Journal of Vegetation Science 13: 395-402, 2002

Regional analysis of litter quality in the central grassland region of North America

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Abstract. The central grassland region of North America is characterized by large gradients of temperature and precipitation. These climatic variables are important determinants of the distribution of plant species, and strongly influence plant morphology and tissue chemistry. We analysed regional patterns of plant litter quality as they vary with climate in grassland ecosystems throughout central North America including tall-grass prairie, mixed grass prairie, shortgrass steppe, and hot desert grasslands. An extensive database from the International Biological Program and the Long-Term Ecological Research Program allowed us to isolate the effects of climate from those of plant functional types on litter quality. Our analysis of grass species confirms a previously recognized positive correlation between C/N ratios and precipitation. Precipitation exhibited a similar positive relationship with lignin/N and percent lignin. Although there was no significant correlation between temperature and C/N, there was a significant positive relationship between temperature and both percent lignin and lignin/N. Among functional types, C_3 grasses had a slightly lower C/N ratio than C_4 grasses. Tall grass species exhibited higher C/N, lignin/N, and percent lignin than short grass species. This understanding of the regional patterns of litter quality and the factors controlling them provides us with a greater knowledge of the effect that global change and the accompanying feedbacks may have on ecosystem processes.

Keywords: C_3 grass; C_4 grass; C/N ratio; Lignin; Precipitation gradient.

Abbreviations: LTER = Long-Term Ecological Research; NUE = Nutrient use efficiency.

Introduction

Plant litter quality is both a determinant and a consequence of the nutrient status of an ecosystem (Chapin 1980; Vitousek 1982; Field et al. 1983; Pastor et al. 1984; Wedin & Tilman 1990). While litter quality has a large influence over carbon and nitrogen dynamics, it is controlled by these same dynamics, as well as a series of abiotic factors. Litter quality is a reflection of the allocation of nutrients and the amount of structural material within a plant, and the overall tissue chemistry of the plant. Plants exhibiting high nutrient use efficiency (NUE) fix large quantities of carbon per unit nitrogen (high C/N) and thus generally produce litter of poor quality (Swift et al. 1979). Similarly, plants that allocate large amounts of carbon to structural components, such as lignin, produce poor quality litter (Fogel & Cromack 1977; Aber & Melillo 1982). Litter of poor quality is decomposed slowly leading to large amounts of carbon stored in the soil. Nitrogen availability may be reduced due to high immobilization potentials (Aber & Melillo 1982), leading to a positive feedback with litter quality (Pastor & Post 1986; Tilman & Wedin 1991).

Although plant communities have a large impact on ecosystem function, many predictions of global change concentrate solely on the direct effects of abiotic factors (e.g. Esser 1990; Melillo et al. 1993). Litter quality is controlled by a variety of biotic and abiotic factors, while influencing some of these same factors. Therefore, understanding the effect of a changing environment, as well as the accompanying feedbacks on litter quality, is vital to predicting overall changes in ecosystem function (Ojima et al. 1993; Owensby 1993; Smith & Shugart 1993; Zak et al. 1993; Kemp et al. 1994). Many current models view litter quality, and thus the biotic influence over carbon and nitrogen turnover, as a static property. At least one simulation model, Century (Parton et al. 1987), includes a precipitation control over litter quality, a relationship that is not validated. We hypothesize that litter quality changes as a function of climate (Parton et al. 1987) both directly by controlling NUE of individual species, and indirectly, by controlling species composition. These climatic controls may have a significant impact on current predictions of the influence of global change on ecosystem function.

In this study we used data from a network of sites to perform a regional analysis of plant tissue chemistry in the central grassland region of North America. Our objectives were twofold. First we wished to test the relationship between climate and patterns of tissue chemistry to determine the climatic controls over litter quality. Resulting relationships should allow us to make predictions about the effect of changing climate on litter quality and the resulting impact on carbon and nitrogen dynamics. Our second objective was to separate the influence of plant species and climate on litter quality by categorizing grass species into functional groups and evaluating patterns of tissue chemistry. These relationships can potentially allow us to assess the impact of changing species composition on regional litter quality.

Methods

A data base was compiled consisting of plant tissue chemistry data from 15 sites across North America, representing 6 grassland regions. These regions include tall-grass prairie, mixed-grass prairie, shortgrass steppe, desert grassland, northwest bunchgrass, and mountain grassland. Although the northwest bunchgrass site is located in eastern Washington, USA, it has been included in our analysis of the central grassland region of North America. The predominant grassland types of the Great Plains (shortgrass steppe, mixed-grass prairie, tall-grass prairie) were represented by sites encompassing a range of climatic combinations (Table 1).

Data for this analysis were obtained from a variety of sources. Most of the data were obtained from the US/IBP Grassland Biome study (Van Dyne 1969; Sims et al. 1978). These data were supplemented by several Long-Term Ecological Research (LTER) (Franklin et al. 1990) sites including the Central Plains Experimental Range, the Konza Prairie Research Natural Area, and the Cedar Creek Natural History Area. Two additional studies (Wedin pers. comm.; Vinton 1994) provided data on other sites (Table 1).

The data base contains tissue chemistry and morphological data for the dominant grass species at each of the sites. Since we were looking for litter quality variables on senesced litter that have the greatest effect on ecosystem function, the data base included percent carbon, percent nitrogen, percent phosphorus, percent lignin, C/N, and lignin/N. Additionally, the grass species were separated into classes based on mean growth height at maturity.

Since the data were collected from a series of studies, the design, methods, and length of study are highly variable. Replication and sample numbers vary between studies as does the completeness of the data set. For example, several of the studies are lacking lignin and/or phosphorus data. Data sets with missing variables were omitted only from analyses involving the missing data. If carbon values were not included in a particular data set, we multiplied biomass by 0.45 in order to determine C/N ratios (Schlesinger 1977). The number of sampling locations within sites also varied between studies. While data were collected from only one location in some studies, other studies separated data by landscape position, texture, and/or community type. In order to simplify the data set, we separated each of the data sets by year and treatment, if applicable, and computed the means. Since some of the data that we obtained were either an average or a composite of an unknown number of samples, we did not determine weighted averages. Instead we treated each average as a single point with power equal to the rest of the data points, regardless of differences in replication or sample number.

In a first set of analyses, we tested the relationships between climatic variables and litter quality. We performed simple regressions between C/N, lignin/N, and percent lignin, and both mean annual precipitation and mean annual temperature. We performed stepwise regression analyses using each of these litter quality variables and mean annual temperature and mean annual precipitation in order to determine the cumulative effect of temperature and precipitation on litter quality. We also separated the data set into discreet classes (200 mm and 500 mm) based on annual precipitation in order to remove the effect of precipitation on litter quality. We regressed temperature against C/N for each of these subsets.

In a second set of analyses, we tested the effects of plant species and morphological characteristics on litter quality. First, we grouped species into functional types based on their physiology. Since it has been recognized that C_3 and C_4 plants allocate nutrients differently (Field & Mooney 1986; Wedin & Tilman 1990; Kemp et al. 1994), we tested the relationship between the litter quality of these functional types and mean annual precipitation and temperature using simple linear regression. We also performed stepwise regressions to determine the cumulative effect of temperature and precipitation on litter quality. Second, we used plant height as an indicator of a plant's investment in structure in order to deter-

Table 1. Description, species and variables measured, mean annual precipitation, and mean annual temperature for 14 grassland sites across North America.

Site	Lat Long	Description	Species	Variables	Precip. (mm)	Temp. (°C)
Ale[1] Washington	46°40' N 119°55' W	Northwest Bunchgrass	*Agropyron spicatum, Poa cusickii, Poa secunda, Stipa thurberiana*	% C*, % N, % P, C/N*	250	12.0
Bridger[1] Montana	45°78' N 110°78' W	Mountain Grassland	*Agropyron subsecundum, Festuca idahoensis*	% C, % N, % P, % lignin, C/N, lignin/N	413	7.4
Cottonwood[1] South Dakota	43°95' N 101°87' W	Mixed Prairie	*Agropyron smithii, Andropogon scoparius, Bouteloua gracilis, Bromus japonicus, Buchloe dactyloides, Carex eleocharis*	% C*, % N, % P, % lignin*, C/N*, lignin/N*	450	8.2
Hays[1,5] Kansas	38°99' N 99°38' W	Mixed Prairie	*Agropyron smithii, Andropogon gerardi, Andropogon scoparius, Aristida longiseta, Bouteloua curtipendula, Bouteloua gracilis, Bromus japonicus*	% C, % N, % lignin, C/N, lignin/N	561	11.8
Jornada[1,2] New Mexico	32°60' N 106°85' W	Desert Grassland	*Aristida longiseta, Bouteloua eriopoda, Muhlenbergia porteri, Sporobolus airoides, Sporobolus cryptandrus, Sporobolus flexuosus*	% C*, % N, % P, % lignin*, C/N*, lignin/N*	259	16.3
Osage[1] Oklahoma	36°95' N 96°55' W	Tallgrass Prairie	*Andropogon gerardi, Andropogon scoparius, Bromus japonicus, Panicum virgatum, Poa pratensis, Sorghastrum nutans, Sporobolus asper*	% C, % N, % P, % lignin*, C/N, lignin/N*	955	15.1
Pantex[1] Texas	35°30' N 101°53' W	Shortgrass Steppe	*Bouteloua gracilis, Hordeum pusillum, Panicum capillare*	% C, % N, % P, C/N	423	13.8
CPER[1,3,5] Colorado	40°82' N 104°77' W	Shortgrass Steppe	*Agropyron smithii, Aristida longiseta, Bouteloua gracilis, Buchloe dactyloides, Carex eleocharis, Carex filifolia, Muhlenbergia torreyi, Sporobolus cryptandrus, Stipa comata*	% C, % N, % P*, % lignin*, C/N, lignin/N*	322	9.8
Konza[4,5] Kansas	39°10' N 96°61' W	Tallgrass Prairie	*Agropyron smithii, Andropogon gerardi, Andropogon scoparius, Bouteloua curtipendula, Bouteloua gracilis, Panicum virgatum, Sorghastrum nutans, Sporobolus asper*	% C, % N, % lignin*, C/N, lignin/N*	835	12.8
Fort Morgan[7] Colorado	40°15' N 103°48' W	Shortgrass Steppe	*Schizachyrium scoparium, Andropogon hallii, Panicum virgatum, Calamovilfa longifolia*	% C, % N, C/N	322	9.8
Sterling[7] Colorado	40°37' N 103°48' W	Shortgrass Steppe	*Andropogon hallii, Panicum virgatum, Calamovilfa longifolia, Bouteloua gracilis*	% C, % N, C/N	456	10.1
Ovid[7] Colorado	40°58' N 102°17' W	Shortgrass Steppe	*Schizachyrium scoparium, Bouteloua curtipendula*	% C, % N, C/N	468	9.5
North Platte[7] Nebraska	41°08' N 100°41' W	Mixed Prairie	*Andropogon hallii, Panicum virgatum, Calamovilfa longifolia, Bouteloua gracilis*	% C, % N, C/N	494	9.0
Valentine[7] Nebraska	42°52' N 100°33' W	Mixed Prairie	*Andropogon hallii, Panicum virgatum, Calamovilfa longifolia, Bouteloua curtipendula*	% C, % N, C/N	479	8.4

[1]US/International Biological Program-Grassland Biome database; [2]Jornada Long Term Ecological Research database; [3]Central Plains Experimental Range-Shortgrass Steppe Long Term Ecological Research database; [4]Konza Prairie Research Natural Area database; [5]Vinton 1994; [6]Cedar Creek Natural History Area database; [7]D. Wedin unpubl. data;*Variable not measured for all samples at a given site.

mine if litter quality changed with increasing structural material. We tested the relationship between mean plant height and C/N, lignin/N, and percent lignin using simple linear regression analysis.

Finally, since there is a positive relationship between plant growth height and precipitation in the grasslands of North America, we attempted to separate the effect that these two factors have on tissue chemistry. First, we analysed variations in the tissue chemistry of individual species across sites. We performed simple regressions between C/N and annual precipitation for four species: *Agropyron smithii*, *Andropogon gerardi*, *Bouteloua gracilis*, and *Panicum virgatum*. Second, we analysed the litter quality of species at individual sites and the variations associated with growth height. We tested the relationship between lignin/N and mean plant height at 4 sites, Central Plains Experimental Range, C_3, Hays, Osage, and Konza, using simple regression analysis.

Results

Comparisons between climate data and tissue chemistry revealed that precipitation was the independent variable most closely related to litter quality for all the litter data (Fig. 1). Mean annual precipitation showed a significant positive relation with C/N, lignin/N, and percent lignin. While mean annual temperature demonstrated a significant positive relationship with both percent lignin and lignin/N, C/N was not significantly altered by differences in temperature (Fig. 2). The addition of temperature to a stepwise regression model comparing climate with C/N did not significantly improve the relationship between precipitation and litter quality. Similarly, the addition of precipitation did not improve the regression model comparing temperature and percent lignin. The combination of temperature and precipitation did however improve the relationship between climate and lignin/N from r^2 = 0.4987 to r^2 = 0.5858.

Both C_3 grasses and C_4 grasses exhibited a positive relationship between C/N and annual precipitation

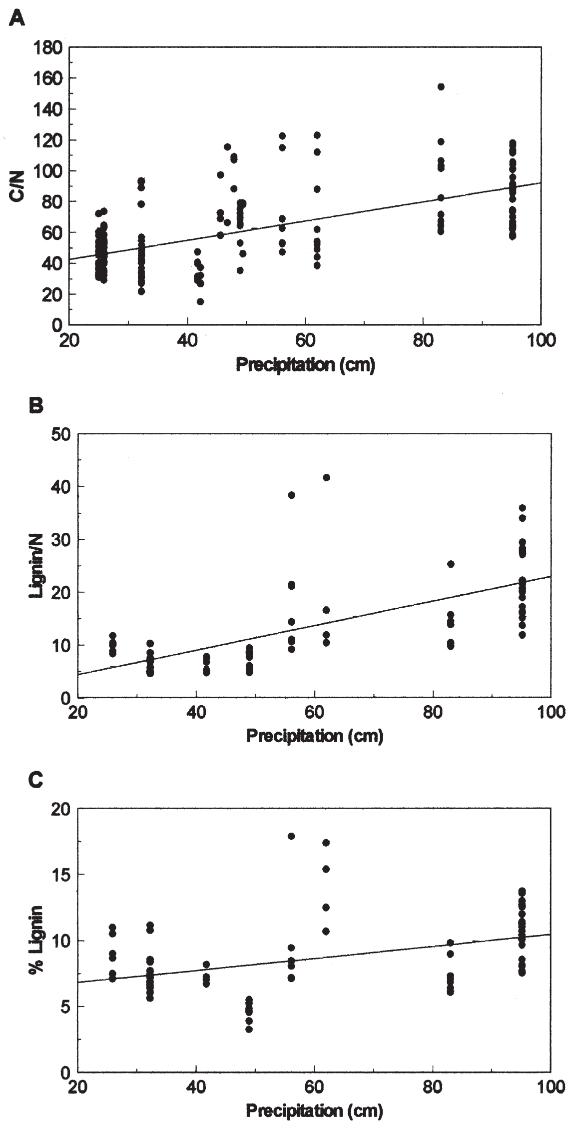

Fig. 1. Relationship between plant litter quality and mean annual precipitation across a series of sites in the central grassland region of the U.S. A positive correlation exists between precipitation and **A.** C/N (r^2 = 0.3555, P < 0.0001), **B.** lignin/N (r^2 = 0.4661, P < 0.0001), and **C.** percent lignin (r^2 = 0.1605, P < 0.0003).

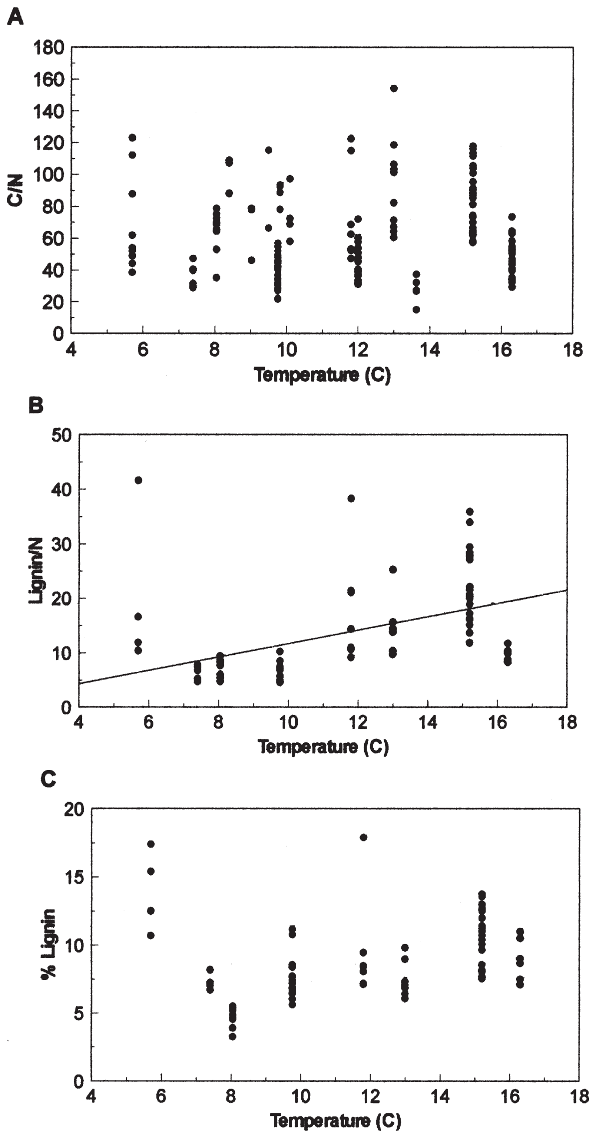

Fig. 2. The relationship between plant litter quality and mean annual temperature across a series of sites in the central grassland region of the U.S. Lignin/N is the only variable to exhibit a significant relationship with temperature alone (r^2 = 0.2081, P < 0.0001).

(Fig. 3). Temperature was not significantly related to C/N of either C_3 grasses ($r^2 = 0.0151$, $P < 0.3900$) or C_4 grasses ($r^2 = 0.0226$, $P < 0.1187$). Temperature slightly improved the relationship between precipitation and C/N for both C^3 ($r^2 = 0.3841$, $P < 0.0001$) and C_4 grasses ($r^2 = 0.3709$, $P < 0.0001$). When compared at similar sites, C_3 species generally exhibited lower C/N than C_4 species (Fig. 3). The C_3 species also showed less variability in litter quality than C_4 species both within and across sites. We also found significant relationships between tissue chemistry and grass species grouped by height. The C/N, lignin/N, and percent lignin increased significantly with increasing plant height (Fig. 4).

We evaluated relationships between C/N and precipitation for 4 individual species that occur across the gradient (Fig. 5). The C/N increased as a function of precipitation for *Agropyron smithii*, *Bouteloua gracilis*, and *Panicum virgatum*. There was no relationship between C/N and precipitation for *Andropogon gerardi*. We also evaluated the relationship between plant height and lignin/N across species at 4 individual sites (Fig. 6). While there was a positive relationship between plant height and lignin/N at Hays, Osage, and Konza, the relationship did not exist for the species at Central Plains Experimental Range.

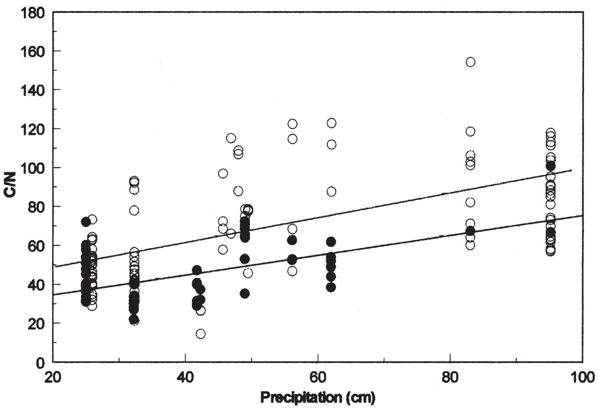

Fig. 3. A comparison of the relationship between precipitation (cm) and plant tissue C/N for C_3 grass species (●) ($r^2 = 0.3157$, $P < 0.0001$, C/N = 25.85 + 0.49(ppt)) and C_4 grass species (○) ($r^2 = 0.3132$, $P < 0.0001$, C/N = 37.54 + 0.57(ppt)).

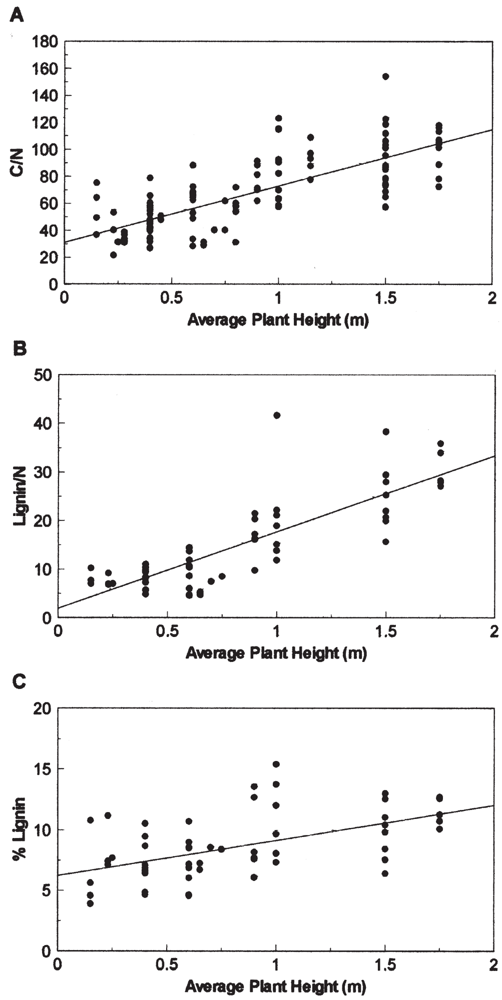

Fig. 4. The relationship between plant litter quality and mean plant height. A positive correlation exists between plant height and **A.** C/N ($r^2 = 0.5279$, $P < 0.0001$), **B.** lignin/N ($r^2 = 0.6739$, $P < 0.0001$), and **C.** % lignin ($r^2 = 0.2823$, $P < 0.0001$).

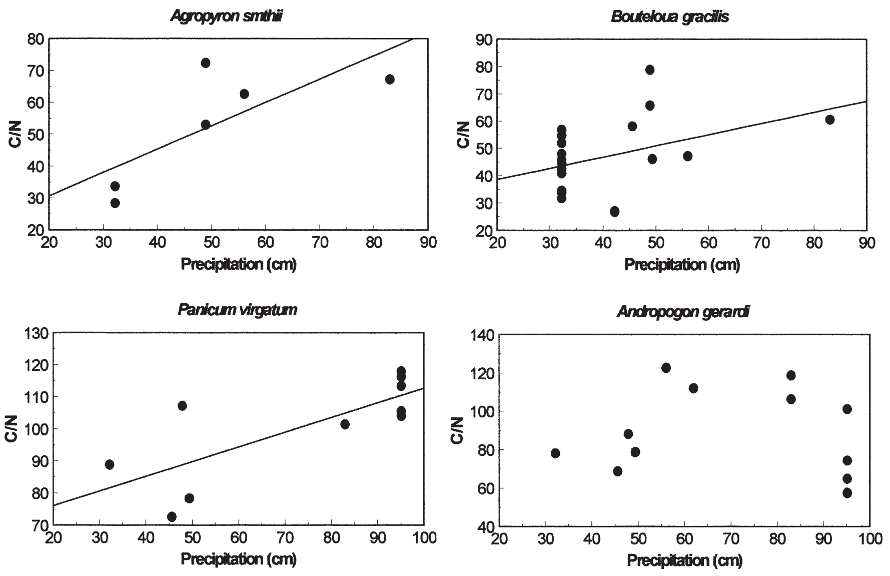

Fig. 5. The relationship between plant tissue C/N and precipitation (cm) for 4 species: *Agropyron smithii* ($r^2 = 0.5739$; $P < 0.0811$); *Bouteloua gracilis* ($r^2 = 0.1598$; $P < 0.0807$); *Panicum virgatum* ($r^2 = 0.5838$; $P < 0.0101$); *Andropogon gerardi* ($r^2 = 0.0291$; $P < 0.5772$).

Discussion

Litter quality varies according to climate and species characteristics (Chapin 1980; Vitousek 1982; Field et al. 1983; Field & Mooney 1986; Schlesinger 1989; Wedin & Tilman 1990; Vinton & Burke 1995). We determined that precipitation has the greatest impact on litter quality in the grasslands of North America. All 3 variables, C/N, lignin/N, and percent lignin, increased with precipitation, indicating increasing NUE, increasing nutrient limitation, and lower quality litter. Temperature generally exhibited little or no relationship with litter quality. Lignin/N was the only litter quality variable that exhibited a significant relationship with temperature. Combining temperature with precipitation improved the models only slightly, if at all. Although there was no relationship between litter quality and temperature, the effect of temperature on species distribution is significant (Epstein et al. 1996), indicating a feedback between temperature, species composition, and litter quality.

When C_3 and C_4 grasses were analysed separately, they each demonstrated a similar relationship to precipitation. However, C_3 grasses generally have lower C/N ratios than C_4 grasses across the gradient, indicating that the physiological differences between these functional types have important ecological consequences (Field & Mooney 1986; Wedin & Tilman 1990; Kemp et al. 1994).

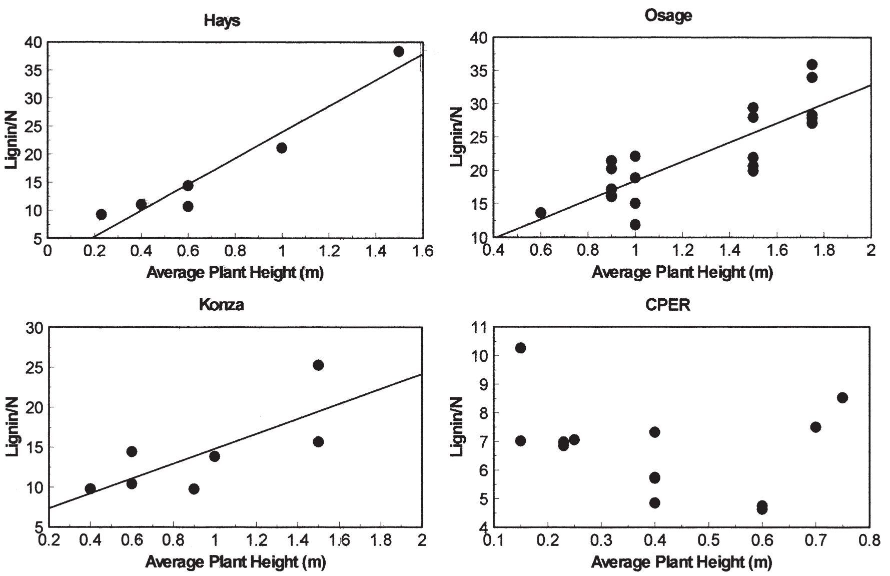

Fig. 6. The relationship between plant tissue lignin/N and plant height for the grass species occurring at 4 grassland sites: Hays ($r^2 = 0.9302$; $P < 0.0019$); Osage ($r^2 = 0.6886$; $P < 0.0001$); Konza ($r^2 = 0.6536$; $P < 0.0518$); Central Plains Experimental Range ($r^2 = 0.0020$; $P < 0.8637$).

Increased precipitation allows plants to utilize nitrogen more efficiently, thereby fixing more carbon per unit nitrogen (Field et al. 1983; Vinton 1994). The plants also produce greater amounts of structural material (i.e. lignin) in order to become more competitive for light in this environment. Increasing precipitation thus invokes processes within plants that produce low quality litter (Vinton 1994; Vitousek et al. 1994). We found that C/N, lignin/N, and percent lignin increased substantially with increasing plant height. These patterns of litter quality across plant functional and morphological types suggest that any changes in species distribution due to shifting climate may have important impacts on ecosystem functioning.

While we are suggesting that litter quality changes as a function of both precipitation and plant height, these variables are confounded in the central grassland region. That is, the occurrence of tall-grass species increases with increasing precipitation (Sims et al. 1978). In order to separate these effects, we analysed (1) single species at a series of sites and (2) single sites for a series of species. Litter quality decreased with increasing precipitation across sites for *Agropyron smithii*, *Bouteloua gracilis* and *Panicum virgatum*. This trend is not universal as suggested by the lack of a relationship between *Andropogon gerardi* and precipitation, but in general, our earlier observation held. Similarly, the trend of decreasing litter quality as a function of increasing plant height held for most of the sites, with Central Plains Experimental Range being one of the few exceptions. We conclude that litter quality varies among species and that some of this variation is attributable to plant height.

As with many regional meta-data analyses (Burke et al. 1998), our study has several limitations: methodologies varied across sites; tissue chemistry data do not reflect senesced litter; data are for representative species of each site and not whole plant communities; and the averaged climatic data for each site may represent different years. Perhaps our results might best be presented as pilot data for a formal hypothesis regarding the control over litter quality by climate. However, we note that although the methods and timing are variable among sites, the relationships of tissue chemistry with precipitation were still robust enough to show significance.

This study suggests that, on a regional basis, changes in climate can have an important impact on litter quality, and presumably on the ecosystem processes that depend on it. Many predictions of climatic change focus on the impact on ecosystem processes, such as primary production and decomposition, while ignoring potentially important feedbacks (Esser 1990; Melillo et al. 1993). For example, decomposition is controlled not only by climate but also by litter quality. If changes in climate produce changes in litter quality by altering plant physiological processes or by changing species composition, predictions of decomposition based solely on changing climate will be in error (Smith & Shugart 1993; Zak et al. 1993; Schimel et al. 1994). We submit that including the effect of climatic change on plant species or functional type composition and litter quality will provide us with a more comprehensive understanding of the effect of global change on ecosystem processes.

Acknowledgements. The National Science Foundation Shortgrass Steppe Long Term Ecological Research Project (BSR 90-11659) supported this work. We thank J. Blair, J. Knops, and W. Parton for their assistance with data acquisition. We also thank H. Epstein and P. Chapman for their assistance with the statistical analysis.

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Received 17 January 2001;
Revision received 20 January 2002;
Accepted 28 March 2002.
Coordinating Editor: P.S. White.