C_3/C_4 Production Shift on Seasonal Burns—Northern Mixed Prairie

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Abstract

This study investigates the potential of fire to manipulate the balance of C_3 (cool-season) and C_4 (warm-season) herbage in 2 northern Mixed Prairie communities. The xeric high prairie community and mesic low prairie community were chosen to represent regional moisture extremes. Treatments included dormant spring burn, mid-summer burn, dormant fall burn, and untreated. The high prairie community appears to be a C_3-dominant type. All 3 burn treatments increased the C_3 herbage fraction relative to untreated sites. Total production, however, was unaffected by treatment. The C_3/C_4 ratio of high prairie communities appears to be the result of long-term adaptation rather than short-term adjustments to fire or weather effects. Spring burning shifted low prairie communities towards C_4 herbage relative to other treatments. This was due to an increase in C_4 herbage (and total) rather than to a decrease in C_3 herbage. The C_3/C_4 ratio of low prairie communities did appear to respond to short-term adjustments in moisture, temperature, and light caused by the spring burn. The response of low prairie C_3/C_4 ratios to mid-summer and dormant fall burns appeared to be related to phenological and indirect weather effects rather than to changes in site microclimate caused by the fires.

Key Words: fire effects, herbage accumulation, δ ^{13}C ratio

Native rangelands of the northern Mixed Prairie region have the potential to provide wild and domestic herbivores with diverse, high quality forage throughout the growing season. Northern Mixed Prairie is characterized by a complex of native mid-height and shortgrass species with C_3 (cool-season) and C_4 (warm-season) photosynthetic pathways (Dix and Smeins 1967, Ode et al. 1980, Singh et al. 1983). C_3 species dominate region-wide. Tallgrass (C_4) species can be locally important on sites remaining moist during the short warm season (Barnes et al. 1983). The eastern ranges of the northern Mixed Prairie can shift strongly towards exotic C_3 species under repeated rest, overgrazing, or summer haying. Maintaining herbage production from 2 temporal guilds with distinct seasonal growth curves should increase nutrient availability for herbivores, while minimizing production declines from seasonal drought.

Several authors (Ehleringer 1978, Teeri and Stowe 1976, Tiezen et al. 1979) have documented predictable relationships in the field between microclimate, latitude, and elevation and C_3 and C_4 plant distribution. In general, C_4 species appear better adapted to the warmer and drier sites with high light intensities and lower leaf CO_2 concentrations. However, Baskin and Baskin (1985) suggest that photosynthetic pathway is only one of a suite of factors determining success or failure of a plant taxon in a particular environment.

In addition to climate, grazing and fire were major factors influencing community structure and function in the pre-settlement northern Mixed Prairie (Hanson 1984, Higgins 1984, Moore 1972). The season and intensity of fire and grazing events were probably interdependent (Steuter 1986). Herbage removal by either event would modify site microclimate (Redmann 1978, Savage and Vermeulen 1983, Owensby and Anderson 1967), and thus growth conditions for C_3 and C_4 species. Ode et al. (1980) and Singh et al. (1983) suggest that grazing will shift northern Mixed Prairie towards C_4 species. Fire suppression may result in accumulation of dead material and self-shading favoring C_3 species (Ode et al. 1980). Spring burning reduces the herbage density of northern Mixed Prairie (Huber and Steuter 1984) allowing more light into the foliage during the growing season. Although not as well documented as in the southern Mixed Prairie, the role of fire in manipulating species composition appears to have useful management implications depending on objectives and burn prescription (Dix 1960, Engle and Bultsma 1984, Gartner et al. 1978, White and Currie 1983).

Native communities with appropriate C_3/C_4 herbage production should meet the diversity and forage quality objectives of natural area and range livestock managers, respectively. The objective of this study was to determine the influence of fire on the production dynamics of C_3 and C_4 plant guilds within 2 communities of the northern Mixed Prairie.

Study Area and Methods

The study was conducted on the Samuel H. Ordway, Jr. Memorial Prairie. This north-central South Dakota (45° 43′ N, 99° 06′W) preserve is a 3,076-ha native grassland owned and managed by The Nature Conservancy. Vegetation has been characterized as northern mixed-grass (Weaver and Albertson 1956). The preserve lies just west of the narrow Tallgrass Transition zone of Küchler (1964). Geology of the glaciated prairie pothole landscape has been described by Christensen (1977). The area has a continental climate of hot summers and cold winters with about 80% of the mean annual precipitation occurring during the April through September growing season. Precipitation during the 2-year study period was below the long-term average (Table 1). The September 1983 through August 1984 period was 18% below, and the September 1984 through August 1985 period was 35% below average precipitation. Spring 1985 was well above average in temperature.

Table 1. Actual cool season (9/1 to 5/31) and warm season (6/1 to 8/31) precipitation (cm) during the study period, and deviation (cm) from the long-term average.

	9/1/83 to 5/31/84	6/1/84 to 8/31/84	9/1/84 to 5/31/85	6/1/85 to 8/31/85	Total
Study Period[1]	24.9	15.7	20.8	11.6	73.0
Deviation from long-term-average[2]	−3.7	−5.2	−7.9	−9.2	−26.0

[1]Recorded at gauge 0.75 km from study plots.
[2]Recorded at U.S. Weather Station (18 yr) Leola, SD-16 km east of site.

The study site consisted of a 0.4-ha, 22° south-facing slope within a 97-ha pasture. The pasture had been ungrazed since May 1982, lightly grazed (0.12 to 0.18 AUM/ha) by bison during October through May from 1980 to 1982, and moderately grazed (0.25 to 0.32 AUM/ha) by cattle during May through October prior to 1980. Plant communities on the study site ranged from a high prairie community on the 5° to 10° south-facing ridge crest through a mid prairie community (30° slope), to a low prairie community near the base of the slope (2° to 5°). This study is restricted to an evaluation of seasonal fire effects on the high

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Table 2. Description of fire treatments applied to two replications each within the study site—untreated not included. Values within the table are treatment means for n = 20 fuel load and % moisture, n = 2 ROS, and n = 4 FL.

Treatment	Date	Community	Fuel Load (g/m^2)	% Moisture[1] Dry Wt. Basis	Ros[2] (m/min)	FL[3] (m)
Summer Burn	8/3/83	High Prairie	339	70	0.4	0.3
		Low Prairie	612	134	0.2	0.2
Fall Burn	10/17/83	High Prairie	480	34	18.8	1.1
		Low Prairie	841	41	14.2	1.4
Spring Burn	4/19/84	High Prairie	433	27	24.0	1.2
		Low Prairie	753	34	21.4	1.8

[1]% moisture derived from composite fuel samples dried for 48 hr at 105° C.
[2]ROS = Rate of fire spread visually timed between two points.
[3]FL = Flame length visually estimated by two observers.

prairie and low prairie communities. Barnes et al. (1983) provide a detailed description of these plant communities on Ordway Prairie with nomenclature following Van Bruggen (1976).

The high prairie community occurred on Vida/Williams loams (silty range site). Vida/Williams loams are fine-loamy, mixed Typic Argiborolls. Major C_4 species are the gramas (*Bouteloua gracilis* (H.B.K.) Griffiths and *B. curtipendula* (Michx.) Torr.), little bluestem (*Andropogon scoparius* Michx.), and plains muhly (*Muhlenbergia cuspidata* (Torr.) Rydb.). Major C_3 species are needlegrasses (*Stipa comata* Trin. & Rupr. and *S. viridula* Trin.) sedges (*Carex filifolia* Nutt. and *C. eleocharis* Bailey), and western wheatgrass (*Agropyron smithii* Rydb.). Untreated high prairie sites had a mean of 302 g/m^2 of pre-1984 litter and standing dead on 28 May 1984 and 169 g/m^2 on 14 Sept. 1984. Pre-1984 litter and standing dead on burned treatments averaged 76 g/m^2 and 21 g/m^2 on the same dates, respectively.

The low prairie community is on a Bowbells loam (overflow range site). Bowbells soils are fine-loamy, mixed Pachic Argiborolls. Major C_3 species are big bluestem (*A. gerardi* Vit.) and switchgrass (*Panicum virgatum* L.). Major C_3 species are slender and western wheatgrass (*A. caninum* (L.) Beauv.), porcupine grass (*S. spartea* Trin.), and bluegrass (*Poa* sp. L.). Untreated low prairie sites had a mean of 907 g/m^2 of pre-1984 litter and standing dead on 28 May 1984 and 761 g/m^2 on 14 Sept. 1984. Pre-1984 litter and standing dead on burned treatments averaged 132 g/m^2 and 86 g/m^2 on the same dates, respectively.

The study site was divided into eight, 15-m by 40-m experimental units, each with a high and low prairie community. Experimental units were randomly assigned to 1 of 2 replications of 4 treatments. Treatments were dormant spring burn, mid-summer burn, dormant fall burn, and untreated (Table 2). Burn dates were designed to approximate peak seasonal fire probabilities based on fuel conditions and ignition sources (Higgins 1984, Moore 1972, Steuter 1986).

Herbage was clipped monthly from May to September in 1984, and at peak cool season (7 June—based on green needlegrass flowering) and warm season (31 July—based on big bluestem flowering) standing crop in 1985. Five sample points were systematically located in each community of each experimental unit. At each sample date a 0.10-m^2 quadrat was clipped radially from around each of the points. Care was taken to maximize the distance between clipped quadrats. The 5 clipped samples of each community/replication combination were air-dried and weighed, then composited and quartered. These reduced samples were sorted into green, current year dead, and past year dead components, then re-weighed. The green component was ground through a 40-mesh screen and stored in plastic canisters pending $\delta^{13}C$ analysis.

The relative contribution of C_3 and C_4 plants to seasonal green herbage was determined from $\delta^{13}C$ values obtained through mass spectrometer analysis (Tieszen et al. 1979, Troughton and Card 1975). Known C_3 and C_4 plants were analyzed to obtain mean $\delta^{13}C$ values (C_3 = −27.1‰, C_4 = −11.4‰) of dominant species in the 2 communities sampled. These mean values were used to estimate the percent composition (C_3 vs C_4) of green herbage by treatment, community, and sample date. Data were analyzed using analysis of variance with Duncan's multiple range mean separation. Significant differences were identified at the 95% confidence level unless otherwise indicated.

Results

High Prairie Community

The percentage of C_3 herbage in the green component was highest during May and September and lowest during July and August for all treatments (Fig. 1). However, during mid-summer the untreated sites had the highest percentage of C_4 herbage in the green component (ca. 60%). The 3 seasonal burn treatments maintained greater than 50% C_3 herbage in the green component throughout the season. During the second season following the burn treatments there was no difference in the green C_3/C_4 percentages. The C_3 fraction on all treatments remained above 50% throughout the peak warm season growth period during the second dry year (Fig. 1).

Green herbage peaked during July of the first season, and June of the second season following burning of high prairie communities (Fig. 2). Total current year herbage (and green) was significantly reduced only on spring and fall burns at the first sample date (Table 3). This reduction was due almost exclusively to a lower C_3 contribution early in the first season following fall or spring burning. However, green C_3 herbage tended to be highest on the fall burns late in the first season. Total current year herbage on fall

Table 3. High Prairie—Total (green and dead) current year herbage (g/m^2) for treatments ($\bar{X}$) by sample date.

Treatment	Sampling Date						
	5/28/84	6/20/84	7/21/84	8/13/84	9/14/84	6/7/85	7/31/85
Summer Burn 1983	75b[1]	127	215	200	167[2]	113	116
Fall Burn 1983	33a	109	223	234	181	107	88
Spring Burn 1984	36a	106	247	237	197	109	95
Untreated	71b	135	238	243	218	125	106

[1]Means within a column followed by the same letter, or no letter, are not significantly different ($P>0.05$).
[2]Summer Burn treatment less than Spring Burn and Untreated ($P<0.10$).

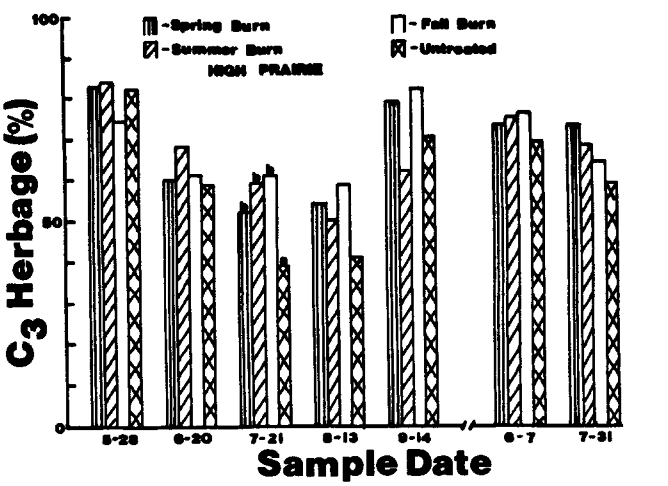

Fig. 1. *High Prairie—Seasonal progression of* C_3 composition for green herbage. The same or no letter atop bars within a sample date (1984–85) indicates treatment means are not different (P>*0.05).*

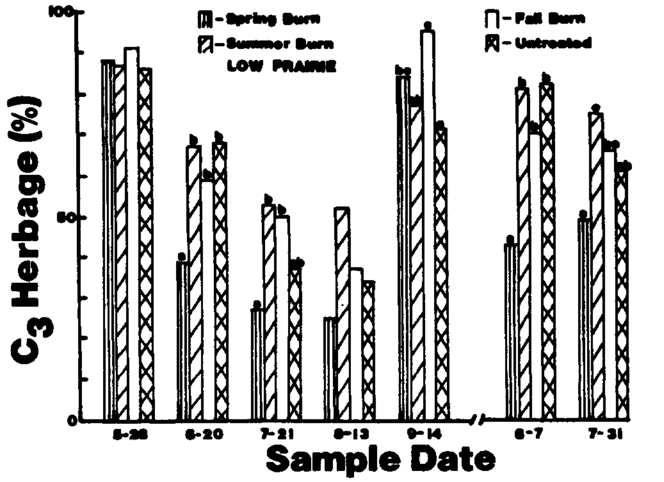

Fig. 3. *Low Prairie-Seasonal progression of* C_3*composition for green herbage. The same or no letter atop bars within a sampling date (1984–85) indicates treatment means are not different (*P>*0.05).*

burned and untreated sites peaked in August of the first season, while the peak on spring and summer burned sites occurred in July (Table 3). Total current year herbage was lowest on summer burned treatments ($P<0.10$) at the end of the first growing season.

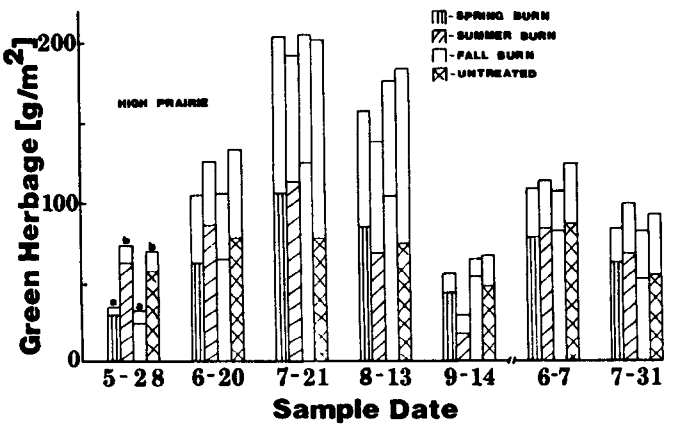

Fig. 2. *High Prairie—Seasonal progression of green herbage. The lower lined, slashed, open, and cross-hatched portion of bars represents the* C_3 *contribution, while the open upper portion represents* C_4 *contribution to green herbage. The same or no letter atop bars within a sampling date (1984–85) indicates treatment means are not different (*P>*0.05).*

Low Prairie Community

The C_3/C_4 ratio and herbage accumulation in low prairie communities were quite responsive to fire treatments (Fig. 3 and 4, Table 4). Again, May and September sample dates had the highest percentage of green C_3 herbage on all treatments (Fig. 3). The spring burn treatment had the highest percentage of green C_4 herbage (ca. 75%) throughout the warm-season growth period. By July the untreated sites had a C_4 herbage fraction similar to the spring burns (Fig. 3). During the September cool-season growth period, the summer burn and the untreated sites had the lowest percentage of green C_3 herbage. All treatments except the summer burn had a less than 50% green C_3 fraction during August of the first year following treatment. The spring burn continued to have the highest green C_4 percentage during the second year following treatment. Rapid growth of the C_4 guild contributed to the green herbage fraction at an earlier date than in the first year following spring burns (Fig. 3).

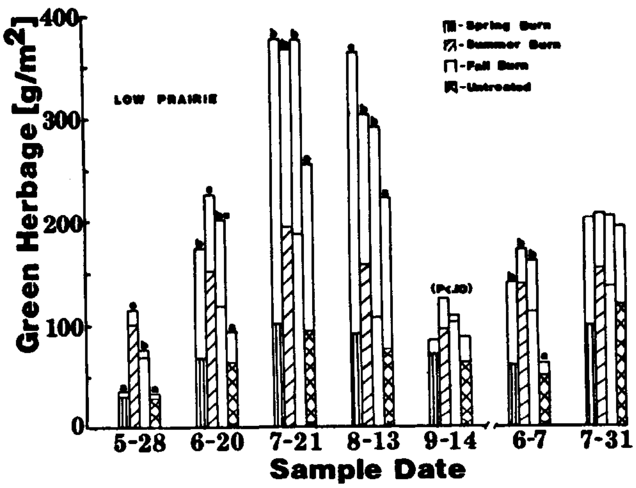

Fig. 4. *Low Prairie—Seasonal progression of green herbage. The lower lined, slashed, open, and cross-hatched portion of bars represents the* C_3 *contribution, while the open upper portion represents* C_4 *contribution to green herbage. The same or no letter atop bars within a sampling date (1984–85) indicates treatment means are not different (*P>*0.05).*

Table 4. Low Prairie—Total (green and dead) current year herbage (g/m²) for treatments ($\bar{X}$) by sample date.

	Sampling Date						
Treatment	5/28/84	6/20/84	7/21/84	8/13/84	9/14/84——	6/7/85	7/31/85
Summer Burn 1983	115c[1]	240c	426b	470b	373b	173b	221
Fall Burn 1983	76b	203b	425b	464b	414bc	162b	225
Spring Burn 1984	36a	178b	416b	497b	444c	141b	215
Untreated	33a	95a	288a	368a	294a	62a	215

[1]Means within a column followed by the same letter, or no letter, are not significantly different ($P>0.05$).

Spring burn and untreated sites had a slower herbage accumulation rate during the May and June period (Fig. 4). This was due primarily to lower C_3 herbage relative to summer and fall burns. High rates of C_4 accumulation during July and August resulted in equivalent, or higher, green and total herbage on spring burns relative to summer and fall burn treatments (Table 4). Growth rates on the untreated sites were substantially less than on burned treatments through August. On these low prairie sites, the summer and fall burn treatments maintained the nearest to a 50:50 ratio between C_3 and C_4 herbage during July and August. Total current year herbage on summer and fall burns was intermediate to the spring burn (highest) and untreated (lowest) sites at the end of the first season. However, spring burned and untreated sites had similar C_3 herbage throughout the season even though current herbage on the spring burns was 135% that of untreated sites during the August peak (Table 4).

Low prairie growth was reduced on all treatments during the second dry year (Table 4). The untreated sites had considerably less current herbage than any of the burn treatments during the cool-season growth period (Table 4). Green C_3 herbage was highest on summer burns, followed by fall and spring burns at the cool-season sampling date (Fig. 4). Untreated sites had the lowest C_3 green herbage, and proportionately much less C_4 herbage at the same date in the second season following treatment. Total current and green herbage was similar across treatments by the middle of the warm-season growth period in this second dry year. Summer burns had the highest C_3 green herbage at that time (Fig. 3).

Discussion

The changes in C_3/C_4 herbage following burning were not always explained by the expected treatment effects on site moisture, temperature, and light status. The C_3/C_4 ratio of high prairie during the cool-season growth period was generally unaffected by burning. Unlike the silty range sites studied by Engle and Bultsma (1984), Kentucky bluegrass *(Poa pratensis* L.) was a minor component of the high prairie community of this study. The large reduction in this exotic C_3 species reported by these authors following late spring burning may have affected the C_3/C_4 ratio. The increase in C_3 herbage on all 3 burn treatments (current study) relative to untreated sites during the warm-season growth period was unexpected. These results are contrary to the hypothesis of Ode et al. (1980) that reduced fire frequencies would favor C_3 species due to increased self-shading and cooler soil temperatures. I interpret the current results as being indicative of a native C_3 guild well adapted to the primary pre-settlement fire seasons. The C_4 species present in high prairie communities appear to be less well adapted to fire disturbance on these dry northern sites. The over-riding influence of a northern continental climate and general dominance of the C_3 pathway produce fire effects quite dissimilar to those from even the extreme northern range of the southern Mixed Prairie (Schacht and Stubbendieck 1985).

The shift to C_3 herbage resulting from burning high prairie appears short lived. The trend towards an increasing C_3 fraction on all treatments during the second dry year emphasizes the dominance of the native C_3 guild. The C_4 guild within high prairie communities appears unable to respond positively to short-term site warming, drying, or increased light whether resulting from fire or weather. The use of fire alone to improve the C_4 herbage component of high prairie communities does not appear feasible. Selective use of C_3 species by herbivores following a fire may improve the competitive position of the C_4 guild above that realized from fire alone (Ode et al. 1980).

Unlike high prairie communities, the species in the C_4 guild of low prairie communities dominate with the increased light and warmer site conditions produced by dormant spring fires. Similar results have been reported following spring burning in a drought year by Engle and Bultsma (1984). Whether this effect continues past the second year is unknown since mulch build-up is rapid in the absence of grazing. The negative phenological impact of the mid-summer burn treatment on the C_4 guild completely over-rode the benefits of higher irradiance and a warmer, drier site. The result of these summer burns was a C_3 dominated low prairie community through the second dry season. The large C_3 fraction on summer burns is especially impressive when compared to the much lower C_3 herbage on the heavily mulched untreated sites.

Why low prairie communities treated with dormant fall burns did not respond more similarly to dormant spring burns is not readily apparent. An obvious difference in the C_3 component of summer versus fall burn treatments was the near absence of Kentucky bluegrass in the fall burns, while summer burns were heavily infested. Yet, fall burned treatments had a C_3 fraction more similar to the summer burns than to the spring burns. This suggests that fall burned treatments had a stronger native C_3 component than summer burns. The fall burn treatments should have been phenologically neutral relative to C_3 and C_4 guilds—similar to the spring burns. Fall burning was as effective as spring burning in removing mulch. Thus light intensity and soil temperatures should have been similar. December 1983 was one of the coldest on record and lack of insulating mulch on the fall burns may have resulted in winter kill of C_4 tallgrasses, and exotic C_3 species. More information is needed on the role of fall burning since this was a peak pre-settlement fire season for much of the northern Mixed Prairie (Moore 1972, Steuter 1986).

The topographic position of low prairie communities (Barnes et al. 1983) insures that they are subirrigated throughout all but the driest growing seasons (e.g., year two of this study). High and mid prairie communities occur on sites characterized by limited soil moisture following the spring rainy season (Dix and Smeins 1967). Unpublished data for Ordway Prairie indicate that optimum soil temperatures for C_4 species growth may be restricted to the July and August period. The co-occurrence of reliable soil moisture and warm soil temperatures results in the potential for the C_4 guild to dominate low prairie communities managed with dormant spring burning even though the region is C_3 dominated. C_4 herbage on spring burns was nearly twice that of untreated sites with 2 years mulch accumulation. The enhancement of the C_4 guild was dramatized by its rapid early growth during the second dry growing season. The summer and fall burned treatments suggest that if the C_4 guild is suppressed or poorly represented, burning will just as effectively enhance C_3 growth relative to untreated sites with heavy mulch loads.

Low prairie communities are more restricted in size and distribution than high and mid prairie communities. However, when present, their productivity is double that of most other northern mixed grass types. Increasing the C_4 (warm-season) herbage from this community with the judicious use of spring burning will provide a more balanced forage resource on C_3 (cool-season) dominated northern Mixed Prairie ranges. As with high prairie communities, the interactive effects of grazing following burning may enhance or negate the simple effects of burning.

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