas exchange (Figure 2) were not significantly different between burned and unburned *S. pectinata* plants. In unburned plants, A and g_{wv} declined more dramatically than in burned plants from midday until evening. Later in the season, unburned plants maintained higher rates of gas exchange from midday into evening (Figure 2). There were no differences in leaf temperatures or incident irradiance between sites during either diurnal measurement.

Specific leaf mass (SLM) in unburned *S. pectinata* decreased significantly ($p<0.01$) from late May to early September (Table 1). Conversely, SLM in burned plants was initially higher and increased significantly ($p<0.001$) over the same time period (Table 1).

Culm densities in burned and unburned *S. pectinata* wetlands increased similarly from mid-May until late July (Figure 3). Peak culm densities in both burned and unburned wetlands occurred in mid-summer. In late season, culm densities decreased in both burned in unburned wetlands. At no time during the season were there significant differences in culm density between burned and unburned *S. pectinata* wetlands.

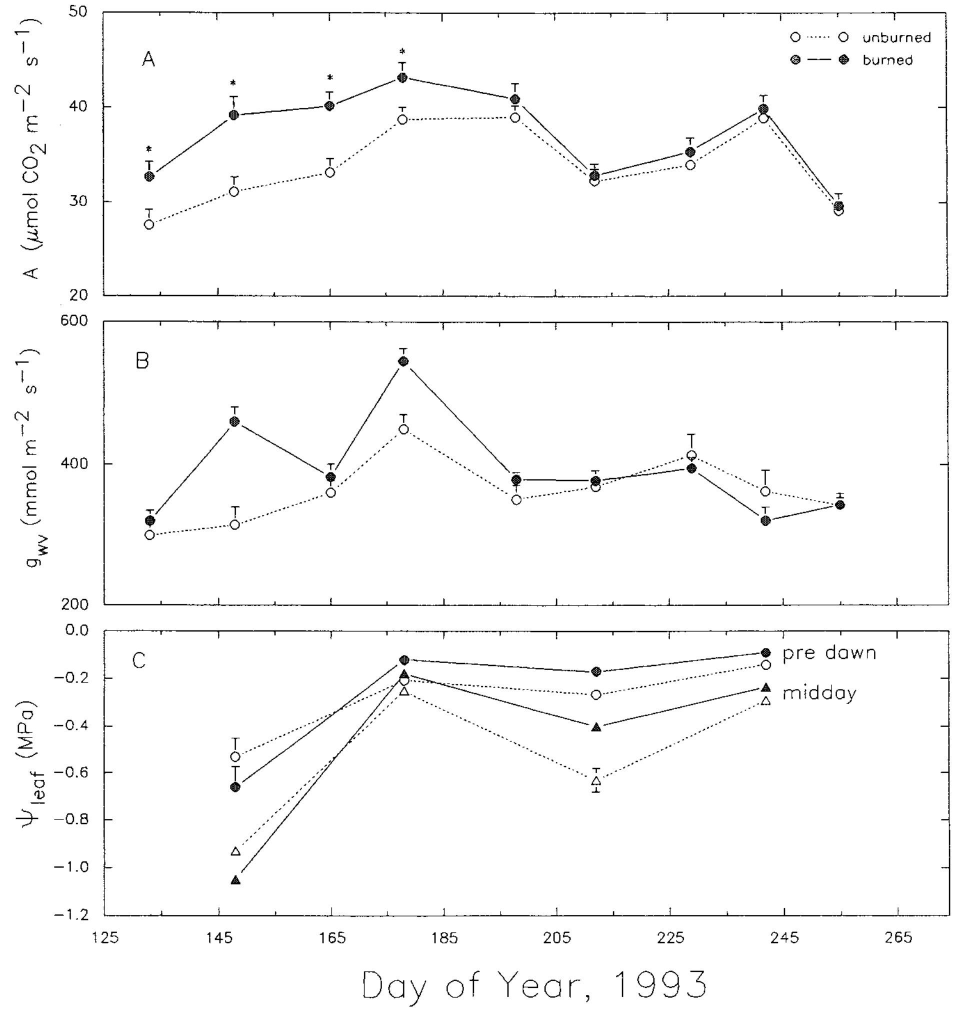

Fig. 1. CO_2 uptake (A; μmol m^{-2} s^{-1}, panel A), stomatal conductance to water vapor diffusion (g_{wv}; mmol m^{-2} s^{-1}, panel B) and leaf water potential (ψ_{leaf}, pre-dawn and midday, panel C) for *Spartina pectinata* in burned (●) and unburned (○) wetlands. * indicates significant ($p<0.0001$) differences between burned and unburned plants for CO_2 uptake and stomatal conductance. Data analyzed by standard ANOVA. Values are means ± 1 SE (n=10).

Mid-June levels of available soil nitrogen differed significantly in regard to nitrate (NO_3) and ammonium (NH_4) in burned and unburned sites (Table 2). Unburned sites had higher levels of NO_3 at both measurement depths ($p<0.001$) and burned sites had higher levels of NH_4 only at 6–25 cm. In contrast, early season levels of % leaf tissue nitrogen did not differ significantly between burned and unburned plants (Table 1). However, when expressed on an area basis, burned plants had almost twice as much N in leaves than unburned plants.

Microhabitat, Biomass, and Reproduction

Early in the season (June), the lowest position along a small topographic gradient within a burned wetland (site 3 in Figure 4) had significantly more ($p<0.001$) leaf tissue nitrogen relative to the other topographic positions (Figure 4). However, at this time, there was no difference in available nitrogen levels in soils between locations (Figure 4). The lowest elevational location (site 3 in Figure 5) had the earliest and highest peak *A* in June. Site 1 (Figure 5) had similarly high peak in *A* later in the season and site 2, with the largest associated litter remnant (Figure 6) had a more stable but lower seasonal *A*. Despite the different seasonal dynamics between these three locations, there was no significant difference in *A* among locations. At the end of the season, biomass at the lowest location (site 3 in Figure 6) was greatest (1645 ± 167 g m^{-2}, $p<0.001$) whereas biomass was lowest at the most upland site (498.2 ± 65 g m^{-2}, site 1, Figure 6). Previous year's litter biomass was greatest at sites 1 and 2 (96 ± 47 and 159 ± 19, respectively, NS) and significantly lower at site 3 (41 ± 10 g m^{-2}, ($p<0.001$) whereas biomass of competing grasses (primarily *Panicum virgatum*) was significantly higher ($p<0.02$) at the upland location (site 1 in Figure 6). Consistent with the highest year-end biomass production, the lowland lo-

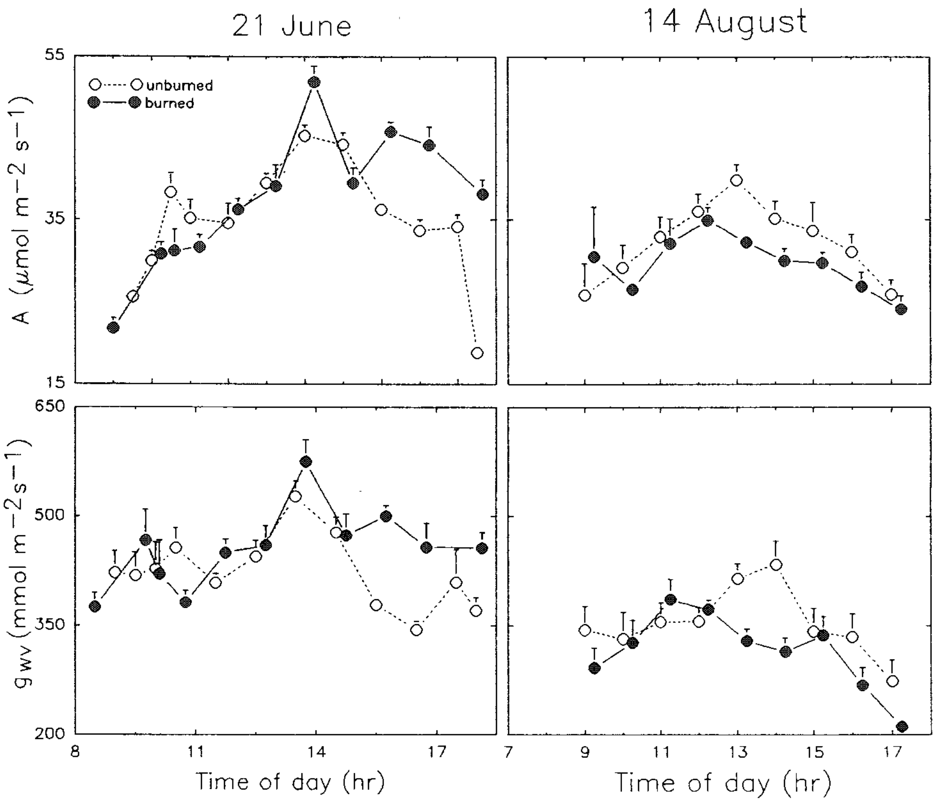

Fig. 2. The diurnal course of CO_2 uptake (A), stomatal conductance (g_{wv}) for annually burned (●) and long-term unburned (○) *Spartina pectinata* on 21 June (Day of year (DOY) = 172; left) and 14 August 1993 (DOY = 226; right). Data analyzed by standard ANOVA. Values are means ± 1 SE (n=10).

cation also had the highest specific leaf mass (Figure 6). In the corresponding analysis of the effect of differences in litter on productivity in unevenly burned wetlands, edges (site 1) without litter had higher biomass (Figure 7) and productivity than sites toward the center (sites 2, 3 and 4) of these wetlands (Figure 7).

Table 1. Differences in leaf width, stem diameter (both measured in late May), biomass, height of flowering culms, density of inflorescences (measured in mid-September), specific leaf mass (SLM, May and September), leaf tissue nitrogen (%) and leaf tissue nitrogen per unit leaf mass (measured in May) between burned and unburned *Spartina pectinata* plants. Data were analyzed by standard ANOVA ($\alpha = 0.05$). Letters indicate significant differences. Values represent mean ± one standard error.

	Burned	Unburned
Stem diameter (cm)	3.02 ± 0.08^a	2.53 ± 0.08^b
Leaf width (cm)	8.09 ± 0.26^a	4.89 ± 0.26^b
Aboveground biomass (g m^{-2})	1735 ± 162^a	672 ± 122^b
Height of flowering shoots (cm)	221.2 ± 6.8^a	173.2 ± 10.64^b
Density of flowering shoots/m^{-2}	45.2 ± 5.4^a	8.5 ± 2.3^b
SLM (May) mg cm^{-2}	8.11 ± 0.8^a	4.46 ± 0.5^b
SLM (September) mg cm^{-2}	11.45 ± 1.9^a	1.78 ± 0.5^b
Leaf tissue N (May) %	1.56 ± 0.16^a	1.74 ± 0.16^a
Leaf N (May) mg cm^{-2}	0.13^a	0.077^b

Early season leaf widths and stem diameters were significantly greater in burned *S. pectinata* stands than in unburned stands (65 and 19%, respectively; $p < 0.0001$; Table 2). Leaves of burned plants were nearly twice as wide as in unburned plants and stem diameters were also greater (Table 1). Litter mass which remains over the winter in unburned *S. pectinata* wetlands averaged 928 ± 52 g m^{-2} and was tightly packed near the soil surface. Depth of litter in these wetlands averaged only 5 ± 0.6 cm. Aboveground biomass production at anthesis was significantly higher (158%) in burned wetlands than in unburned wetlands ($p<0.0001$; Table 2). Biomass accumulation varied from 1520 ± 162 g m^{-2} to 2007 ± 170 g m^{-2} in stands of burned *S. pectinata* and from 525 ± 118 g m^{-2} to 785 ± 125 g m^{-2} in unburned stands. Similarly, plant height at anthesis and flowering culm density were significantly higher in burned than in unburned plants ($p<0.001$; Table 2). Burned plants were 22% taller and flower stalk density increased by more than 5-fold in burned compared to unburned wetlands.

DISCUSSION

Spartina species in coastal wetlands are often characterized as occurring in large monotypic stands with high levels of productivity (Morris and Haskin 1990).

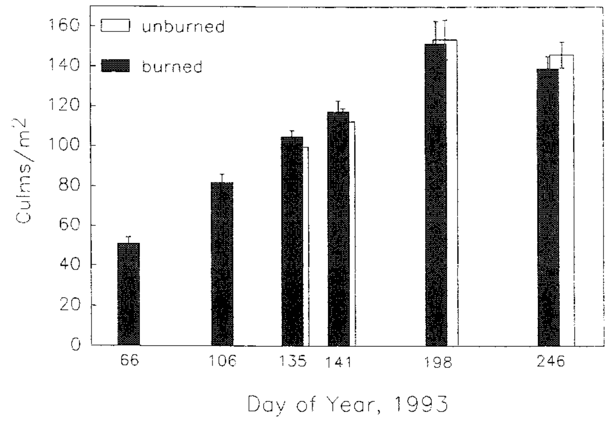

Fig. 3. Seasonal dynamics of culm density within annually burned and long-term unburned *Spartina pectinata* wetlands. Burning occurred on April 30 (Day of year (DOY) = 120). Data analyzed by standard ANOVA. Values are means ± 1 SE (n=20 quadrats).

While coastal *Spartina* wetlands are by far the best studied, inland S. *pectinata* wetlands may be equally productive on a per unit area basis (Table 1), but these wetlands are limited in extent by physical barriers and low rainfall. Indeed, annual biomass production in either annually burned or long-term unburned *S. pectinata* wetlands compare well with reported values of net primary production in the eastern coastal *Spartina* congeners *S. cynosuroides* and *S. alterniflora* (Odum and Fanning 1973).

Significant increases in flowering culm density, and aboveground production in burned compared to unburned wetlands indicate that annual fire enhances the reproductive effort and competitive ability of *S. pectinata* due to increased size of plants (Grace 1985). These findings are consistent with those from similar studies of highly productive wetland species such as *Spartina bakeri* (Schmalzer et al. 1991), *Typha glauca* (Mallik and Wein 1986) and *Phragmites australis* (Thompson and Shay 1985; 1989).

Results from this study clearly show that *S. pectinata* wetlands can be positively affected by spring fire. Average biomass production in long-term unburned *S. pectinata* was less than 50% of that in annually burned stands. This high productivity in *Spartina* wetlands may increase their use by many wildlife species, as well as cattle (Teal and Teal 1969; McAtee et al. 1978; Zimmerman 1990; Sedgwick and Knopf 1991).

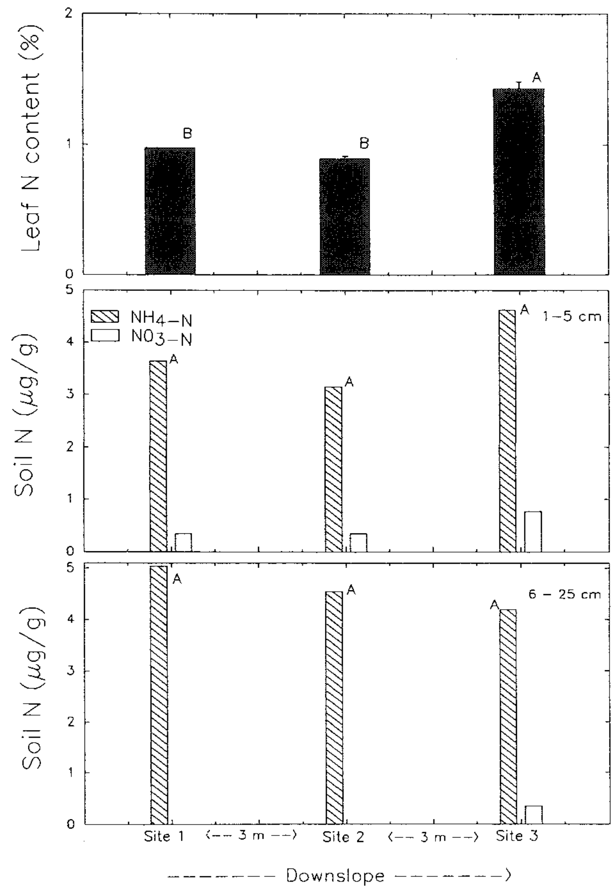

Fig. 4. Leaf tissue nitrogen and extractable soil nitrogen (NH_4 and NO_3, at depths of 0–5 cm and 6–25 cm) along a microelevational gradient (<1.5 m) in an annually burned *S. pectinata* wetland. See text for details of sampling. Different letters indicate significant differences within a panel. Data analyzed by standard ANOVA. Values for soil N represent a pooled mean of 20 soil samples. Values for leaf tissue N are means ± 1 SE (n=10).

CO_2 uptake (*A*) and stomatal conductance (g_{wv}) of burned *S. pectinata,* were similar to measured rates in the western coastal congener, *S. foliosa* (Pearcy and Ustin 1984), and to that of the tall form of *S. alterniflora* (43.2 vs 41 μmol m^{-2} s^{-1}), respectively (Giurgevich and Dunn 1982). Furthermore, the differences in CO_2 uptake, g_{wv} and year end biomass accumulation between burned and unburned *S. pectinata* wetlands are similar to differences between streamside and inland *S. alterniflora* marshes (Pezeshki and DeLaune 1988). Such differences in rates between inland and streamside *S. alterniflora* may be related to differences in the ability of plants to uptake soil nutrients (Gallagher 1975; Mendelssohn and Postek 1982). A similar difference in nu-

Table 2. Comparison of extractable soil nitrogen (NO_3-N or NH_4-N) in three burned and three unburned *Spartina pectinata* wetlands in mid-June 1993. Data were analyzed with ANOVA at α = 0.05. Letters indicate significant differences between burned and unburned sites. Values represent mean ± one standard error.

	Burned	Unburned
NH_4-N 1-5 C m (µg/g)	4.09 ± 1.19^a	3.15 ± 0.42^a
NO_3-N 1-5 cm	2.36 ± 0.70^a	4.83 ± 0.24^b
NH_4-N 6-25 cm	3.92 ± 0.63^a	2.36 ± 0.42^a
NO_3-N 6-25 cm	1.31 ± 0.77^a	3.43 ± 0.84^b

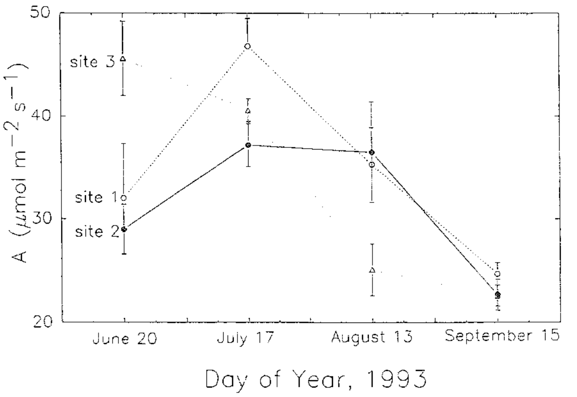

Fig. 5. Seasonal changes in peak CO_2 uptake (A) and seasonal average A in *S. pectinata* along a microelevational gradient (<1.5 m) in an annually burned wetland. * indicates significant differences between microelevational locations. Data analyzed by standard ANOVA. Values are means ± 1 SE (n=10).

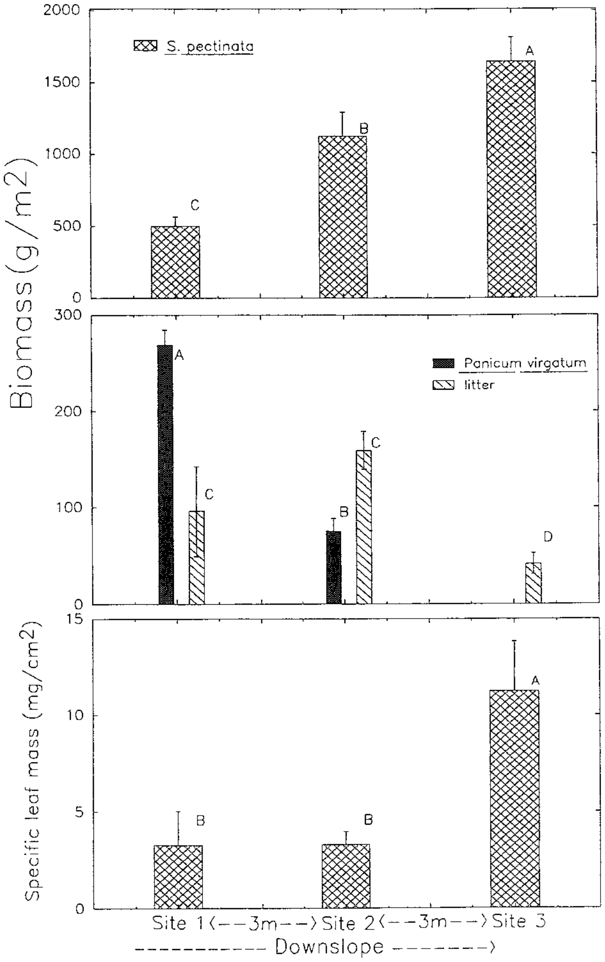

Fig. 6. Aboveground biomass of *S. pectinata* in relation to previous year's litter mass and biomass of a competing grass, *Panicum virgatum*, along a microelevational gradient (<1.5 m) in an annually burned wetland at the Konza Prairie Research Natural Area. Different letters indicate significant differences within a panel. Data analyzed by standard ANOVA. Values are means ± 1 SE (n=10).

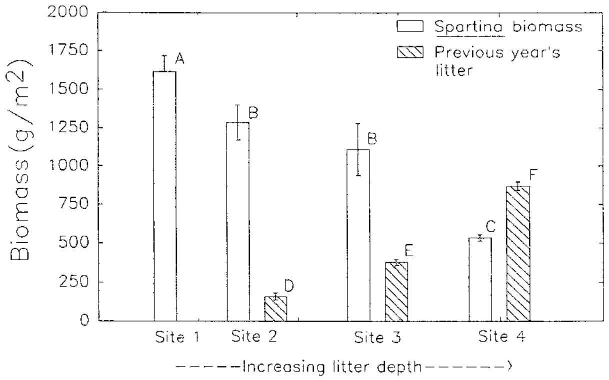

Fig. 7. Aboveground biomass of *Spartina pectinata* from completely burned wetland edge (with all litter consumed by fire, site 1) through incompletely burned wetland zones with increasing accumulations of previous year's litter (sites 2, 3, 4). Values means ± 1 SE (n=10). Different letters indicate significant differences among biomass or litter at the different sites. Data analyzed by standard ANOVA.

trient uptake ability may also play a part in the differences in gas exchange and biomass between burned and unburned *S. pectinata.* The lower concentrations of NO_3-N in mid-June in annually burned wetlands suggests a depletion of nitrate nitrogen corresponding to enhanced uptake. Since NO_3 is highly mobile in soils and is brought to plant roots along with water used for transpiration (Barber 1984), and because mid-June stomatal conductance in burned plants was significantly higher than that of unburned plants (Figure 1), the significantly lower concentration of nitrate in soils of burned wetlands may be related to greater uptake of nitrate and concomitant soil nitrate depletion (Cramer and Lewis 1993). Furthermore, because plants of burned wetlands are more productive than plants of unburned wetlands (Table 1), this suggests nitrate depletion rather than inherently lower concentrations of inorganic N typically associated with annually burned prairie communities (Seastedt et al. 1991).

The results from the study of microhabitat differences within wetlands suggest that a strong positive relationship exists between early season maximum *A,* aboveground biomass production and the amount of previous year's litter present. Burned wetlands had the highest early season *A* and the largest biomass accumulation at the end of the season. In contrast, where previous year's litter mass was largest (unburned sites), biomass production was lowest. In unevenly burned sites, larger remnant litter mass correlated with a later seasonal peak in *A* and also to lower end-of-season biomass accumulation (Figures 6 and 7). This may relate to litter effects on incident irradiance and soil temperature (Knapp 1984; Knapp and Gilliam 1985). Previous year's litter accumulation in unburned wetlands was in a compact zone, with as much as 900 g m^{-2} of litter compressed to a depth of just over 5 cm. This compact zone allowed little light to pass to the soil surface. For example, on a clear day in late May, with ambient light levels above the canopy greater than 1700 μmol m^{-2} s^{-1}, and light levels on the litter surface exceeding 500 μmol m^{-2} s^{-1}, only 26 ± 9 μmol m^{-2} s^{-1} (< 5 %) penetrated the litter layer. In burned stands, more than 150 μmol m^{-2} s^{-1} (> 6 times more) penetrated to the soil surface. This difference in light penetration would have been more striking in early spring, prior to grass canopy development and when burned wetlands had black soil exposed to full sunlight. Although not consistently measured in this study, soil temperature differences would likely also be greatest at that time (Knapp 1984). Indeed, in late June, there was still a 3° C difference in afternoon soil temperatures (S. Johnson, pers. obs.). Differences between burned and unburned sites in soil microbial activity, mineralization and/or immobilization of inorganic nitrogen may also affect N availability and, thus, productivity. Also, the greater integrated seasonal amount of CO_2 uptake in burned *S. pectinata* (Figure 1) may lead to earlier and more rapid root growth in burned plants (Mäkelä and Sievänen 1987; Hilbert 1990) which would allow an earlier and greater whole season uptake of extractable soil N. Increased N per unit leaf area in burned sites is consistent with this scenario.

In relatively mesic tallgrass prairie sites, net primary productivity and gas exchange are also higher in burned areas primarily because fire removes the large detrital layer which acts as a light and nutrient filter in unburned sites (Hulbert 1969; Knapp 1985; Knapp and Seastedt 1986; Seastedt 1988). Indeed, similar leaf-level physiological responses to fire have been documented for *Andropogon gerardii,* the dominant tallgrass prairie species that often grows adjacent to *S. pectinata.* This species also exhibited increased CO_2 uptake, biomass and flowering culm density in response to fire (Knapp 1985; Knapp and Hulbert 1986). While responses to fire are similar in burned *A. gerardii* and burned *S. pectinata,* their respective responses in unburned sites are more distinct. A reduction in culm density in the absence of fire occurs in *A. gerardii* (Knapp and Hulbert 1986) whereas no reduction occurred in *S. pectinata.* The lack of variation in culm density between burned and unburned *S. pectinata* may be a generalized response to stabilizing wetland substrates that may otherwise be severely eroded during high water flow (Gleason et al. 1979; Reidenbach 1983). From these studies, we conclude that differences in light (energy) availability via litter removal by fire may be the most important factor determining responses of *S. pectinata* and other grasses to fire.

In summary, fire enhances productivity in tallgrass prairie wetlands dominated by *S. pectinata.* Indeed, even after 20 years of annual burning, *S. pectinata* wetlands are as productive as sites less frequently burned (Johnson and Knapp, unpubl. data). Protection of these wetlands from fire decreases production and may lead to increases in woody species (*Salix* spp.) and other forbs (S. Johnson, unpubl. data.). Thus, from a management perspective, fire is a tool that can be quite effective in maintaining *S. pectinata* dominance in tallgrass prairie wetlands.

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