RELATIONSHIP BETWEEN COMMUNITY CARBON ISOTOPE VALUES AND NUTRIENT CONCENTRATIONS IN A NORTHERN MIXED PRAIRIE

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ABSTRACT

Grasses which photosynthesize by the C_3 and C_4 pathways differ in their nutrient concentrations and digestibilities. The biomass of these photosynthetic groups varies in a predictable manner with time of season, topographic position, latitude, and in response to fire. Since C_3 and C_4 composition can be quantitatively and conveniently assessed by measuring the carbon isotopic composition of the bulk vegetation, we proposed to test hypotheses relating community nutrient availability and digestibility to community C_3 and C_4 composition by estimating this composition with stable carbon isotopes.

Nitrogen (N), Phosphorus (P) and acid-detergent fiber (ADF) were determined for composite green biomass samples collected from seasonally burned and control plots in three upland communities. Community N, P, and ADF were correlated with growing season date, $\delta^{13}C$ values and fire season. N and P were most highly correlated with growing season date. The $\delta^{13}C$ value accounted for small but significant additional variation in N and P in some communities. ADF was most highly correlated with $\delta^{13}C$ values, and growing season date accounted for a relatively large amount of additional variation. Trends in plant nutrient availability were similar in high and low prairie communities. Communities with increasing amounts of C_4 biomass possessed lower nutrient concentrations and more ADF, thereby confirming at the ecosystem level the hypotheses generated from information at the species level.

INTRODUCTION

The Northern Mixed Prairie of North America is characterized by C_3 and C_4 plant groups within communities and considerable variation in the dominance of these respective types with topographic position and season (Barnes et al., 1983). The C_3 and C_4 composition of temperate zone grasslands is generally predictable from climatic, mainly temperature and moisture, data (Ehleringer, 1978; Ode et al., 1980; Terri and Stowe, 1976; Tieszen et al., 1979). C_3 species increase in abundance as temperature decreases and often as moisture increases along both altitudinal and latitudinal clines. Some of these environmental factors which govern floristic composition also affect yield differences in these two groups. C_4 species can often photosynthesize at higher rates at limiting CO_2 concentrations, and, therefore, are often at a competitive advantage when canopies are open (Monteith, 1978).

Research at Ordway Prairie has shown a wide range in productivities among different community types (Barnes et al., 1983) This variation was basically not related to C_3 and C_4 composition and the data showed no relationship between biomass and $\delta^{13}C$ values or C_4 cover (Tieszen and Boutton, 1989). However, Barnes et al. (1983) indicated that C_4-dominated communities also tended to occur on nutrient poor topographic positions. Therefore, in these systems Tieszen has suggested that C_4 species occupy resource poor parts of the landscape.

Our understanding of the physiology of C_4 species also suggests that these two types might possess different nutrient requirements and contents. C_4 species use an auxiliary enzymatic system to pump CO_2 into the bundle sheath cells thereby overcoming oxygen inhibition. This allows a high photosynthetic rate with less photosynthetic machinery. Wilson (1984) has reviewed the nitrogen status of grasses and indicates that the high nitrogen use efficiencies of C_4 species can lead to a large dilution of N. This can result in protein levels as low as 6 to 8% for actively growing C_4 leaf material. It is also established that *in vitro* dry matter digestibility of C_4 leaf material is less than C_3 species due to anatomical differences (Wilson and Hacker, 1987). These differences consist largely of more abundant vascular bundles and suberinized bundle sheath cells in C_4 species.

Analyses of the nutrient status of species representing different photosynthetic pathways have been largely confined to individual species comparisons or comparisons between single species swards (Wilson, 1984). These comparisons are often difficult because these two types do not always grow together and climate itself affects nutrient status. The implications of differing nutrient contents, however, for both selection by native herbivores and as an explanation for species distributions may be quite important. The spatial and temporal variation in aboveground production (Ode et al., 1980; Redman, 1975) and the potential for protein (Brown, 1978), digestibility (Caswell et al., 1973; Wilson and Ford, 1971; Wilson and Hacker, 1987), and phosphorus (Morris et al., 1982; Wilson and Haydock, 1971) differences between C_3 and C_4 species suggests that both biomass and nutrient concentration are influenced by community composition.

We undertook this study to utilize published isotopic data and exisiting biomass samples from two independent projects (Ode et al., 1980 and Steuter, 1987) to test some community level hypotheses about nutrients in these photosynthetic types. We proposed to test whether nutrient levels were related to time of season in various communities at Ordway Prairie and to test the hypothesis that nutrient availability at the community level was positively correlated with the prevalence of the C_3 pathway as estimated by community $\delta^{13}C$ values.

MATERIALS AND METHODS

Study sites were located on a 3,076 ha prairie preserve (Samuel H. Ordway, Jr. Memorial Prairie) in north-central South Dakota (45° 43' N, 99° 06' W). The preserve lies just west of Kuchler's Tallgrass Transition zone and is characterized as northern mixed-grass (Weaver and Albertson, 1956) on glaciated prairie pothole landscape (Christensen, 1977). Detailed climatic, vegetation, and soils information are provided by Ode et al. (1980), Steuter (1987) and Barnes et al (1983).

Data were obtained from three major upland communities during two growing seasons. The upland and lowland communities described by Ode et al. (1980) are here properly renamed high prairie and mid prairie. These were replicated in their 1977 study. The seasonal isotopic data have been presented and related to biomass. We are now reporting for the first time the nutrient analysis on those same samples. The second data set was secured from a fire management study. High prairie and low prairie communities were subjected to 3 treatments and were evaluated in 1984. They were replicated. Treatments consisted of a dormant spring burn (4-19-84), a summer burn (8-3-83) and a dormant fall burn (10-17-83). These were selected to approximate peak seasonal fire probabilities based on fuel conditions and ignition sources (Higgins, 1986; Steuter, 1986, 1987). Again, the isotope data have been published and interpreted as shifts in community composition (Steuter, 1987).

Sites were selected from native pastures in high range condition with no evidence of plowing or haying. Grazing was moderate by bison (*Bison bison*) and cattle. All sites were ungrazed for the two growing seasons prior to and during the sampling periods.

Aboveground biomass was clipped at frequent intervals near the soil surface from 0.1 m^2 quadrats within experimental and control units. Material from five quadrats was composited to form one sample which was mixed, quartered and sorted into green and dead. Green biomass was air-dried and ground to pass a 40-mesh sieve. The proportion of C_3 and C_4 biomass was determined from the $\delta^{13}C$ values of the clipped samples. Mean values for pure C_3 and C_4 test samples in 1977 (Ode et al., 1980) and 1984 (Steuter, 1988) were -26.7°/$_{\infty}$ and -12.9°/$_{\infty}$, and -27.1°/$_{\infty}$ and -11.4°/$_{\infty}$ respectively. Nutrients and ADF were determined with standard methods (AOAC 1975). ADF (lignocellulose) is used as an indirect measure of ruminant digestibility (Rao et al., 1973) and energy available to herbivores. For purposes of analyses the growing season date (GSD) is assumed to start 15 April in all years.

RESULTS

The results from Ode's samples collected in 1977 (Ode et al., 1980) illustrate marked seasonal changes in protein, phosphorus and carbon isotope ratio (Figure 1). Protein concentrations were 17 to 18% in the high and mid prairies during the beginning of the growing season (GSD = 20, early May) and then dropped to values as low as 7 to 8% in September. The two-factor ANOVA (Table 1) shows the large effect of growing season day (GSD) and that the two communities did not differ significantly with respect to protein.

The seasonal kinetics for phosphorus concentration are generally similar to those for protein with values around 0.3% in early May to values as low as 0.1% in late summer in the high prairie community. GSD was also very highly significant as a predictor for phosphorus. The communities differed with respect to phosphorus concentrations; mid prairie had a seasonal average slightly higher than that of high prairie.

Table 1. Two Factor ANOVA for samples from high and mid prairie communities sampled by Ode in 1977. Each component sampled is analyzed as a function of Community and Growing Season Date.

Component	GSC		Community	
	F	p	F	p
Protein	105.7	.0001	1.04	.32
Phosphorus	42.1	.0001	13.9	.003
CIR	3.2	.03	65.5	.0001

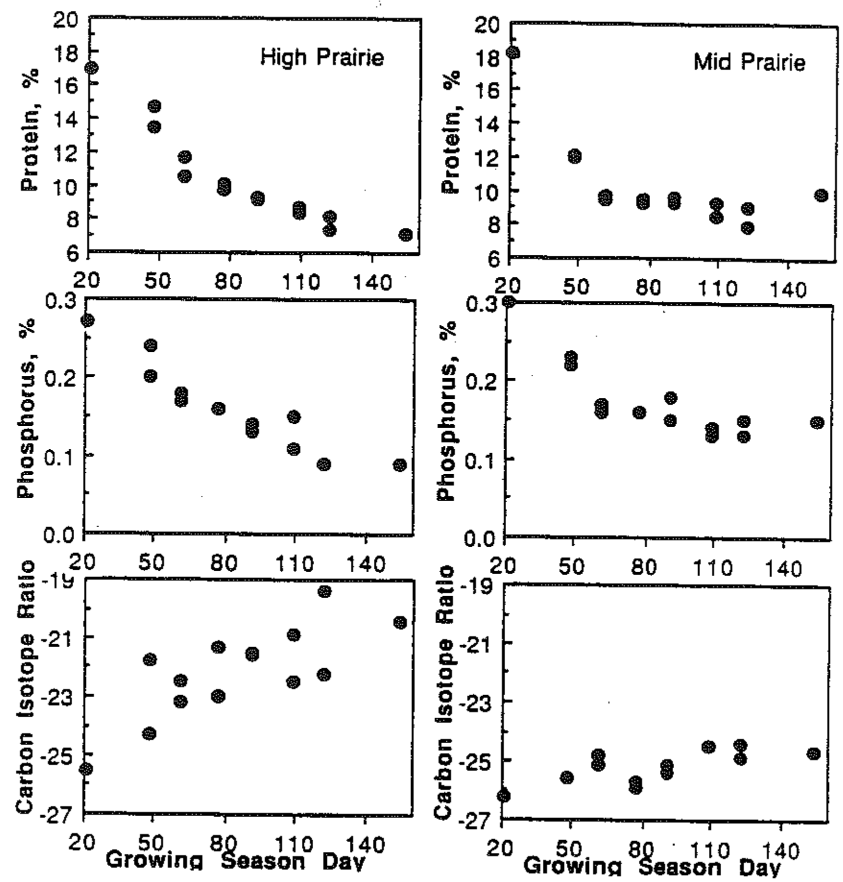

Figure 1. The seasonal course of protein and phosphorus concentrations and carbon isotope ratios, °/$_{\infty}$, from high and mid prairie communities sampled by Ode in 1977. CIR are from Ode et al. (1980).

Carbon isotope ratios varied from very negative values, around -26°/$_{\infty}$, characteristic of C_3 communities in early spring to around -20°/$_{\infty}$ in late summer in high prairie. The ANOVA (Table 1) illustrated that GSD was a significant predictor but not as important as community. The mid prairie community maintains its C_3 signal throughout the growing season indicating a low contribution by C_4 species. In contrast, the high prairie community shows a significant input of C_4 biomass as the season progresses thereby diluting the early season C_3 signal.

A linear regression analysis was performed in order to test the relationships among nutrients and the carbon isotope ratio (CIR). Protein and phosphorus concentrations are clearly and tightly correlated (Figure 2) with R^2 values of 0.93 and 0.91 for the two communities. Although the slopes do not differ, the intercepts do, indicating the higher phosphorus concentration of the mid prairie. Protein and phosphorus concentrations are also clearly and significantly related to CIR. As the CIR becomes more positive, protein and phosphorus concentrations decrease.

The results of a multiple regression analysis relating nutrients to GSD and CIR are presented in Table 2. In all cases GSD accounts for the largest amount of the variance; however in all cases CIR adds significantly to the regression. The multiple R^2 is substantially greater in the high prairie where the range of CIR was much greater than in mid prairie.

Tissue samples were analyzed from the biomass collections secured in the 1984 fire management project at Ordway. These effects of fire on seasonal biomass production and standing crop in control and three experimental groups in both high and low prairie communities have been published (Steuter, 1986, 1987). Since treatment effects were often small, all groups were pooled in the analysis of seasonal patterns. The seasonal patterns for protein and phosphorus (Figure 3) were similar to those obtained from Ode's samples. In addition, we were able to measure acid detergent fiber (ADF) on these samples. These started from a low around 25 to 30% in spring to a high around 35 to 40% in early summer. Then the values dropped slightly in fall. CIR patterns were

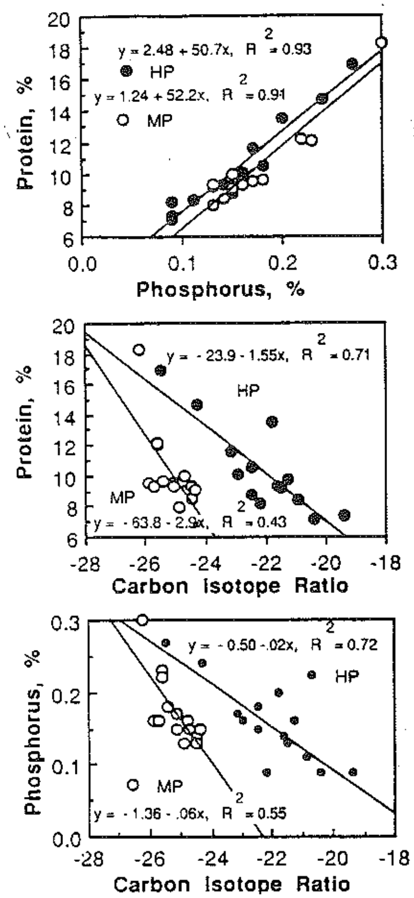

Figure 2. Linear regressions relating protein and phosphorus and protein and phosphorus concentrations to CIR, °/$_{oo}$, in high and mid prairies. CIR are from Ode et al. (1980).

marked with early season values again indicative of C_3 biomass, around -24°/$_{oo}$ to -26°/$_{oo}$. These values became more positive until day 120 after which both communities again became more negative. The two-factor ANOVA (Table 3) again clearly indicates the strong effect of GSD on all parameters measured.

Table 2. Multiple regression analysis of the importance of Growing Season Date and Carbon Isotope Ratio on the Protein and Phosphorus concentrations of Ode's high and mid prairies, 1977. r^2 represents simple coeffecients of determination; R^2 represents multiple coefficients of determination. In all cases slopes were very significantly different from 0.

	r^2		R^2
	GSD	CIR	
High Prairie			
Protein	.85	.71	.89
Phosphorus	.88	.72	.92
Mid Prairie			
Protein	.48	.43	.52
Phosphorus	.62	.55	.68

Table 3. Two-Factor ANOVA for high and low prairie communities sampled by Steuter in 1984: Each component sampled is analyzed as a function of Fire Treatment and Growing Season Date. CIR from Steuter (1988).

Component	GSD		Fire Treatment	
	F	p	F	p
High Prairie				
Protein	264	.0001	3.7	.028
Phosphorus	199	.0001	0.2	.86
ADF	193	.0001	12.9	.0001
CIR	28.7	.0001	3.7	.029
Low Prairie				
Protein	319	.0001	18.4	.0001
Phosphorus	227	.0001	11.9	.0001
ADF	150	.0001	4.1	.019
CIR	112	.0001	12.1	.0001

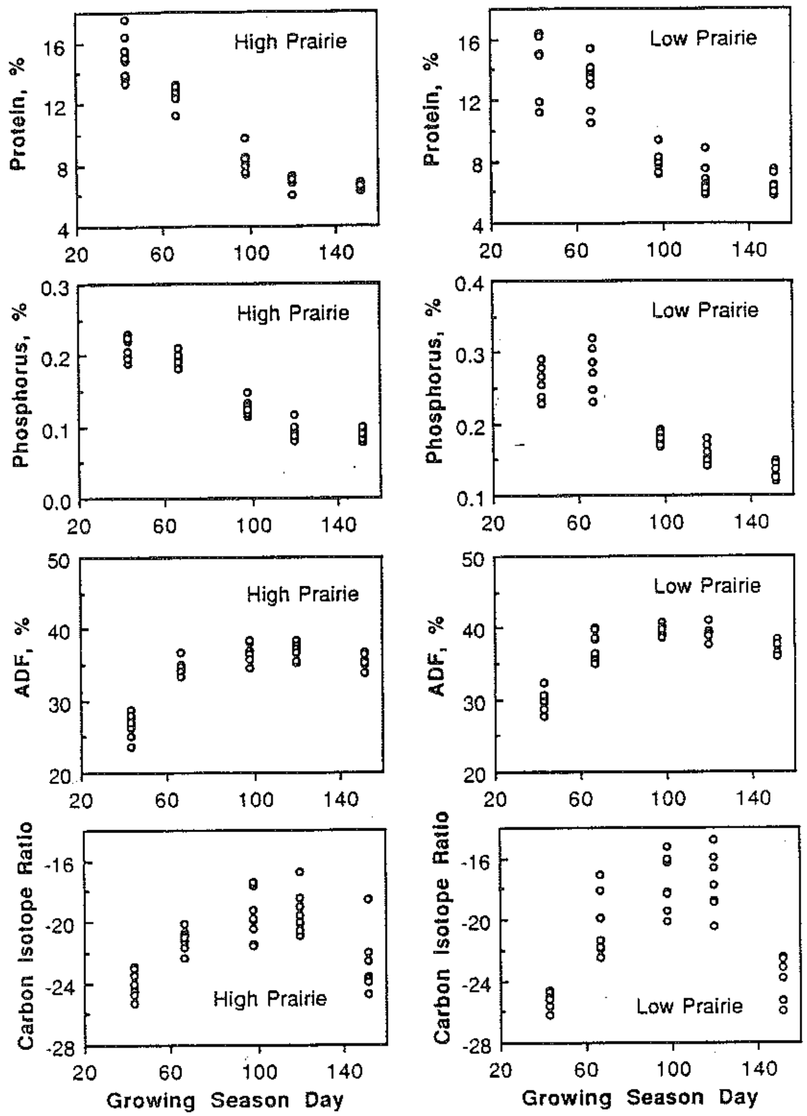

Figure 3. The seasonal course of protein and phosphorus concentrations, ADF, and carbon isotope ratios, °/∞, from high and low prairie communities sampled by Steuter in 1984. Individual data points from replicated controls and fire treatments are presented. CIR are from Steuter (1988).

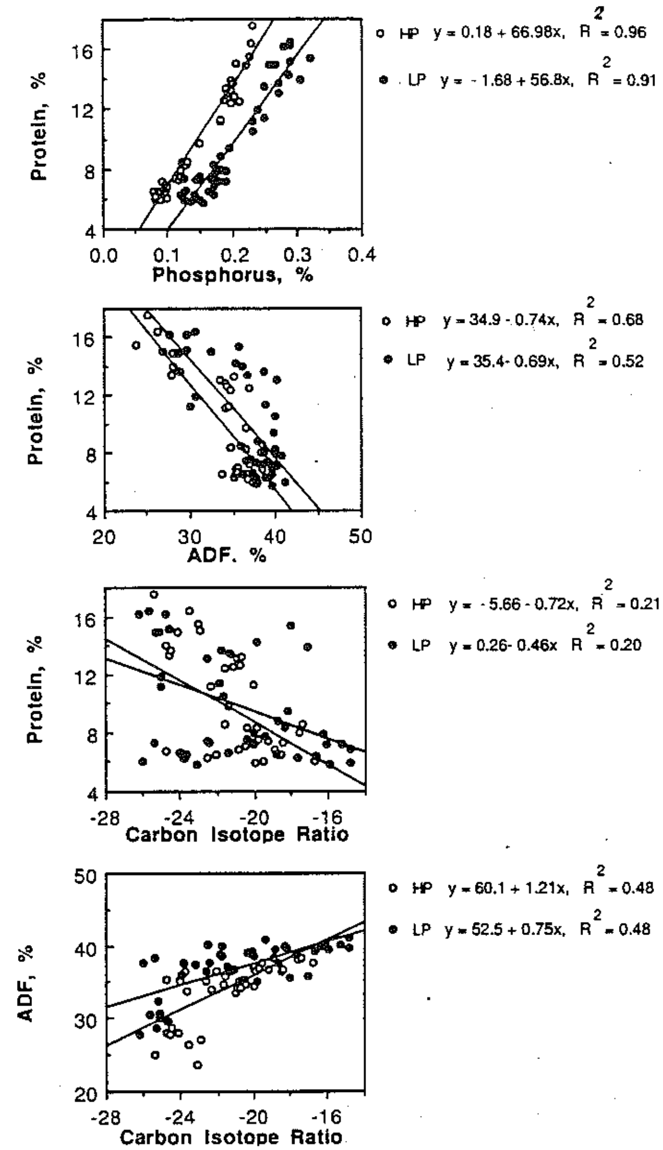

Figure 4. Linear regressions relating protein concentration to phosphorus concentration, ADF concentration, and CIR, °/∞, and ADF to CIR in high and low prairies. All control and fire treatment results were combined in the analysis. CIR are from Steuter (1988).

As was the case with the 1977 data, protein and phosphorus values are significantly and highly correlated in both communities with the low prairie possessing a higher season average phosphorus content. There is also a strong inverse relationship between protein and ADF in both communities. ADF is more highly correlated with CIR than is protein, but in both cases the slopes are significantly different from zero. As CIR increases, that is as C_4 biomass increases, protein decreases and ADF increases.

The multiple regression analysis (Table 4) shows relationships among CIR and GSD and all parameters that are similar to those found in the 1977 data set. GSD is a much greater predictor of protein and phosphorus than is CIR but in all cases CIR is significant and adds to the explanation. With respect to ADF the carbon isotope ratio is a better predictor than is GSD in low prairie and an equivalent predictor in high prairie.

Table 4. Multiple regression analysis of the importance of Growing Season Date and Carbon Isotope Ratio on the Protein, Phosphorus and ADF concentrations of Steuter's high and mid prairies, 1984. r^2 represents simple coeffecients of determination; R^2 represents multiple coeffecients of determination. In all cases except phosphorus vs CIR in low prairie, slopes were very significantly different from zero. Original CIR from Steuter (1988).

	r^2		R^2
	GSD	CIR	
High Prairie			
Protein	.86	.21	.91
Phosphorus	.8	.13	.91
ADF	.49	.48	.78
Low Prairie			
Protein	.77	.15	.83
Phosphorus	.83	.03	.83
ADF	.37	.44	.69

DISCUSSION

The CIR data confirm the strong dominance of C_3 grasses in the mid prairie and the greater abundance of C_4 species in the high and low prairies (Ode et al., 1980; Steuter, 1987). This interesting relationship results because of the presence of short and mid-grass species in the high prairie and the near exclusive presence of tallgrass species in the low prairie. The seasonal kinetics of the CIR in both high and low prairie is likely a fairly quantitative measure of the contribution to biomass by C_3 species in spring, the increasing contribution to biomass by C_4 species as summer progresses and the increased C_3 production once again in late fall. It is therefore clear that changes in proportional contributions of C_3 and C_4 species are a common feature of the northern Mixed Prairie and that these changes are superimposed on the normal seasonally related growth and senescent relationships.

Some of the differences associated with topographic position at Ordway result from environmental differences related to the toposequence. Soil moisture stress is most significant in the high prairie and least in the low prairie (Barnes et al., 1983). Soil N and soil nitrate (Barnes et al., 1983) are higher in the mid prairie than high prairie, but this did not result in community differences in the protein concentration of green biomass. We were not able to analyze recent dead compartment to determine if growth and senescence might have been influenced. The lower herbage P in high prairie corresponds to soil P levels 6 to 7 times less than those in mid prairie.

The results from two completely independent data sets at Ordway clearly establish a relationship between the nutrient contents and digestibilities of green biomass and the C_3 and C_4 composition as estimated by the CIR. Protein and phosphorus contents both increase as the CIR becomes more negative. Thus, the nutritive value of the biomass in these communities is higher when the proportion of C_3 biomass increases. Although this relationship is clear, the magnitude of the effect is not as great as that of GSD which is a strong predictor of nutritive value.

The relationship between indigestible fiber at the community level and the $\delta^{13}C$ value is much less ambiguous. The high, and independent portion of the variability in ADF accounted for by the CIR, as distinct from that associated with GSD, indicates that C_3-dominated communities will have lower fiber (higher digestibility) levels than those with increasing C_4 composition. Our data thereby confirm the community level hypotheses which were generated from differences in the physiological performances and anatomical characteristics of individual species which differed in their photosynthetic pathways.

These community level differences associated with the photosynthetic pathways have implications for both herbivore utilization and the role of natural fires. The seasonal declines in nutrient availability represent differentially maturing green biomass in the three adjacent community types. Large herbivores are not restricted by community boundaries in the northern Mixed Prairie. However, they should respond to a change in energetics which occurs as they cross these boundaries (Wiens et al., 1985). The increased nutrient availability associated with the C_3 pathway suggests the possibility that herbivore diversity, biomass, and utilization may be relatively high in mid prairie communities.

Intense herbivore selection for biomass (Caswell et al., 1973; McNaughton, 1984) may shift community composition towards C_4 species (Evans and Tisdale, 1972; Sims et al., 1978). An increase in the C_4 biomass would reduce nutrient availability to herbivores, but reduced utilization of the C_4 component would result in fuel accumulation and increased probability of fire spread. Fire maintains or increases the C_3 component of northern Mixed Prairie (Steuter, 1987), thus counteracting the effects of herbivory. Although this scenario is plausible, it depends on strong and consistent selection against C_4 species. The evidence (Tieszen et al., 1983) suggests that bison are good generalist grazers except during the winter season when the utilization of C_3 species is pronounced. The effect of this "dormant" season selectivity on community dynamics is not known.

Although nutrient availability at the community level is negatively correlated with the C_4 pathway, nutrient concentrations within the C4 component should increase with fire in the system (Britton and Steuter, 1983; Kucera and Ehrenreich, 1962; Ohr and Bragg, 1985), especially if herbivores maintain regrowth at an immature stage. Enhanced nutrient availability following fire in a northern Mixed Prairie may also reduce herbivore selection between communities by masking the boundaries between them (Wiens et al., 1985). It appears that without the proximate influence of both fire and grazing, changes in community structure will lead to reduced aboveground nutrient availability in the northern Mixed Prairie.

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