DISSERTATION

THE INFLUENCE OF INDIVIDUAL PLANTS ON SOIL NUTRIENT DYNAMICS IN THE CENTRAL GRASSLAND REGION OF THE UNITED STATES

Submitted by

Mary Ann Vinton

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

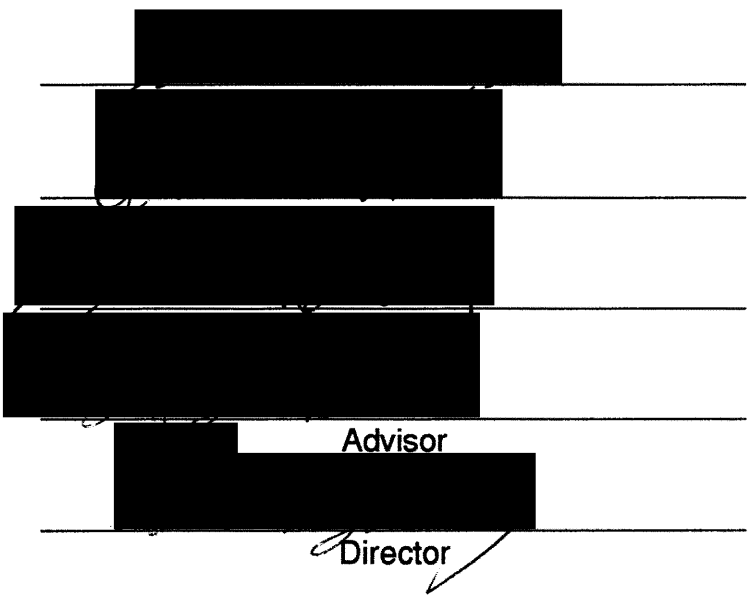
Summer 1994

COLORADO STATE UNIVERSITY

July 1, 1994

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY MARY ANN VINTON ENTITLED THE INFLUENCE OF INDIVIDUAL PLANTS ON SOIL NUTRIENT DYNAMICS IN THE CENTRAL GRASSLAND REGION OF THE UNITED STATES BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work



ABSTRACT OF DISSERTATION

THE INFLUENCE OF INDIVIDUAL PLANTS ON SOIL NUTRIENT DYNAMICS IN THE CENTRAL GRASSLAND REGION OF THE UNITED STATES

The extent to which plant community structure influences ecosystem nutrient cycling is an important but poorly understood element of ecosystem ecology. I studied the effects of two aspects of vegetation structure, plant cover patterns and plant species composition, on nutrient cycling in soils of shortgrass-steppe, mid- and tallgrass prairie, and desert grassland in the Great Plains. My general objective was to identify the importance of plant cover patterns and species composition, especially in the context of other environmental variables, to soil nutrient dynamics in these grasslands.

In the dry shortgrass-steppe and desert grasslands, plant cover patterns were very important in determining patterns of soil nutrient dynamics. Soils under plants had generally higher rates of carbon and nitrogen pool sizes and turnover rates than soils from adjacent bare ground areas between plants. Individual plant characteristics, such as lifespan and growth form, explained the degree of soil heterogeneity in some cases, with the most long-lived, productive species fostering the most plant-interspace soil heterogeneity. Also, abiotic

environmental variables explained patterns in plant-induced soil heterogeneity. The desert grassland with the largest proportion of bare ground, and thus possibly the most soil erosion, had the largest plant-interspace soil heterogeneity. The wet grasslands, the mid- and tallgrass prairies, had more continuous plant cover; thus plant cover did not impose strong control over soil nutrient patterns in these ecosystems.

Plant litter quantity and quality of tissue for decomposers differed between species and grassland ecosystems and, in some cases, affected soil nutrient cycling. *Kochia scoparia*, an introduced species in shortgrass steppe, had high quality tissue (low carbon:nitrogen and lignin:nitrogen) and had relatively high rates of nitrogen and carbon mineralization in its soils. Precipitation affected plant tissue quality, with a general decrease in average quality and increase in inter-species variation in quality from dry to wet grasslands.

Vegetation structure, and its interaction with site-based abiotic variables such as precipitation, had important effects on soil carbon and nitrogen dynamics in these grassland ecosystems. Results indicate that information about plant community structure may be critical to large-scale estimates of ecosystem function.

Mary Ann Vinton
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Summer 1994

ACKNOWLEDGEMENTS

Many people have fostered and enriched my graduate education at Colorado State University. First, I want to express my sincere appreciation to my advisor, Dr. Ingrid Burke, for her many contributions to my academic and personal development. She helped shape much of my thinking about scientific issues and her unflagging enthusiasm for ideas helped me maintain my excitement for scholarly activity. I gratefully acknowledge her guidance and support throughout my program. We enjoyed many wonderful conversations about political and sociological issues in science, particularly the role of women in science. Indy's openness and willingness to share her experiences helped me gain perspective and insights not otherwise possible.

I want to acknowledge my graduate committee, Drs. Debra Coffin, Jim Detling, Dan Binkley and Chuck Grier for their constructive comments and advice on my work, and their willingness to tailor their requirements to better fit my needs and goals. Also, I want to thank Drs. William Lauenroth, Osvaldo Sala, Tim Seastedt and Dean Urban for their useful advice and their contributions to my work.

I have many people to thank for technical advice and assistance. Dr. Phillip Chapman helped with statistical analyses of my data. Dan Reuss, Paul

Hook, Serita Frey, Neal Scott and Mark Lindquist provided advice on laboratory and field methods. I want to thank Tamiko Ihori, Howie Epstein, Martin Aguiar, Julie Faire and Amy Rupp for their good humor and help on field trips. I am very grateful to Lea Spears, for her tireless dedication to completing routine laboratory work. Thanks go to Carole Travis for her flexibility and willingness to help me with budget matters.

My friends and fellow graduate students enlivened and enriched my time here at CSU, by providing stimulating and enjoyable conversation and much-needed moral support. I am very grateful to all of them: Laura Stump, Neal Scott, Paul Hook, Mike Arbaugh, Tamiko Ihori, Diana Garcia, Carol Miller, Dave Bluhm, Chuck Rhodes, Xiaoming Zou, Maurya Faulkner, Robin Kelly, Marcos Robles, Tamera Minnick, Diana Lane and others. I want to particularly thank Laura Stump, Maurya Faulkner and Robin Kelly for their emotional support and willingness to share their insights, as well as listen to my views, on career and women's issues. I also want to thank Paul Hook and Neal Scott, both members of my graduate school "cohort", for particularly useful support and advice. I am very grateful to Drs. Frank Vattano and Jack Avens for their ardent love of teaching and scholarly service, and for reminding me that academia can be a very honorable and worthwhile pursuit.

I want to acknowledge sources of financial support for this project. I received funding from a National Science Foundation (NSF) Doctoral

Dissertation Improvement Award (DEB-9213180) and NSF grant BSR-8114822 for the shortgrass steppe Long-Term Ecological Research Program.

Finally, I want to express my deepest gratitude to my husband, John Noble. His empathy, patience and enthusiasm, as well as his unwavering love and support, contributed greatly to my successful completion of graduate study.

TABLE OF CONTENTS

I. INTRODUCTION

The relationship between ecosystem structure and function is a dominant theme of ecological research and a current manifestation is the wide-spread interest in the effects of plant community structure on ecosystem function (e.g. Mooney and Schulze 1993). Several lines of evidence suggest that plant community structure might be critical to our understanding of aspects of ecosystem function, such as soil nutrient dynamics. One line of evidence is comprised of the numerous studies suggesting that plant species composition can be an important factor in determining nutrient cycling patterns in soils (Pastor and Post 1986, Johnson and Damman 1991, Tilman and Wedin 1989). Physiological attributes of plants such as growth rate, biomass allocation and tissue chemical composition appear to be important in regulating soil nutrient cycling. These physiological attributes frequently differ between plant species or growth forms (Chapin 1993), and may be the mechanism by which plant species differentially affect nutrient cycling.

Another aspect of vegetation structure that can be important in influencing soil nutrient dynamics is that of plant cover patterns. In arid to semi-arid areas, patterns of plant-covered microsites vs. bare-ground microsites are a major determinant of soil nutrient patterns (Charley and West 1975, 1977,

Burke 1989, Burke et al. 1989, Schlesinger et al. 1990, Hook et al. 1991). This pattern is attributed to plants collecting resources from a large rooting radius, and depositing those resources as aboveground and belowground litter in a smaller radius beneath the plant. Also, physical erosional processes can result in depletion of soil resources in bare areas between plants, or net movement of resources from bare soil areas to canopy-covered areas. Patterns of plant cover may differ between species because of life history or growth-form differences. For example, short-lived plants with high recruitment rates may confer less spatial heterogeneity on soil properties than long-lived plants which occupy the same location year after year. Also, growth forms with highly localized points of aboveground biomass, e.g. bunchgrasses, may confer more heterogeneity on soil nutrients than growth forms with more diffuse, evenly distributed biomass, e.g. rhizomatous grasses.

I studied the effects of these two aspects of vegetation structure, plant cover patterns and plant species composition, on ecosystem nutrient cycling in soils of central United States grasslands. My general objective was to identify the importance of plant cover patterns and species composition, especially in the context of other environmental variables, to soil nutrient dynamics in these grasslands.

My objective in the first study was to test the effects of a variety of plant species and lifeforms, as well as their cover patterns, on soil nutrient cycling on a local- and plot-scale in shortgrass-steppe grasslands. I used historically

fertilized and watered plots which had undergone large changes in vegetation structure to see if feedbacks between vegetation structure and soil properties persisted through time. I hypothesized that demographic and physiological characteristics of plants would be related to the amount and spatial pattern of soil organic matter across the landscape. Furthermore, I tested the importance of these local, plant-induced soil patterns to soil patterns at a larger, plot scale. This study is described in Chapter 2.

My objective in the second study was to test the effects of precipitation on the plant-soil patterns that I had observed in the first study. In particular, I was interested in testing the regional generality of the ideas and their dependence on water availability. Consequently, I sampled plants and soils in three sites along a precipitation gradient in the central Great Plains. My central hypothesis was that the importance of plant cover patterns to soil properties would decrease from the semi-arid grassland to the sub-humid grassland, while the importance of plant tissue chemistry would increase along this gradient. This study is described in Chapter 3.

The results of my first two studies emphasized the importance of plant-induced soil heterogeneity, especially in semi-arid grasslands. For my third study, I was interested in testing the dependance of this plant-induced soil heterogeneity on plant species characteristics (such as lifespan and productivity) and the interaction between these species characteristics and site-based abiotic variables. I studied the plant-soil patterns associated with two species of

Bouteloua over a temperature gradient reflecting the extremes and the shared sites in the geographic distribution of the two species. These three sites ranged from arid desert grasslands to semi-arid shortgrass steppe. The two species were similar lifeforms (warm-season, perennial bunchgrasses) but previous studies suggested that they had different lifespan and dispersal characteristics (Lauenroth et al. in press). I expected these differences to result in different degrees of plant-induced soil heterogeneity. Also, I expected site characteristics, by affecting plant productivity and erosional characteristics, to interact with the species differences to determine plant-soil patterns in these ecosystems.

LITERATURE CITED

Burke, I.C., W.A. Reiners, and D.S. Schimel. 1989. Organic matter turnover in a sagebrush steppe landscape. Biogeochemistry 7:11-31.

Burke, I.C. 1989. Control of N mineralization in a sagebrush steppe landscape. Ecology 70(4): 1115-1126.

Chapin, F.S. 1993. Functional role of growth forms in ecosystem and global processes. *in* J.R. Ehleringer and C.B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, London.

Charley, J.L., and N.E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. Journal of Ecology 63: 945-963.

Charley, J.L., and N.E. West. 1977. Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. Soil Biology and Biochemistry 9: 357-365.

Hook, P.B., I.C. Burke, and W.K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North

American shortgrass steppe. Plant and Soil 138: 247-256.

Johnson, L.C. and A.W.H. Damman. 1991. Species-controlled Sphagnum decay on a South Swedish raised bog. Oikos 61: 234-242.

Lauenroth, W.K., D.P. Coffin, I.C. Burke, and R.A. Virginia. in press. Interactions between demographic and ecosystem processes: a challenge for functional types. *in* T.M. Smith, I.A. Woodward and H.H. Shugart, editors. Plant Functional Types. Cambridge University Press, Cambridge.

Mooney, H.A., and E. Schulze. 1993. Biodiversity and ecosystem function. Springer Verlag. New York. 525 p.

Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycle. Biogeochemistry 2: 3-27.

Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.G. Whitford. 1990. Biological feedbacks in global desertification. Science 247: 1043-1047.

Wedin, D.A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84: 433-441.

II. INTERACTIONS BETWEEN INDIVIDUAL PLANT SPECIES AND SOIL NUTRIENT STATUS IN SHORTGRASS-STEPPE

ABSTRACT

The extent to which community structure (i.e. plant species composition and distribution) interacts with nutrient cycling is fundamental to our understanding of ecosystem function. I examined plant-soil interactions and tested the importance of individual plant species identity and plant presence vs. absence on nutrient cycling in semi-arid shortgrass-steppe of northeastern Colorado. The shortgrass steppe has both discontinuous plant cover and a variety of plant species and lifeforms; I tested the effects of both plant cover (i.e. plant covered microsites vs. bare soil) and different species on soil nitrogen and carbon cycling. I tested these effects in an area of undisturbed shortgrass-steppe as well as an area that had undergone nitrogen and water additions from 1971-1974, resulting in significant shifts in plant species composition.

The presence of plant cover had strong effects on soil properties, with soil under plants having consistently higher rates of carbon and nitrogen mineralization, and in some cases, higher levels of total C and N and microbial biomass C and N, than soils from bare ground between plants. Four native, perennial grasses, one native sedge and one native shrub differed from one

another in the quantity and quality of above- and belowground biomass but differences among the six species in soil nutrient cycling under their canopies were slight. However, soils under bunchgrasses tended to have higher rates of carbon mineralization and higher levels of microbial biomass carbon than soil under the rhizomatous grass, *Agropyron smithii.* Also, the one introduced annual in the study, *Kochia scoparia*, differed from the other species significantly, both in the degree of plant-induced soil heterogeneity and in soil nutrient cycling properties. Soils associated with *Kochia scoparia* had less plant-induced heterogeneity and higher rates of carbon and nitrogen mineralization as well as higher levels of microbial biomass carbon than soils associated with the other species. This species was abundant only on the historical water and nitrogen addition plots (where it has persisted in the absence of resource additions for 20 y), suggesting a positive feedback between plant species persistence and soil nutrient status.

Plant cover patterns had larger effects on ecosystem-scale estimates of soil properties than the attributes of a particular plant species. In this semi-arid ecosystem, the importance of plant presence may overshadow that of plant species in ecosystem-level soil process estimates because 1) plant presence is discontinuous and 2) decomposition and nutrient availability are primarily limited by water, not by plant species-mediated characteristics such as litter quality. That local plant-induced patterns in soil properties significantly affected ecosystem scale estimates indicates that consideration of structural attributes,

particularly plant cover patterns, is critical to estimates of ecosystem function in shortgrass steppe.

INTRODUCTION

Individual plant characteristics, such as lifespan, biomass allocation and tissue chemical composition have been shown to have significant effects on ecosystem processes such as soil organic matter and nutrient dynamics (Melillo et al. 1982, Pastor et al. 1984, Pastor and Post 1986, Vitousek et al. 1987, Berendse et al. 1989, Matson 1990, Binkley and Valentine 1991, Johnson and Damman 1991). Many of these studies showing significant plant species effects on nutrient cycling have been conducted in forests or in systems undergoing primary succession. Recent work in tallgrass prairie suggests that grass species have differential effects on nutrient availability, with important potential consequences for species interactions and successional processes (Tilman 1986, Inouye and Tilman 1988, Wedin and Tilman 1990, Tilman and Wedin 1991). In dryer shrub and grassland ecosystems, individual plants concentrate biomass in soils beneath their canopies, forming islands of soil fertility (eg. Charley and West 1977). Individual plants, both by virtue of their tissue quantity and quality, as well as their presence in systems with sparse plant cover, may play important roles in ecosystem-level nutrient cycling.

The importance of these plant species-ecosystem relationships lies in the potential for positive feedbacks to exist between species and ecosystem

variables, for example between species litter quality and decomposition rate (Pastor and Post 1986, Hobbie 1992), and thus for species-induced changes to persist and be important regulators of ecosystem structure and function. Pastor and Post (1986) used a simulation model of forest nutrient cycling to demonstrate that feedbacks between plant species litter characteristics and soil nutrient levels have important implications for forest species dynamics and ecosystem development through time. This feedback potential is particularly important for systems undergoing significant changes in species composition, such as those resulting from human intervention or global climate change.

Individual plant canopy presence or absence can also be an important cause of small-scale patterns of nutrient availability (Charley and West 1977, Robertson et al. 1988, Burke 1989, Burke et al. 1989, Jackson and Caldwell 1993). In arid to semi-arid areas, patterns of plant-covered microsites vs. bare-ground microsites are a major determinant of soil nutrient patterns (Charley and West 1977, Bolton et al. 1990, Schlesinger et al. 1990), and may affect subsequent plant establishment (Padien and Lajtha 1992). In shortgrass steppe, patterns in plant presence or absence of the dominant plant species have significant effects on patterns of microbial activity and nutrient availability (Hook et al. 1991). Population factors (i.e. seed dispersal and plant lifespan), by influencing the spatial patterning and turnover of plants, may determine the degree of spatial heterogeneity in resource availability (Lauenroth et al. in press) and, potentially, ecosystem stability (Schlesinger et al. 1990).

The literature summarized above on individual plant effects on soil properties can be divided into two groups: 1) studies on the relationships and feedbacks between plant tissue chemical content and soil nutrient availability and 2) studies, largely in semi-arid to arid areas with discontinuous plant cover, relating plant canopy presence to properties of the soil beneath the canopy. In the shortgrass-steppe of northeastern Colorado, both discontinuous plant cover and a mix of plant lifeforms and species are present, allowing for both plant presence as well as plant lifeform and tissue chemistry to have important effects on soils. This system is characterized by the dominant C_4 bunchgrass, *Bouteloua gracilis*, with a mix of other grasses, forbs and shrubs, with a significant amount of bare ground between individual plants.

Our primary objective in this study was to examine the influence of individual plants, by virtue of their species identity and their physical presence, on the local pattern of carbon and nitrogen cycling in the soil of shortgrass steppe. I was interested in determining what characteristics of individual plant species, such as tissue chemical composition, biomass allocation or life history qualities, were most important in explaining effects on soil properties. I expected plant litter characteristics such as lignin, lignin to nitrogen ratios or carbon to nitrogen ratios would reflect litter quality for decomposers and thus explain patterns in decomposition rate and nutrient availability (Melillo et al. 1982). Similarly, I expected plant production and allocation measures to reflect the amount of material available for decomposition and nutrient release. I

expected plant lifespan to influence the spatial pattern of plants on the landscape through time, with short-lived plants in place for less time than long-lived plants. Plant lifeform should also affect the spatial pattern of biomass on the landscape, with bunchgrasses forming more concentrated locations of biomass than rhizomatous grasses. Thus, I expected both plant lifespan and lifeform to affect the spatial pattern of soil resources.

A secondary objective was to evaluate these plant-soil relationships in the context of a major historical disturbance to soil resources, the addition of water and nitrogen from 1970-1974, which may have significantly changed these plant-soil relationships. The addition of these resources changed species composition dramatically, and some of the changes persisted into the current time, 20 years after the resource addition ceased. This persistent response represents a potential example of a positive feedback between plants and soils, i.e. soil fertility was enhanced via artificial additions, plant species composition or physiology changed in response to the enhanced resources and in turn, plants may have subsequently altered or maintained this enhanced resource regime. Comparisons of species effects on soils in the unaltered plots versus species effects on soils in the historically resource-amended plots indicate how native, shortgrass steppe species influence soils under more or less "steady state" conditions as well as how plant species and soils interact under a perturbed nutrient regime.

Our third objective was to examine the importance of these local plant-

induced effects on soils for determining larger-scale (1 ha) estimates of ecosystem processes. If individual plant species do indeed affect local patterns of soil carbon and nitrogen dynamics, how do these small-scale, plant-induced patterns scale up to ecosystem-level nitrogen and carbon budgets? To estimate large-scale budgets, is it necessary to sample small-scale heterogeneity? Again, I evaluated this question in the context of the historical resource disturbance to see if, under dynamic resource and plant conditions, the action of individual plant species could contribute to significant changes in soil carbon and nitrogen levels and turnover rates.

METHODS

Site Description

Studies were conducted at the Central Plains Experimental Range (CPER, 40°49'N latitude, 107°46'W longitude), 61 km northeast of Fort Collins on the north-central Colorado piedmont. The mean annual precipitation at the site is 309 mm and mean monthly temperatures range from -3°C in January to 22°C in July (Parton and Greenland 1987). The vegetation of the area is typical of shortgrass steppe and is dominated by the perennial bunchgrass, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths. Other common species include the perennial grass, *Buchloë dactyloides* (Nutt.) Engelm.; the half-shrubs, *Gutierrezia sarothrae* (Pursh) Britt. & Rusby and *Artemisia frigida* Willd.; the forb, *Sphaeralcea coccinea* (Pursh) Rydb.; and the succulent, *Opuntia polyacantha*

Haw. All plant nomenclature follows the Great Plains Flora Association (1986).

We sampled plants and soils on an area that was part of a fertilization and irrigation experiment in the early 1970's (Lauenroth and Dodd 1978). The experiment consisted of a factorial combination of four treatments with two replicates: control (no resource addition), water (W), nitrogen (N) and nitrogen+water (NW) additions. The eight cells of the design were contiguous plots of 1 ha each, randomly assigned within the two blocks. Water and nitrogen fertilizer were applied from 1970 to 1974. Water was applied to maintain soil water potential at a depth of 10 cm between 0 and -0.08 MPa from 1 May to 1 September (Lauenroth and Dodd 1978). Soil water was checked daily and, if needed, water was added at night with sprinklers. The amount of water added per year ranged from 458-707 mm (Lauenroth and Dodd 1978). Nitrogen fertilizer (33% nitrogen as ammonium nitrate) was added to maintain a difference between the treatment and control plots of at least 50 kg/ha of soil mineral nitrogen (NO_3^- + NH_4^+). This resulted in addition of 100-200 kg/ha of nitrogen to the nitrogen treatment plots in each of the four years. Water and nitrogen additions were stopped in 1974 and since then, except for some vegetation and soil sampling, the plots have been unaltered. The plots have been protected from cattle grazing since 1968.

The major effects of resource additions were a 5-10 fold increase in net primary production and large changes in species composition via colonization by alien species and shifts in the relative dominance of native species

(Lauenroth et al. 1978, Dodd and Lauenroth 1978, Lauenroth and Dodd 1979). When resource additions were stopped, the plant community in the treated areas had reached a new state in terms of relative abundance of species (Lauenroth et al. 1978, Dodd and Lauenroth 1978, Lauenroth and Dodd 1979) which has persisted, with some fluctuations in species relative abundance, into the present time (Milchunas et al. 1990, Milchunas and Lauenroth in review).

Tissue Sampling and Analyses

We sampled plant tissue and soils under plants of 5 species on each of the historical treatment plots (Table 2.1). These species were selected because they represented the majority of the biomass on the plots and because they represented a variety of lifeforms. The species were: *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, a perennial C_4 bunch grass; *Aristida longiseta* Steud., a perennial C_4 bunch grass; *Stipa comata* Trin. & Rupr., a perennial C_3 bunch grass; *Agropyron smithii* Rydb., a perennial C_3 rhizomatous grass; and *Artemisia frigida* Willd., a perennial half-shrub. Two other species, *Carex eleocharis* Bailey, a perennial C_3 sedge, and *Kochia scoparia* (L.) Schrad., an annual C_4 forb, were sampled only on the NW historical treatment plots. These two species were abundant on the NW historical treatment plots, but were rare or not present in the other plots (Table 2.1).

Aboveground biomass and cover estimates were obtained for each target species by randomly locating six 0.1 m^2 rectangular quadrats along transects

in each replicate of the historical treatment plots. I estimated percent basal cover, counted the number of individuals and clipped all aboveground plant material of each target species in each quadrat. The plant material was sorted into leaves, stems and seeds and was dried at 55°C for 48 h before weighing.

Belowground biomass was sampled by removing a 2.2 cm diameter, 30 cm deep core from the soil immediately underneath each plant. Cores were taken from 32 individuals of each species on each plot of only one replicate of the historical treatment area. One transect was formed diagonally across each 1 ha historical treatment plot, and individual plants were chosen along the transect in a stratified, random manner at sixteen locations. Root cores from two individual plants at each of the sixteen locations were composited to provide enough root material for each sample. The belowground plant material was separated from the soil with the flotation method of Lauenroth and Whitman (1971), using a 0.5 mm mesh sieve to catch fine roots. Roots were separated from culms or stem bases and all parts were dried at 55°C and weighed. The roots and stem bases were ground in a Wiley mill to pass through #40 mesh and subsamples were ashed at 550°C.

Total percent carbon and nitrogen were determined on both aboveground and belowground plant tissue using a Carlo-Erba automated combustion analyzer. Lignin analyses were conducted on composited subsets of the tissue samples, using a modified Van Soest (1963) procedure (Waldern 1971).

Soil Sampling and Analyses

We sampled soils directly under plants of each species and in adjacent openings between plants by taking 5 cm diameter, 10 cm deep soil cores. Samples from between plants were taken on bare ground at least 10 cm away from the target plant and neighboring plant canopies. Samples from under plants were taken at the location where a stem or a group of stems emerged from the soil. I took "under" and "between" cores from a total of 4 plants of each species, randomly located along transects, from each replicate of the historical treatment plots. Cores from two plants were composited for the laboratory analyses. This resulted in four soil samples analyzed for each historical treatment*species*position combination. Soil samples were placed in coolers immediately and were transported to a laboratory refrigerator within 7 hours after collection. All fresh soil analyses were performed within 3 days after collection.

Fresh soils were sieved to separate plant material and fragments greater than 2 mm in diameter. The soils were then weighed, mixed and subsampled for 4 analyses: water content, initial inorganic N, incubations to determine potential net N and C mineralization, and microbial biomass N and C. Inorganic N was extracted from a 10 g subsample with 50 ml of 2 N KCl (with phenylmercuric acetate added to prevent microbial growth) for 30 min on an orbital shaker to measure initial inorganic N. The extracts were allowed to settle for 10 min and were filtered through Whatman #40 paper. The extracts were

refrigerated until analyzed for nitrate and ammonium on a Lachat autoanalyzer (EPA 1979).

For the soil incubation, a 25 g subsample was placed in a small beaker, brought to field capacity with deionized water and placed in a closed mason jar with 20 ml of deionized water in the bottom to maintain a saturated atmosphere (Schimel 1986). Five ml of 2 N NaOH in a small vial was added to the jar to serve as a base trap for CO_2 respired by soil microbes (Schimel 1986). The samples were incubated at 25°C for 30 days. At the end of the incubation, soils were extracted with KCl, filtered and analyzed for nitrate and ammonium as described above. The base trap was titrated with 1 N HCl to determine the amount of CO_2 released during incubation, or the potential C mineralization (Snyder and Trofymow 1984). Potential net N mineralization was calculated as the difference between initial and final inorganic N of the soil.

The chloroform fumigation-extraction procedure (Powlson and Jenkinson 1976 and Brookes et al. 1985) was used to measure microbial biomass in the soil samples. A 10 g subsample of fresh, sieved soil was extracted with 50 ml of 0.5 M K_2SO_4 for 30 min on a 200 rpm orbital shaker and filtered through Whatman #40 paper. Another 10 g subsample of soil was fumigated with chloroform for 18 h, vented for 5 h, and extracted and filtered as described above. The control and fumigated soil extracts were frozen until they could be analyzed. Samples were thawed in warm water, agitated for 10 minutes and allowed to settle overnight before they were analyzed the following day.

Microbial biomass nitrogen was analyzed by the ninhydrin method (Amato and Ladd 1988). Microbial biomass carbon was obtained by a wet oxidation diffusion procedure (Snyder and Trofymow 1984) performed on the extracts. The air-dried soil samples were ground and dried at 55°C before total carbon and nitrogen contents were measured using a Carlo-Erba automated combustion analyzer.

Statistical Analyses

For all of the soil response variables, the experimental design was treated as a split-split plot with historical treatment as the whole plot factor (with the whole plot factor being a randomized complete block), species as the sub-plot factor and position (under vs between) as the sub-sub-plot factor. I used the GLM procedure in SAS (SAS Institute 1985) to perform a 3-way analysis of variance (ANOVA) on the data. I used transformed data when necessary to satisfy the assumptions of the ANOVA. When ANOVA indicated a significant effect, I tested differences between means with techniques specific to split-split plot designs (Gomez and Gomez 1984), and the Scheffe procedure. I used contrast statements for specific comparisons between watered and unwatered plots (i.e. the W and NW plots vs. the control and N plots) and fertilized vs. unfertilized plots (i.e. N and NW vs. the control and W plots). In the statistical analyses of soil variables, I tested for the effects of the five species sampled across the historical treatment area by restricting the analysis only to soils taken

from under plants. This resulted in a split plot design, with historical treatment as the whole plot factor and species as the sub-plot factor. I used planned contrasts to analyze species lifeform effects (e.g. bunchgrass vs. non-bunchgrass and C_4 vs. C_3) on soil properties.

For the aboveground biomass and tissue chemistry response variables for the five species on all historical treatment plots, the design was a split plot with historical treatment as the whole plot factor (the whole plot being a randomized complete block) and species as the sub-plot factor (Table 3).

We tested statistical hypotheses about the two species (*Carex eleocharis* and *Kochia scoparia*) that only occurred on the NW historical treatment plot by restricting the analysis to the NW plots. In this case, the design for the soil response variables was a split plot with species as the whole plot factor and position as the sub-plot factor. I used planned contrasts to compare the effects of the annual *Kochia scoparia* to the effects of the other, perennial species on soil properties. For the aboveground mass and tissue chemistry response variables, the design was a randomized complete block with the two NW replicates forming the blocks and species being the factor of interest.

For belowground mass and tissue chemistry response variables, I sampled only one of the historical treatment replicates, due to time constraints on root washing and sorting. I considered the historical treatment as the whole plot factor and the species as the subplot factor in a split plot design. In this case, I had no replication of the historical treatment, so statistical inferences

about the effects of historical treatment on belowground mass and tissue chemistry cannot be made. However, I spatially replicated as much as possible, by sampling 32 individuals across each entire historical treatment plot (1 ha), so inferences about historical treatment are unlikely to be affected by errors from local plot effects.

Ecosystem-level estimates of local plant-soil patterns

To estimate the impact of individual plants and species on larger-scale ecosystem properties, I scaled up the individual plant-level soil data using information about soil properties under and between plants and information about the relative cover of the plant species and bare ground in the historical treatment area (Table 2.1). I obtained the estimates of plant species cover using my own cover data (methods described above) and data from another study (Daniel Milchunas, pers. comm.), that provided an estimate of the relative cover of bare ground on each treatment plot. I standardized percentage basal cover estimates for the five species (seven in the NW historical treatment plots) plus bare ground to 100%. I neglected the other species in the estimates since the 5-7 sampled species represent >80% of plant cover in the plots (Daniel Milchunas, pers. comm.).

We calculated three estimates of ecosystem-level soil properties for each of the historical treatment areas. The first estimate, the "Bare Soil Estimate" is the "between" canopy soil properties applied to the entire area and represents

the scaled-up soil property in a plot without the influence of individual plants. However, Bare Soil Estimate values could be affected by past influence of plants, since currently "between" microsites could have been occupied by plants in the past. This is especially likely in the historical nitrogen and water addition plots. In many nutrient cycling studies of systems with discontinuous plant cover, only soils between plants are sampled, yet results are scaled up to represent the entire ecosystem, bare as well as plant-covered areas. Thus, this estimate is useful in demonstrating the implications of such a technique. The second estimate, the "Plant Estimate", is the sum of average properties of soils under all plants, multiplied by the average plant cover, and the average properties of soils between plants multiplied by average bare ground cover. The Plant Estimate takes into account the soil properties under the canopies of plants as well as the soil properties in the "between microsites", but does not take into account the cover or nutrient cycling differences among species. The third estimate, the "Species Estimate", is the sum of the average soil property under each species, multiplied by the percent cover of that species, and the average between-plant soil property, multiplied by percent cover of bare ground. Thus, the Species Estimate takes into account not only average plant effects, but the different effects that plant species, by virtue of their cover and nutrient cycling properties, may have on ecosystem-level soil properties. These different scaling techniques represent a range of information, from no information (Bare Soil Estimate) to detailed information (Species Estimate), about current plant-

and species-specific effects on soil processes. Comparing results from the different estimates allowed us to assess the contribution of plant-specific information to ecosystem level conclusions. I used a 2-way ANOVA to see if historical treatment or estimate method significantly affected the results (Table 4).

RESULTS

Plant and soil patterns on the control plots

Soil properties were affected by the five native, shortgrass species, and these effects were consistent over the historical treatments, i.e. there were no historical treatment*species interactions except for microbial biomass carbon (Table 2.2). Therefore, I will restrict the presentation of the effects of the five native, shortgrass species on soils to only the soils in the unaltered shortgrass-steppe (Fig. 2.1). The five native shortgrass species did not differ from one another in their effects on total soil pools of carbon or nitrogen in soils beneath their canopies (Fig. 2.1a and 2.1b). Species did differ in their effects on C mineralization, with the bunchgrass, *Stipa comata*, having significantly higher C mineralization rates in soils under its canopy than did the rhizomatous grass, *Agropyron smithii* (Fig. 2.1c). Also, soils under the bunch grasses, *Stipa comata*, *Aristida longiseta*, and *Bouteloua gracilis*, collectively had significantly higher carbon mineralization rates than did the soils under *Agropyron smithii* (Fig. 1c). Species identity had no effect on potential nitrogen mineralization rate

or microbial biomass nitrogen (Fig. 2.1d and 2.1f). Microbial biomass carbon showed a response similar to carbon mineralization rates, with the rhizomatous grass having one of the lowest levels in its soils (Fig. 2.1e).

More striking differences existed between species in their biomass quantity and quality (Table 2.3, Fig. 2.2) than in soil properties under their canopies (Table 2.2, Fig. 2.1). The shrub, *Artemisia frigida*, had significantly more aboveground biomass than the grass species, with the exception of *Stipa comata* (Fig. 2.2a). The tall bunchgrass, *Stipa comata*, had the most aboveground biomass among the grasses. The dominant grass species of the shortgrass steppe, *Bouteloua gracilis*, had significantly more total belowground biomass than the other species (Fig. 2.2b). All of the bunchgrasses and the shrub had more belowground biomass than the rhizomatous grass, *Agropyron smithii* (Fig. 2.2b). *Bouteloua gracilis* had much higher root to shoot ratios than the other species, which did not differ significantly from one another (Fig. 2.2c). Plant species also differed in tissue quality, or carbon:nitrogen and lignin:nitrogen ratios of above- and belowground tissue (Table 2.3). *Aristida longiseta* had significantly higher leaf C:N ratios than the other species, and higher root C:N ratio than the other species, with the exception of *Bouteloua gracilis* (Fig. 2.2d and 2.2e). *Agropyron smithii* had significantly higher root lignin/nitrogen ratios than two of the other four species (Fig. 2.2f).

Plant position (under vs. between plants) exerted a strong and consistent effect on pools and turnover rates of soil carbon and nitrogen in unaltered

shortgrass steppe (Table 2.2, Fig. 2.1). Soils under plants had significantly higher rates of carbon and nitrogen mineralization and significantly more soil carbon, nitrogen and microbial biomass nitrogen than soils from between plants (Fig. 2.1). Although species*position was not statistically significant for all the historical treatment plots, on the control plots the contrast in the between and under plant positions was greater for bunchgrasses than non-bunchgrasses.

Plant and soil patterns on the NW plots

The historical NW plots had very different relative abundances of species than the historically unaltered control plots (Table 2.1). The NW plots had much of the plant cover composed of the species, *Kochia scoparia* and *Carex eleocharis*, and correspondingly much less cover was composed of the other native shortgrass steppe species than in the control plots (Table 2.1). The non-invasive species in general had the same relative ranking in biomass quantity and quality on the NW plots as on the control plots (Fig. 2.2 and 2.3). However, there were some exceptions, and these contributed to the significant historical treatment*species interaction in the ANOVA for plant characteristics (Table 2.3). On the control plots, *Bouteloua gracilis* had much more belowground biomass than the other species, but on the NW plots, the amount of belowground biomass of *Bouteloua gracilis* was less than or similar to that of the other 5 native species (Fig. 2.2b and 2.3b). Also, *Agropyron smithii* had less aboveground biomass than most of the other species on the control plots, but

ranked relatively high in aboveground biomass among the five native species on the NW plots (Fig. 2.2a and 2.3a). Although plants on the NW plots in general had lower tissue C:N than plants on the control plots, the relative rankings of the species tissue chemistry were similar between the control and NW plots (Fig. 2.2 and 2.3).

The major difference, between the control and NW plots was the presence of the two invasive species on the NW plots and their virtual absence on the control plots. Thus, I compared the influence of the two invasive species, *Kochia scoparia* and *Carex eleocharis*, to the influence of the other five species on plant and soil characteristics, all on the NW plots (Fig. 2.3 and 2.4). *Kochia scoparia* had significantly more aboveground biomass than the other species on the NW plots and both *Kochia scoparia* and *Carex eleocharis* had significantly more belowground biomass per m^2 than the other species (Fig. 2.3a and 2.3b). *Carex eleocharis* had significantly higher root to shoot ratios than the other species (Fig. 2.3c). Both of these invasive species had lower belowground carbon to nitrogen ratios than the other species, except *Agropyron smithii*, (Fig. 2.3d) and both had significantly lower belowground lignin/nitrogen ratios than *Agropyron smithii* and *Bouteloua gracilis* (Fig. 2.3f). Neither invasive species had significantly different effects on total soil carbon or nitrogen in soil beneath their canopies than the other species (Fig. 2.4a and 2.4b). However, soils associated with *Kochia scoparia* had significantly higher nitrogen mineralization rates, carbon mineralization rates and microbial biomass carbon

than soils beneath the other species (Fig. 2.4c, 2.4d and 2.4e).

The effect of position, i.e. the under vs. between plant soil pattern, on soils was much less on the NW plots than on the control plots (Fig. 2.1 and 2.4). Also, *Kochia* had less of a contrast among soils under and between its canopy than did the other species on the NW plots. This trend was significant for carbon mineralization rates and microbial biomass nitrogen levels (Fig. 2.3c and 2.3f).

Plant and soil patterns among all historical treatment plots

Historical resource addition significantly affected current aboveground plant biomass and tissue chemistry of the five species (Table 2.3). Total aboveground biomass was significantly higher on the N plots than on the other plots (Fig. 2.5a). Much of this increase in biomass on the N plots can be attributed to the very large and frequent individuals of the shrub, *Artemisia frigida*, on the N plots; this factor contributed to the significant historical treatment*species interaction effect on biomass (Table 2.3). Total belowground biomass of the five species was significantly lower on the NW plots than on control and N plots, with the W plots having intermediate levels (Fig. 2.5b). Root to shoot ratios were also influenced by historical treatment, with ratios significantly lower on the N plots than on the Control and W plots (Fig. 2.5c). Carbon/nitrogen ratios of plant roots were significantly lower and root lignin to nitrogen ratios showed a lower trend than the ratios on the other plots (Fig. 2.5d

and 2.5f). Carbon/nitrogen ratios of aboveground plant material were significantly lower on the NW plots than the other plots (Fig. 2.5e).

Although the four historical treatment plots were not significantly different from one another in total soil carbon and nitrogen, the plots that had received water (i.e. the NW and the W plots) had higher soil carbon and nitrogen than the those that did not receive water, the control and N plots (Fig. 2.6a). Also, historical treatment interacted with plant position to affect soil carbon and nitrogen (Table 2.2), in that the increase in carbon and nitrogen under plants relative to between plants was less pronounced or reversed in the NW and W plots (Fig. 2.6a and 2.6b). So, the plots that received water had much less of a plant-induced island of fertility effect on soils than the plots that did not receive water. Historical treatment did not affect C mineralization (Fig 2.6c), but again interacted with plant presence (Table 2.2) to affect C mineralization; the NW and W plots had significantly less of a contrast between positions in C mineralization than the other plots (Fig. 2.6c). Historical treatment affected nitrogen mineralization, with the N and NW plots having higher rates of nitrogen mineralization than the control and W plots (Fig. 2.6d). As with total soil pools and carbon mineralization rates, nitrogen mineralization rates were significantly higher in soils from under than from between plants, and the historical addition of water interacted with position (Table 2.2) to significantly decrease this contrast (Fig. 2.6d). No historical treatment main effects were present in microbial biomass carbon or nitrogen (Table 2.2, Fig. 2.6e and 2.6f), but again

the W plots had less of a contrast in between vs. under plant levels of microbial biomass nitrogen.

Ecosystem-level implications of local plant-soil patterns

Soil properties expressed on a local scale, without accounting for cover proportions of plant species and bare ground, did not exhibit many differences among historical treatments (Table 2.2, Fig. 2.6), whereas soil properties expressed on a plot-scale were, in most cases, significantly affected by historical treatment (Table 2.4). The NW plots had significantly more soil carbon and nitrogen on a plot basis than the control plots (Table 2.5). Nitrogen mineralization rates on a plot scale were significantly higher in the NW and N plots than the W and the control plots (Table 2.5). The N plot had higher rates of plot-scale carbon mineralization than the control plot, with the NW and the W plot being intermediate (Table 2.5). The NW plots had significantly higher plot-scale microbial biomass carbon than the W plots with the control and N plots intermediate. Historical treatment did not affect levels of microbial biomass nitrogen on a plot scale (Table 2.4 and 2.5).

Different methods of calculating estimates, i.e. the consideration of individual plant or species effects, did not significantly affect the plot-scale estimates of total soil carbon and nitrogen (Table 2.4). For both carbon and nitrogen mineralization, the estimates incorporating both average plant and plant species information (Plant and Species Estimates) resulted in significantly

higher plot-scale rates than the Bare Soil Estimate, an estimate that considered only bare ground (Table 2.5). The three estimates did not result in different levels of microbial biomass carbon or nitrogen (Table 2.5).

DISCUSSION

Plant species and lifeform effects on soils

This study provided evidence that plant species, via either tissue chemistry, biomass allocation, or lifespan (influencing spatial pattern and turnover on the landscape), affected local soil properties in shortgrass steppe. These species effects, however, were most obvious when species were grouped into categories and compared, i.e. bunchgrass vs. rhizomatous grass or annual vs. perennial; thus grouping species into growth forms or functional types in this system may be an adequate representation of their effects on the ecosystem (see for example Mooney and Schulze 1993, Chapin 1993). Furthermore, the species (*Kochia scoparia*) most clearly different from the rest in terms of its effects on soil properties, was introduced into the native ecosystem as a result of large increases in the soil resource regime; thus it does not play a dominant role in the native, shortgrass-steppe ecosystem. The soil properties affected by most species tended to be the more labile pools, and not the total pools, of carbon and nitrogen. This result is consistent with Wedin and Pastor (1993), who found that species effects were most obvious in the labile rather than in the recalcitrant portions of soil nitrogen. The most

responsive soil property seemed to be the indexes of labile carbon, and the most consistent pattern among the native species was that soils under the rhizomatous grass, *Agropyron smithii* had lower carbon turnover rates and lower levels of carbon in microbial biomass than did the soils under the other, mostly bunchgrass, species. The low above- and belowground biomass of *Agropyron smithii* may explain these patterns in soil carbon.

Frequently, plant lignin or lignin/nitrogen and carbon/nitrogen ratios are viewed as important variables determining soil nutrient availability and cycling, particularly nitrogen mineralization rates (Melillo et al. 1982, Pastor and Post 1986, Wedin and Tilman 1990, Stump and Binkley 1993). In general, I found that species with the highest nitrogen mineralization rates in soils beneath their canopy also had the lowest root lignin/nitrogen and carbon/nitrogen ratios (e.g. *Stipa comata* and, in the NW plots, *Kochia scoparia*). Nitrogen mineralization in the soil beneath the plant canopy reflects combined effects of a number of potentially controlling and interacting factors, including tissue chemical quality as well as tissue quantity. Van Vuuren and van der Eerden (1992) have demonstrated that plant species can have differential effects on both microbial immobilization and microbial release of nutrients. In this study, *Bouteloua gracilis* had fairly low nitrogen mineralization rates in its soils but did not have the highest root lignin/nitrogen or leaf and root carbon/nitrogen ratios. *Bouteloua gracilis* also had fairly high belowground biomass and root/shoot ratios, suggesting that microbial immobilization of nitrogen may have

significantly decreased net nitrogen mineralization in the incubations of *Bouteloua gracilis* soil and other species' soil with large amounts of fine root litter. In a root exudation study, (Biondini et al. 1988) *Bouteloua gracilis* released more C and N from roots in sterile media than *Agropyron smithii*; however, I did not detect any significant differences in microbial levels or activity between the two.

Plant species effects were also apparent in the degree of between vs. under plant canopy differences in soil properties. *Kochia scoparia*, the only annual in the study, had significantly less plant canopy-induced soil variation in carbon mineralization rates and microbial biomass nitrogen than did the perennial species. As an annual, *Kochia scoparia* plants presumably occupy microsites only briefly, with different microsites occupied each year. Also, bunch grasses tended to have more of a contrast in soil properties in between vs. under plant canopy positions than did the non-bunch lifeforms. This difference could be explained by the spatial arrangement of stems. Bunch grasses tend to have very localized points of biomass, in contrast to more diffuse or "stemy" herbaceous lifeforms, such as rhizomatous grasses. Mazzarino et al. (1991), in a dry chaco ecosystem in Argentina, also showed differences in plant-associated soil heterogeneity, depending upon the plant type. In that system, soils under trees were significantly higher in nitrogen mineralization than soils in interspaces, whereas soils under grasses were similar to the interspace soils. Lauenroth et al. (in press) showed differences

in plant-associated soil heterogeneity, apparently determined by the lifespan of the plant, with the shorter-lived plant, *Bouteloua eriopoda*, having less between vs. under canopy difference in soils than the longer-lived plant, *Bouteloua gracilis*. In a study of the scale of soil heterogeneity around individual plants in a sagebrush-steppe ecosystem, Jackson and Caldwell (1993) found stronger spatial patterning in soils associated with tussock grasses than soils associated with sagebrush plants.

Plant cover effects on soils

Discontinuous plant cover is an obvious feature of shortgrass steppe ecosystems and this spatial heterogeneity in plant presence had strong and consistent effects on soil properties, particularly the active soil pools. Soil under plants had higher total and mineralizable carbon and higher microbial biomass and mineralizable nitrogen. Individual plants concentrate biomass and thus carbon and nitrogen in the soil beneath their canopy, leading to a plant-induced "island of soil fertility" effect, often observed in arid and semi-arid areas (Charley and West 1975 and 1977, Barth and Klemmedson 1978, Klopatek 1987, Burke et al. 1989, Bolton et al. 1990 and 1993, Schlesinger et al. 1990, Hook et al. 1991). Historical addition of resources, particularly water, in many cases diminished or eliminated this plant-induced heterogeneity. This breakdown in plant-induced soil pattern is probably due to increased turnover of plants on the landscape, resulting from increased mortality of native plants and increased

recruitment of new plants, especially those with an annual lifespan. Increased turnover of plants on the landscape may have resulted in plants occupying given locations for a shorter period of time. Bolton et al. (1990), in studies of a semi-arid grassland in south-eastern Washington, also showed less plant-induced soil heterogeneity in annual plant stands than in perennial shrub-steppe stands. Schlesinger et al. (1990) have suggested that increased plant-induced soil heterogeneity, initiated by grazing in the south-western U.S. desert system, leads to ecosystem degradation and desertification. This heterogeneity seems to be a feature of native shortgrass-steppe, and the disruption of that heterogeneity, initiated by nutrient and water addition in this case, was associated with unprecedented changes in plant production and species composition.

Historical treatment effects on plants and soils

The historical addition of soil resources to shortgrass-steppe in the early 1970's affected plant biomass and allocation in the early 1990's. Numerous experiments and reviews (e.g. Mooney 1972, Chapin 1980, Tilman and Cowan 1989) have shown that plant root/shoot ratios decrease under conditions of enhanced belowground resources, and data from this study show the same pattern. Apparently, 20 years after fertilization, the additional nitrogen on the N plots is still available to plants and allows them to maintain high levels of tissue nitrogen relative to carbon as well as to invest relatively less in production

of roots. Such a response may involve a positive feedback between the plant characteristics of biomass allocation and litter quality and soil resource availability. Although responses of plant nutrient allocation to resource additions are often observed, this study shows that responses can persist through time and may be stabilized by interactions between plants and soils.

Historical resource addition has also caused persistent changes in soil characteristics, via the activity of plants. The addition of water in the early 1970's resulted in large increases in net primary production (Lauenroth et al. 1978); the high current levels of soil carbon on the historical W plots likely reflect this production pulse twenty years ago. Although current total pools of soil nitrogen were not detectably larger in the plots which received nitrogen from 1970-1974, active pools (sensu Parton et al. 1987), as indicated by nitrogen mineralization rates, were significantly higher in these plots. Furthermore, the plants on the historical nitrogen addition plots had lower carbon/nitrogen tissue ratios. This suggests that at least a portion of the added nitrogen is still present in active soil pools and has been incorporated into plant tissue. In turn, during the 20 years since fertilization, the labile plant tissue has probably contributed to the active soil pool of nitrogen. This result represents further evidence for linkages and feedbacks between soils and plants in this system and is consistent with earlier work showing tight linkages in the nitrogen cycle between *Bouteloua gracilis* plants and soil (Clark 1977).

Plant-soil patterns on the historically resource-amended area suggest that

positive feedbacks between plants and soil nutrients may be initiated and persist for many years, even in an ecosystem traditionally viewed as being limited primarily by water. *Kochia scoparia* was only able to invade and dominate this ecosystem under artificially high soil resource conditions, resulting from water and nitrogen fertilizer additions. However, when additions were stopped (20 years ago), the abundance or productivity of *Kochia* did not drop to previous levels. These data suggest that high nitrogen availability in soils beneath *Kochia* may be maintained in part by tissue chemistry favorable to microbial decomposition and release of nitrogen. The continued persistence of *Kochia*, in turn, may involve its superior competitive ability on nutrient-rich soils and/or possible allelopathic effects on other species (Karachi and Pieper 1987). The fact that invasive plant species, such as this one, can initiate and maintain profound changes in ecosystem function has important implications for disturbed or island systems, or any ecosystem undergoing large changes in plant species composition (Vitousek 1986 and 1990, Vitousek et al. 1987).

Effects of plants on ecosystem-level soil property estimates

Our ecosystem-level estimates of soil properties serve to emphasize the importance of local plant effects on soils. The estimate (Bare Soil) that did not incorporate local plant presence effects on soils resulted in very different calculated plot-level properties than the estimates (Plant and Species) that did include plant information. However, despite some of the large effects of plant

species on local soil properties, the addition of information about plant species in most cases did not have large effects on estimates of plot-level soil properties. This result indicates that, although plant species may have differential local effects on soils, it is the presence, and not so much the identity of the plant occupying a given space, that may be most important to plot-level estimates of soil properties in this semi-arid grassland. In some cases (e.g. perennial vs. annual) the plant species identity determines the year-to-year pattern in plant presence. Padien and Lajtha (1992) found similar results in that the presence or absence of a canopy in pinyon-juniper communities was more important to soil nitrogen dynamics on a local scale than differences among the particular species forming the canopy. In this semi-arid ecosystem, the importance of plant presence may overshadow that of plant species in ecosystem-level estimates because 1) plant presence is discontinuous and 2) decomposition and nutrient availability are primarily limited by water, not by plant species-mediated characteristics such as litter quality.

This study has shown that perturbations in soil resources can persist for long periods of time (>20 years) and furthermore, these perturbations to soil resources may persist and be maintained through feedbacks between soil organic matter and plant species characteristics. In addition this study has shown that plant species may have differential effects on soil properties but, in this system, the presence of a plant rather than the identity of the plant is the most important determinant of ecosystem-level soil property estimates. That

local plant-induced patterns in soil properties significantly affected ecosystem scale estimates indicates that consideration of structural attributes, particularly plant cover patterns, is critical to estimates of ecosystem function in shortgrass steppe.

LITERATURE CITED

Amato M., and J.N Ladd. 1988. Assay for microbial biomass based on ninhydrin-reactive nitrogen in extracts of fumigated soils. Soil Biology and Biochemistry 20: 107-114.

Barth, R.C., and J.O. Klemmedson. 1978. Shrub-induced spatial patterns of dry matter, nitrogen and organic carbon. Soil Science Society of America Journal 42: 804-809.

Berendse, F., R. Bobbink, and G. Rouwenhorst. 1989. A comparative study on nutrient cycling in wet heathland ecosystems II: Litter decomposition and nutrient mineralization. Oecologia 78: 338-348.

Binkley, D., and D. Valentine. 1991. Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. Forest Ecology and Management 40: 13-25.

Biondini, M., D.A. Klein, and E.F. Redente. 1988. Carbon and nitrogen losses through root exudation by *Agropyron cristatum*, *A. smithii* and *Bouteloua gracilis*. Soil Biology and Biochemistry. 20: 477-482.

Bolton, H, J.L. Smith, and R.E. Wildung. 1990. Nitrogen mineralization potential of shrub-steppe soils with different disturbance histories. Soil Science Society of America Journal. 54: 887-891.

Bolton, J., J.L. Smith, and S.O. Link. 1993. Soil microbial biomass and activity of a disturbed and undisturbed shrub-steppe ecosystem. Soil Biology and Biochemistry 25: 545-552.

Brookes, P.C., A. Landman, G. Pruden, and D.S. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology and

Biochemistry 17: 837-842.

Burke, I.C., W.A. Reiners, and D.S. Schimel. 1989. Organic matter turnover in a sagebrush steppe landscape. Biogeochemistry 7:11-31.

Burke, I.C. 1989. Control of N mineralization in a sagebrush steppe landscape. Ecology 70(4): 1115-1126.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233-260.

Chapin, F.S. 1993. Functional role of growth forms in ecosystem and global processes. *in* J.R. Ehleringer and C.B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, London.

Charley, J.L., and N.E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. Journal of Ecology 63: 945-963.

Charley, J.L., and N.E. West. 1977. Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. Soil Biology and Biochemistry 9: 357-365.

Clark, F.E. 1977. Internal cycling of ^{15}Nitrogen in shortgrass prairie. Ecology 58: 1322-1333.

Dodd, J.D., and W.K Lauenroth. 1978. Analyses of the response of a grassland ecosystem to stress. p. 43-58. *in* N.R. French, editor. Perspectives in grassland ecology. Springer-Verlag. New York, New York, USA.

EPA. 1979. Methods for chemical analysis of water and wastes. EPA-600/4-79-020, March 1979, U.S. Environmental Protection Agency. U.S. Government Printing Office, Washington, D.C.

Franklin, J.F., C.S. Bledsoe, and J.T. Callahan. 1990. Contributions of the Long-Term Ecological research program. Bioscience 40: 509-523.

Gomez K., and A. Gomez. 1984. Statistical Procedures for Agricultural Research. Wiley Interscience, New York, New York, USA.

Great Plains Flora Association. 1986. Flora of the Great Plains. Univ. Press of Kansas, Lawrence, Kansas, USA.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, England.

Hobbie, S.E. 1992. Effects of plant species on nutrient cycling. Trends in Ecology and Evolution 7: 336-339.

Hook, P.B., I.C. Burke, and W.K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. Plant and Soil 138: 247-256.

Inouye, R.S., and D. Tilman. 1988. Convergence and divergence of old-field plant communities along experimental nitrogen gradients. Ecology 69: 995-1004.

Jackson, R.B. and M.M. Caldwell. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. Journal of Ecology 81: 683-692.

Johnson, L.C., and A.W.H. Damman. 1991. Species-controlled Sphagnum decay on a South Swedish raised bog. Oikos 61: 234-242.

Karachi, M., and R.D. Pieper. 1987. Allelopathic effects of kochia on blue grama. Journal of Range Management 40: 380-381.

Karimian, N., and K. Razmi. 1990. Influence of perennial plants on chemical properties of arid calcareous soils in Iran. Soil Science 150: 717-721.

Klemmedson, J.O. 1991. Oak influence of nutrient availability in pine forests of central Arizona. Soil Science Society of America Journal 55: 248-253.

Klopatek, J.M. 1987. Nitrogen mineralization and nitrification in mineral soils of pinyon-juniper ecosystems. Soil Science Society of America Journal 51: 453-457.

Lauenroth, W.K., and W.C. Whitman. 1971. A rapid method for washing roots. Journal of Range Management 24: 308-309.

Lauenroth, W.K., and J.L. Dodd. 1979. Response of native grassland legumes to water and nitrogen treatments. Journal of Range Management 32: 292-294.

Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978, The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid

grassland. Oecologia 36: 211-222.

Lauenroth, W.K., D.P. Coffin, I.C. Burke, and R.A. Virginia. 199_. Effects of plant mortality on population dynamics and ecosystem structure: a case study. *in* T.M. Smith, H.H. Shugart, and F.I. Woodward, editors. Plant Functional Types. Cambridge University Press. in press.

Matson, P. 1990. Plant-soil interactions in primary succession at Hawaii Volcanoes National Park. Oecologia 85: 241-246.

Mazzarino, M.J., L. Oliva, A. Nunez, G. Nunez, and E. Buffa. 1991. Nitrogen mineralization and soil fertility in the dry Chaco ecosystem (Argentina). Soil Science Society of America Journal 55:515-522.

Melillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621-626.

Milchunas, D.G., W.K. Lauenroth, P.L. Chapman, and M.K. Kazempour. 1990. Community attributes along a perturbation gradient in a shortgrass steppe. Journal of Vegetation Science 1: 375-384.

Milchunas, D.G., and W.K. Lauenroth. in review, Ecological Applications. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress.

Monk, C.D. 1966. An ecological significance of evergreeness. Ecology 47: 504-505.

Mooney, H.A. 1972. The carbon balance of plants. Annual Review of Ecology and Systematics 3: 315-346.

Mooney, H.A., and E. Schulze. 1993. Biodiversity and ecosystem function. Springer Verlag. New York. 525 p.

Padien, D.J., and K. Lajtha. 1992. Plant spatial pattern and nutrient distribution in pinyon-juniper woodlands along an elevational gradient in northern New Mexico. International Journal of Plant Science 153: 425-433.

Parton, W.J., and D. Greenland. 1987. Central Plains Experimental Range Site, Colorado. Pages 23-27 *in* D. Greenland, editor. The climates of the long-term ecological research sites. Occasional Paper No. 44, Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, USA.

Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51: 1173-1179.

Pastor, J., J.D. Aber, C.A. McClaugherty, and J.M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin, Ecology 65: 256-268.

Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycle. Biogeochemistry 2: 3-27.

Pastor, J., B. Dewey, R.J. Naiman, P.F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74: 467-480.

Powlson D.S., and D.S. Jenkinson. 1976. The effects of biocidal treatments on metabolism in soil-II. Gamma irradiation, autoclaving, air-drying and fumigation. Soil Biology and Biochemistry 8: 179-188.

Reiners W.A., I.A. Worley, and D.B. Lawrence. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecology 52: 55-69.

Rice, E.L., and S.K. Pancholy. 1972. Inhibition of nitrification by climax ecosystems. American Journal of Botany. 59: 1033-1040.

Robertson, G.P., M.A. Huston, F.C. Evans, and J.M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology 69: 1517-1524.

SAS institute. 1985. SAS Statistics. SAS Institute, Cary, N.C.

Schimel, D.S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry 2:345-357.

Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.G. Whitford. 1990. Biological feedbacks in global desertification. Science 247: 1043-1047.

Snyder, J.D., and J.A. Trofymow. 1984. A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil samples. Communications in Soil Science and Plant Analysis. 15: 587-597.

Stump, L.M., and D. Binkley. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Canadian Journal of Forest Research 23: 492-502.

Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. Ecology 67: 555-563.

Tilman, D., and M.L. Cowan. 1989. Growth of old field herbs on a nitrogen gradient. Functional Ecology 3: 425-438.

Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72: 1038-1049.

Van Soest P.F. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. Journal of the Association of Official Analytical Chemists 46: 829-835.

Van Vuuren, M.M.I., and L.J. van der Eerden. 1992. Effects of three rates of atmospheric nitrogen deposition enriched with ^{15}N on litter decomposition in a heathland. Soil Biology and Biochemistry 24: 527-532.

Vitousek. P.M. 1986. Biological invasions and ecosystem properties: can species make a difference. Pages 163-176 *in* H.A. Mooney and J. Drake, editors. Biological invasions of North America and Hawaii. Springer USA.

Vitousek, P.M., L.R. Walker, L.D. Whiteaker, D. Mueller-Dombois, and P.A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238: 802-804.

Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57: 7-13.

Waldern, D.E. 1971. A rapid micro-digestion procedure for neutral and acid detergent fiber. Canadian Journal of Animal Science 51: 67-69.

Wedin, D.A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84: 433-441.

Wedin, D.A., and J. Pastor. 1993. Nitrogen mineralization dynamics in grass monocultures. Oecologia 96: 186-192.

Wilson, J.R., and J.B. Hacker. 1987. Comparative digestibility and anatomy of

some sympatric C3 and C4 arid zone grasses. Australian Journal of Agricultural Research 38: 287-295.

Table 2.1. Plant species characteristics and relative percent basal cover of plant species and bareground in 1991 on plots in shortgrass steppe receiving no addition (Control), nitrogen addition (N), water addition (W), or both nitrogen and water addition (NW) from 1971-1974.

Species	Phenology*	Lifespan and Growth Form	Relative Basal Cover (%)			
			Control	N	NW	W
Agropyron smithii	cool season	perennial, mid rhizomatous grass	4.9	5.3	4.6	5.1
Stipa comata	cool season	perennial mid bunchgrass	11.3	10.5	5.0	19.2
Bouteloua gracilis	warm season	perennial short bunchgrass	31.6	31.1	6.3	24.8
Aristida longiseta	warm season	perennial mid bunchgrass	12.2	6.1	3.3	16.8
Artemisia frigida	cool season	perennial half shrub	19.2	30.7	4.5	14.2
Carex eleocharis	cool season	perennial sedge			38.0	
Kochia scoparius	warm season	annual forb			35.5	
Bare ground			20.9	16.3	2.9	19.8

* Phenology indicates the season of maximum growth and in most cases is associated with the C_3 (cool season) or C_4 (warm season) photosynthetic pathway.

Table 2.2 Results of a 3-way ANOVA using a split-split plot design, showing the significance of the effects of historical treatment (control, nitrogen, water or nitrogen+water additions from 1970-1974), species (both under and between plants of 5 different species), position (under vs. between plants) and factor interactions on soil response variables expressed on a m^2 basis. The soil variable means are illustrated for species and positions for the control plots in Figure 2.1 and for the NW plots in Figure 2.4 Also, means for the historical treatments and postions are shown in Figure 2.6.

	FACTORS											
	Historical Treatment		Species		Position		Historical Trt. *Species		Historical Trt. *Position		Species*Position	
RESPONSE	F Ratio	Prob.	F Ratio	Prob.	F Ratio	Prob.	F Ratio	Prob.	F Ratio	Prob.	F Ratio	Prob.
Total Soil Carbon	4.488	.1246	0.9800	.4459	12.554	.0020	0.8324	.6202	15.211	.0001	1.263	.3172
Total Soil Nitrogen	2.308	.2551	1.152	.3683	1.275	.2721	1.051	.4533	8.992	.0006	0.9298	.4665
Carbon Mineralization	1.5075	.3720	9.525	.0004	119	.0001	1.3458	.2847	5.3011	.0075	2.1256	.1153
Nitrogen Mineralization	93.4826	.0018	1.8612	.1666	30.923	.0001	0.5663	.8385	3.0877	.0505	0.1385	.9660
Microbial Biomass Carbon	9.7889	.0466	1.3194	.3051	3.1156	.0928	2.7102	.0325	0.8036	.5065	0.1733	.9495
Microbial Biomass Nitrogen	0.7792	.5788	4.2577	.0155	37.380	.0001	0.4624	.9093	2.9921	.0553	0.2473	.9079

Table 2.3. Results of a 2-way ANOVA using a split-plot design, showing the significance of the effects of historical treatment (control, nitrogen, water or nitrogen+water additions from 1970-1974), plant species (5 different species), and their interaction on plant biomass characteristics. Figure 2.2 shows the species means for plant biomass characteristics only on the control plots and Figure 2.3 shows the species means for the nitrogen+water plots. The means or plant biomass characteristics for the historical treatment plots are shown in Figure 2.5. Lignin analyses were only performed for all species on one level of the historical treatment factor (control), so the historical treatment*species interaction for root lignin:N could not be estimated.

	FACTOR					
	Historical Treatment		Species		Hist.Trt.*Species	
RESPONSE	F Value	Prob.	F Value	Prob.	F Value	Prob.
Aboveground Biomass (g/m^2)	96.0612	.0018	44.9373	.0001	11.1727	.0001
Belowground Biomass (g/m^2)	6.5900	.0003	37.2800	.0001	6.9200	.0001
Root:Shoot	11.2000	.0001	77.2500	.0001	3.5600	.0001
Root C:N	23.7400	.0001	7.5300	.0001	0.3000	.9869
Leaf C:N	41.2619	.0001	47.7635	.0001	3.7317	.0001
Root Lignin:N	2.9400	.0765	3.1000	.0274		

Table 2.4. Results of 2-way ANOVA, showing the significance of the effects of historical treatment (control, nitrogen, water or nitrogen+water additions from 1970-1974) and the estimate method used to scale up local measurements of soil properties to the plot-scale. Three estimate methods were used: the Bare Soil Estimate represents no consideration of plant effects on soils; the Plant Estimate includes effects of plant presence or absence, without consideration of differential cover among species; and the Species Estimate includes the effects of all major plant species, including their relative cover and nutrient cycling characteristics. See text in Methods for an explanation of how each estimate was calculated.

RESPONSE	FACTOR	df	MS	F	P
Total Soil Carbon	Historical Treatment (T)	3	33610	14.86	.0002
	Estimate (E)	2	5203	2.30	.1426
	T*E	6	5726	2.53	.0805
	Error	12	2261		
Total Soil Nitrogen	Historical Treatment (T)	3	515	5.47	.0133
	Estimate (E)	2	5.7	0.06	.9414
	T*E	6	33.8	0.36	.8911
	Error	12	94		
Carbon Mineralization	Historical Treatment (T)	3	0.3009	5.78	.0111
	Estimate (E)	2	0.5889	11.31	.0017
	T*E	6	0.0303	.058	.7388
	Error	12	0.0521		
Nitrogen Mineralization	Historical Treatment (T)	3	0.0016	10.78	.0010
	Estimate (E)	2	0.0011	7.29	.0085
	T*E	6	0.0001	0.88	.5353
	Error	12	0.0001		
Microbial Biomass C	Historical Treatment (T)	3	14.35	4.53	.0240
	Estimate (E)	2	1.38	0.44	.6566
	T*E	6	0.99	0.31	.9176
	Error	12	3.17		
Microbial Biomass N	Historical Treatment (T)	3	0.0073	0.32	.8137
	Estimate (E)	2	0.0073	0.32	.7347
	T*E	6	0.0007	0.03	.9998
	Error	12	0.0232		

Table 2.5. Three estimates of whole-plot values of total soil carbon, total soil nitrogen, carbon mineralization rates, potential nitrogen mineralization rates, microbial biomass carbon, and microbial biomass nitrogen on plots in shortgrass steppe receiving no addition (Control), nitrogen addition (N), water addition (W), or both nitrogen and water addition (NW) from 1971-1974. The Bare Soil Estimate represents no consideration of plant effects on soils. The Plant Estimate includes effects of plant presence or absence, without consideration of differential cover or nutrient cycling characteristics among species. The Species Estimate includes the effects of all major plant species, including their relative cover and nutrient cycling characteristics. See text in Methods for an explanation of how each estimate was calculated. One SE is shown in parentheses. Estimates with the same letter superscript are not significantly different ($p>.05$) when averaged over historical treatments. Historical treatments with the same letter are not significantly different ($p>.05$) when averaged over estimate.

Response	Estimate	Historical Treatment			
		Control	N	NW	W
Total Soil Carbon (kg/ha)		b	a	a	a
	Bare Soil[a]	5350 (21)	6259 (618)	7973 (256)	7615 (687)
	Plant[a]	6560 (276)	7502 (277)	7804 (178)	7119 (130)
	Species[a]	6369 (347)	7646 (135)	7930 (164)	6996 (266)
Total Soil Nitrogen (kg/ha)		b	ab	a	ab
	Bare Soil[a]	491 (12)	534 (10)	755 (21)	626 (152)
	Plant[a]	560 (45)	609 (52)	732 (2)	563 (96)
	Species[a]	538 (51)	626 (63)	746 (24)	554 (104)
Carbon Mineralization (kg/ha/day)		b	a	ab	ab
	Bare Soil[b]	4.7 (0.1)	9.5 (3.9)	10.8 (0.9)	7.4 (1.1)
	Plant[a]	11.4 (0.8)	15.8 (1.2)	13.5 (1.3)	10.6 (1.6)
	Species[a]	11.5 (0.9)	15.8 (1.8)	13.3 (1.1)	10.5 (1.5)
Nitrogen Mineralization (kg/ha/day)		b	a	a	b
	Bare Soil[b]	0.56 (0.01)	0.76 (0.09)	0.97 (0.03)	0.63 (0.06)
	Plant[a]	0.84 (0.09)	1.11 (0.01)	1.01 (0.08)	0.75 (0.09)
	Species[a]	0.84 (0.10)	1.10 (0.09)	1.06 (0.07)	0.71 (0.09)
Microbial Biomass Carbon (kg/ha)		ab	ab	a	b
	Bare Soil[a]	78 (3)	61 (11)	89 (3)	40 (7)
	Plant[a]	85 (10)	74 (19)	79 (10)	55 (12)
	Species[a]	80 (9)	81 (23)	83 (15)	55 (11)
Microbial Biomass Nitrogen (kg/ha)		a	a	a	a
	Bare Soil[a]	1.2 (0.9)	1.0 (0.3)	1.9 (1.2)	1.8 (0.7)
	Plant[a]	1.9 (1.2)	1.7 (0.6)	2.6 (1.7)	1.9 (0.7)
	Species[a]	1.9 (1.2)	1.8 (0.8)	2.4 (1.7)	1.9 (0.7)

Figure 2.1. Total soil carbon (**a**), total soil nitrogen (**b**), carbon mineralization rate (**c**), potential nitrogen mineralization rate (**d**), microbial biomass carbon (**e**), and microbial biomass nitrogen (**f**) in soils from under and between plants of the species, *Agropyron smithii, Stipa comata*, *Bouteloua gracilis*, *Aristida longiseta*, and *Artemisia frigida* on the control plots (unfertilized and unwatered) of a historical treatment area in shortgrass steppe. The vertical line on each bar indicates 1 SE. The letters over the "under plant" bars indicate cases where significant differences ($p<.05$) existed among species in soil properties under their canopies.

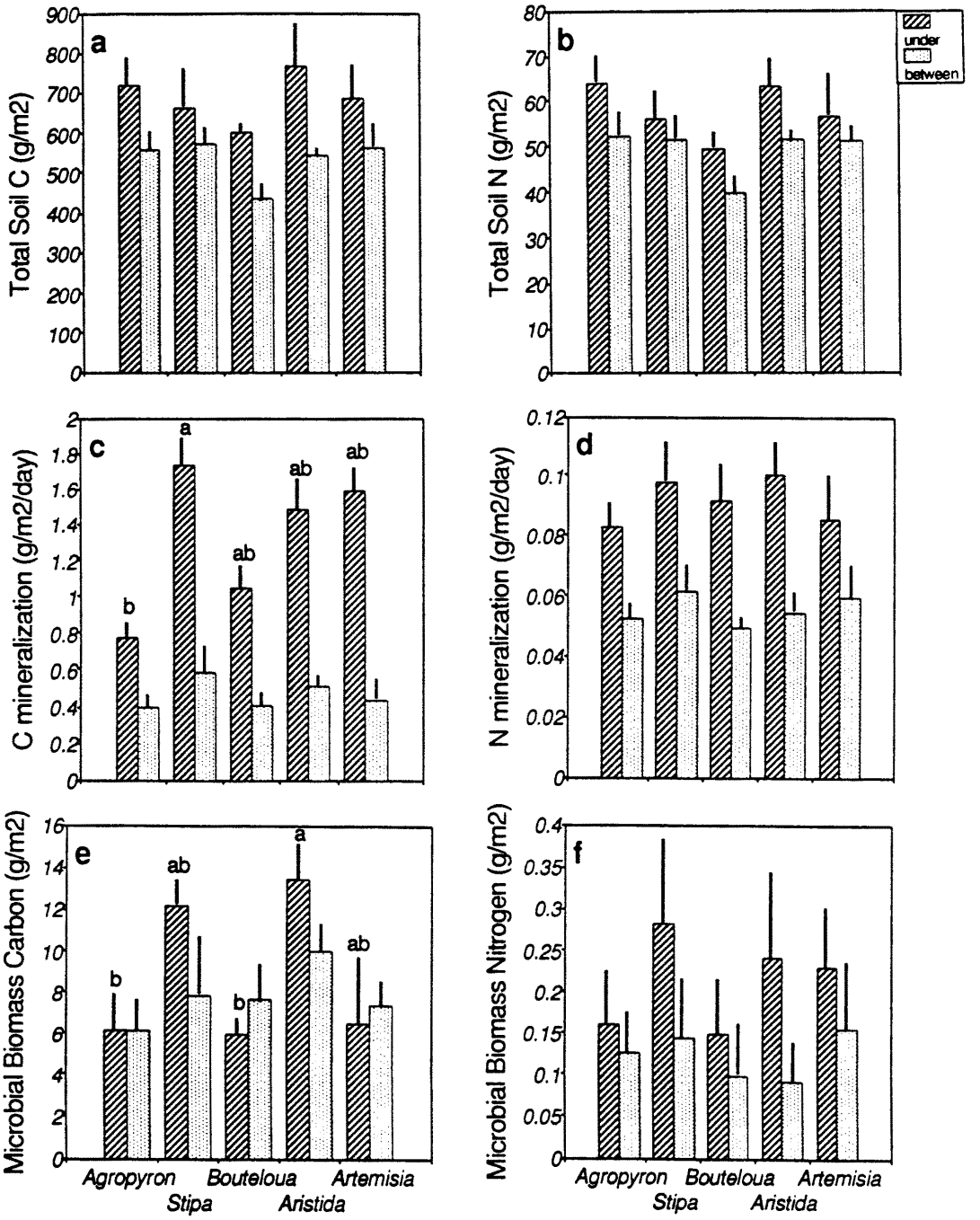

a
b
c
d
e
f
Total Soil C (g/m2)
Total Soil N (g/m2)
C mineralization (g/m2/day)
N mineralization (g/m2/day)
Microbial Biomass Carbon (g/m2)
Microbial Biomass Nitrogen (g/m2)
under
between
Agropyron
Stipa
Bouteloua
Aristida
Artemisia

Figure 2.2. Aboveground biomass (**a**), belowground biomass (**b**), root/shoot biomass ratio (**c**), root carbon/nitrogen ratio (**d**), leaf carbon/nitrogen ratio (**e**), and root lignin/nitrogen ratio (**f**) of *Agropyron smithii, Stipa comata*, *Bouteloua gracilis*, *Aristida longiseta*, and *Artemisia frigida* on the control plots (unfertilized and unwatered) of a historical treatment area in shortgrass steppe. The vertical line on each bar indicates 1 SE. Bars with the same letters are not significantly different ($p \geq .05$).

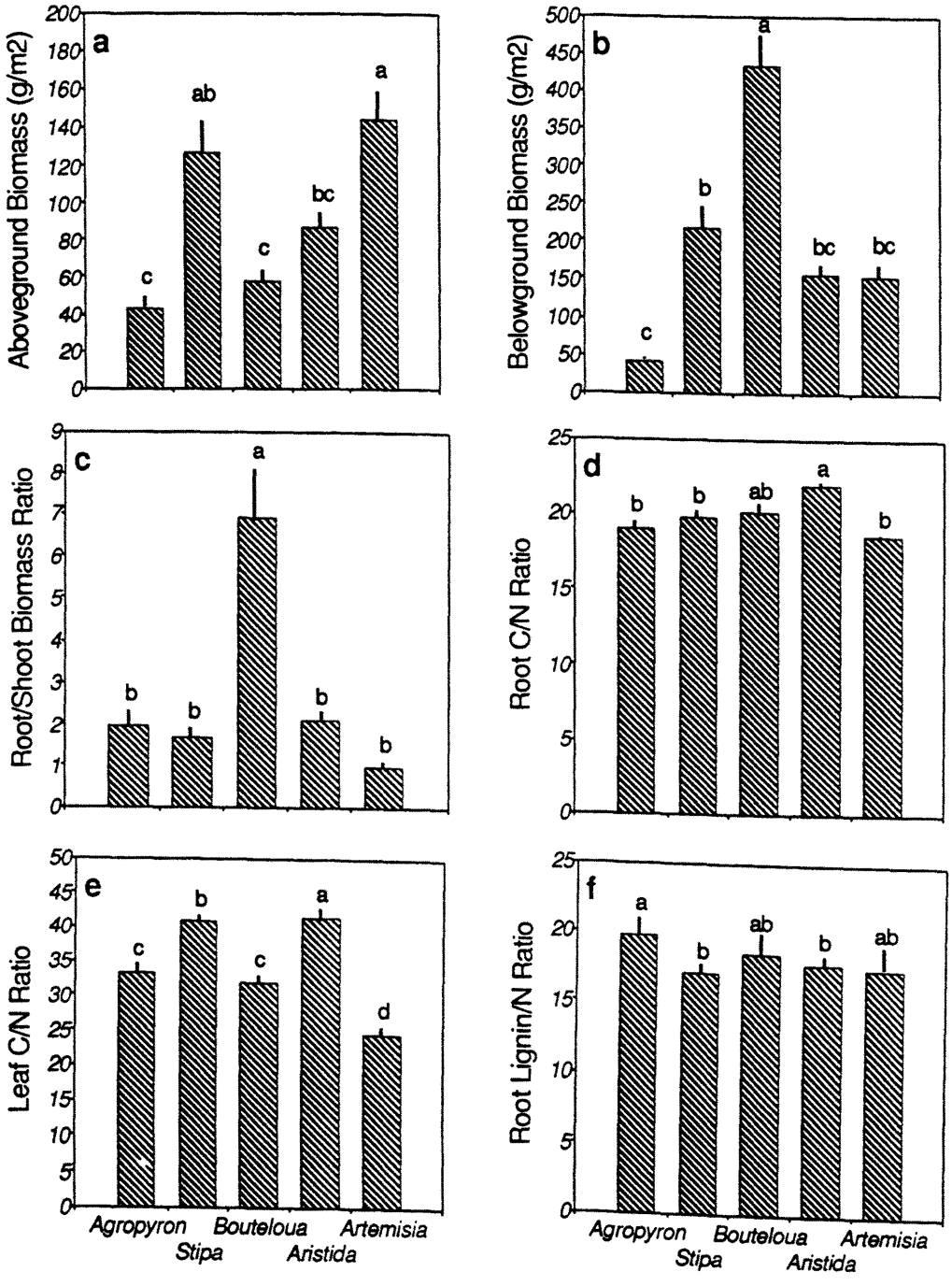

a
Aboveground Biomass (g/m2)
200
180
160
140
120
100
80
60
40
20
0
c
ab
c
bc
a
b
Belowground Biomass (g/m2)
500
450
400
350
300
250
200
150
100
50
0
c
b
a
bc
bc
c
Root/Shoot Biomass Ratio
9
8
7
6
5
4
3
2
1
0
b
b
a
b
b
d
Root C/N Ratio
25
20
15
10
5
0
b
b
ab
a
b
e
Leaf C/N Ratio
50
45
40
35
30
25
20
15
10
5
0
c
b
c
a
d
f
Root Lignin/N Ratio
25
20
15
10
5
0
a
b
ab
b
ab
Agropyron
Stipa
Bouteloua
Aristida
Artemisia

Figure 2.3. Aboveground biomass (**a**), belowground biomass (**b**), root/shoot biomass ratio (**c**), root carbon/nitrogen ratio (**d**), and aboveground biomass carbon/nitrogen ratio (**e**) of *Agropyron smithii, Stipa comata*, *Bouteloua gracilis*, *Aristida longiseta*, and *Artemisia frigida*, *Carex eleocharis* and *Kochia scoparia* on plots receiving nitrogen+water from 1970-1974 on shortgrass steppe. The vertical line on each bar indicates 1 SE. Bars with the same letters are not significantly different ($p \geq .05$).

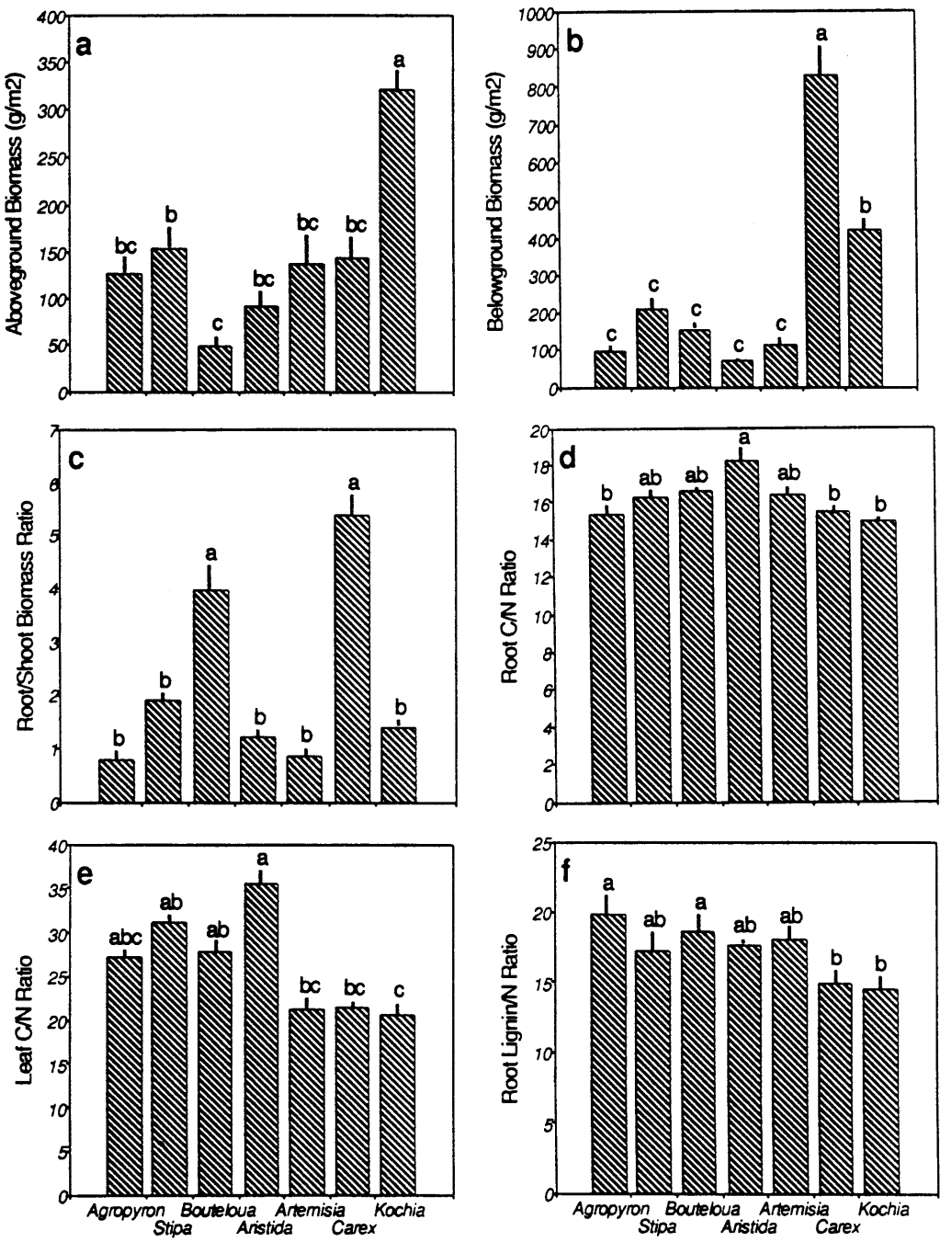

a
Aboveground Biomass (g/m2)
400
350
300
250
200
150
100
50
0
bc
b
c
bc
bc
bc
a
b
Belowground Biomass (g/m2)
1000
900
800
700
600
500
400
300
200
100
0
c
c
c
c
c
a
b
c
Root/Shoot Biomass Ratio
7
6
5
4
3
2
1
0
b
b
a
b
b
a
b
d
Root C/N Ratio
20
18
16
14
12
10
8
6
4
2
0
b
ab
ab
a
ab
b
b
e
Leaf C/N Ratio
40
35
30
25
20
15
10
5
0
abc
ab
ab
a
bc
bc
c
Agropyron
Stipa
Bouteloua
Aristida
Artemisia
Carex
Kochia
f
Root Lignin/N Ratio
25
20
15
10
5
0
a
ab
a
ab
ab
b
b
Agropyron
Stipa
Bouteloua
Aristida
Artemisia
Carex
Kochia

Figure 2.4. Total soil carbon (**a**), current total soil nitrogen (**b**), carbon mineralization rates (**c**), potential nitrogen mineralization rates (**d**), microbial biomass carbon (**e**), and microbial biomass nitrogen (**f**) in soils from under and between plants of seven species on plots in shortgrass steppe receiving nitrogen+water from 1970-1974. The vertical line on each bar indicates 1 SE. Significant differences ($p<.05$) between soils associated with *Kochia scoparius* and soils under the other plant species are indicated with asterisks.

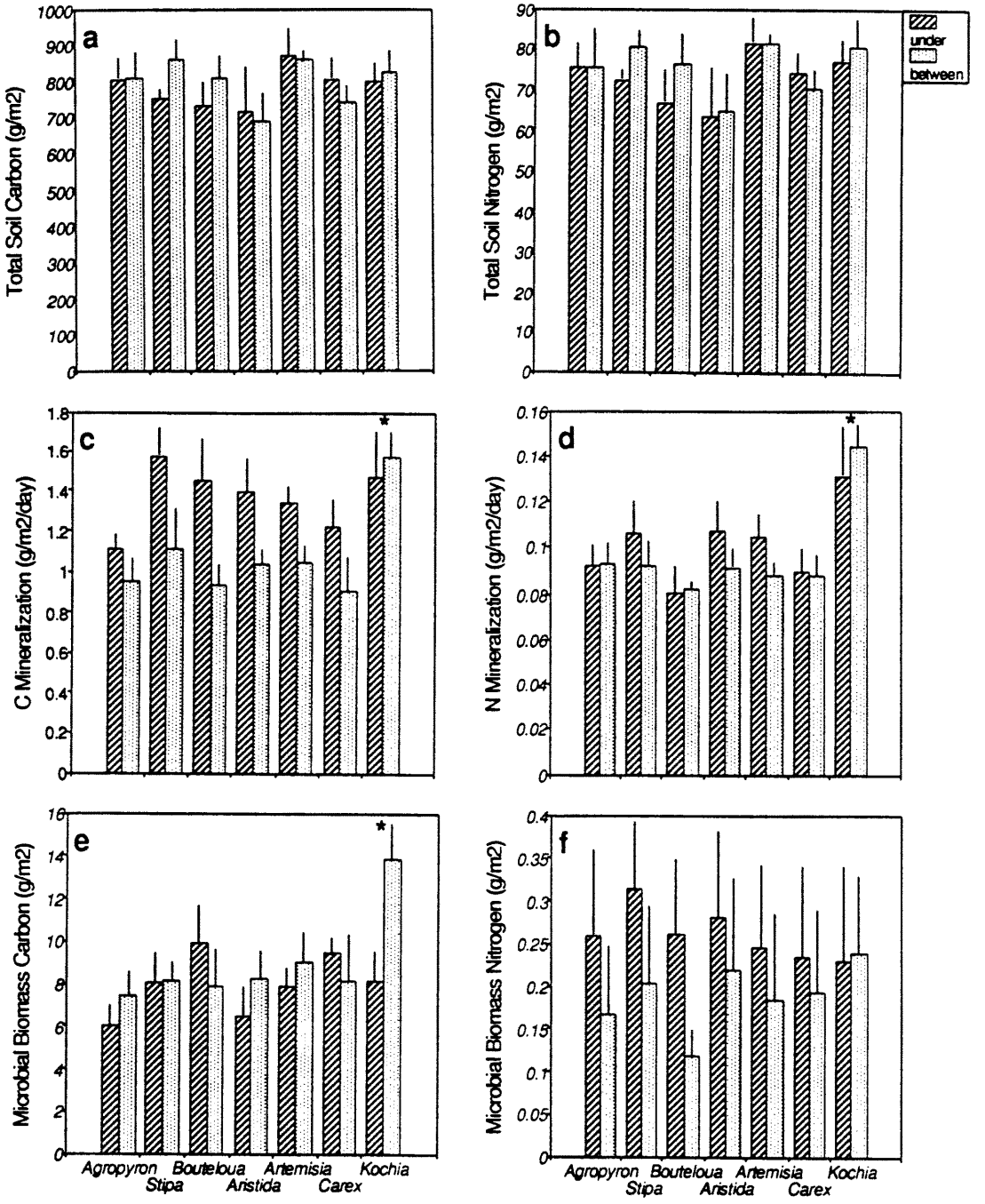

a
b
c
d
e
f
Total Soil Carbon (g/m2)
Total Soil Nitrogen (g/m2)
C Mineralization (g/m2/day)
N Mineralization (g/m2/day)
Microbial Biomass Carbon (g/m2)
Microbial Biomass Nitrogen (g/m2)
under
between
*
Agropyron
Stipa
Bouteloua
Aristida
Artemisia
Carex
Kochia

Figure 2.5. Aboveground biomass (**a**), belowground biomass (**b**), root/shoot biomass ratio (**c**), root carbon/nitrogen ratio (**d**), leaf carbon/nitrogen ratio (**e**) and root lignin/nitrogen ratio (**f**) averaged across five plant species (only *Bouteloua gracilis* for root lignin:N) on plots in shortgrass-steppe receiving no addition (Control), nitrogen addition (N), water addition (W), or both nitrogen and water addition (NW) from 1971-1974. The vertical line on each bar indicates 1 SE. Bars with the same letters are not significantly different ($p \geq .05$).

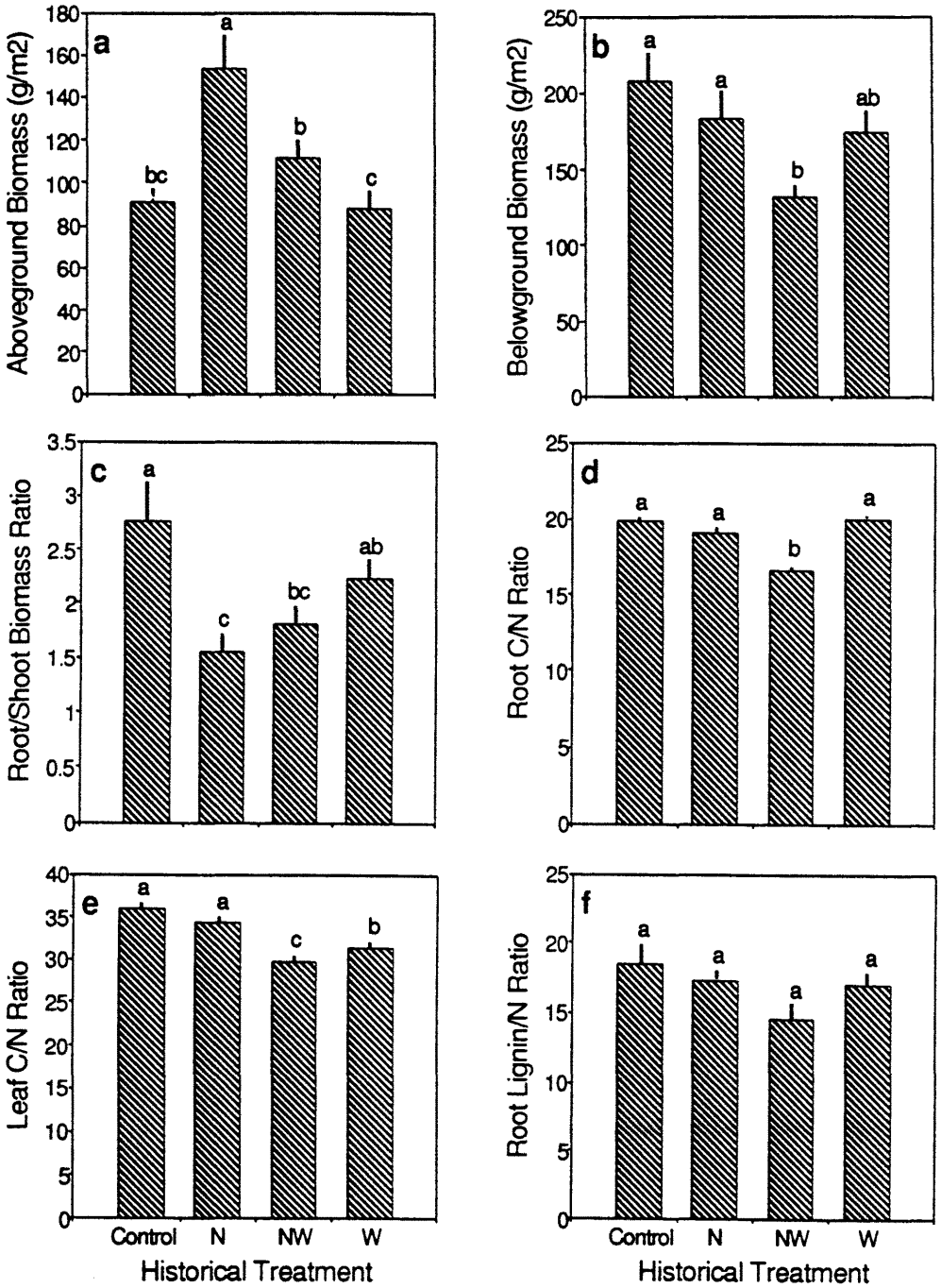
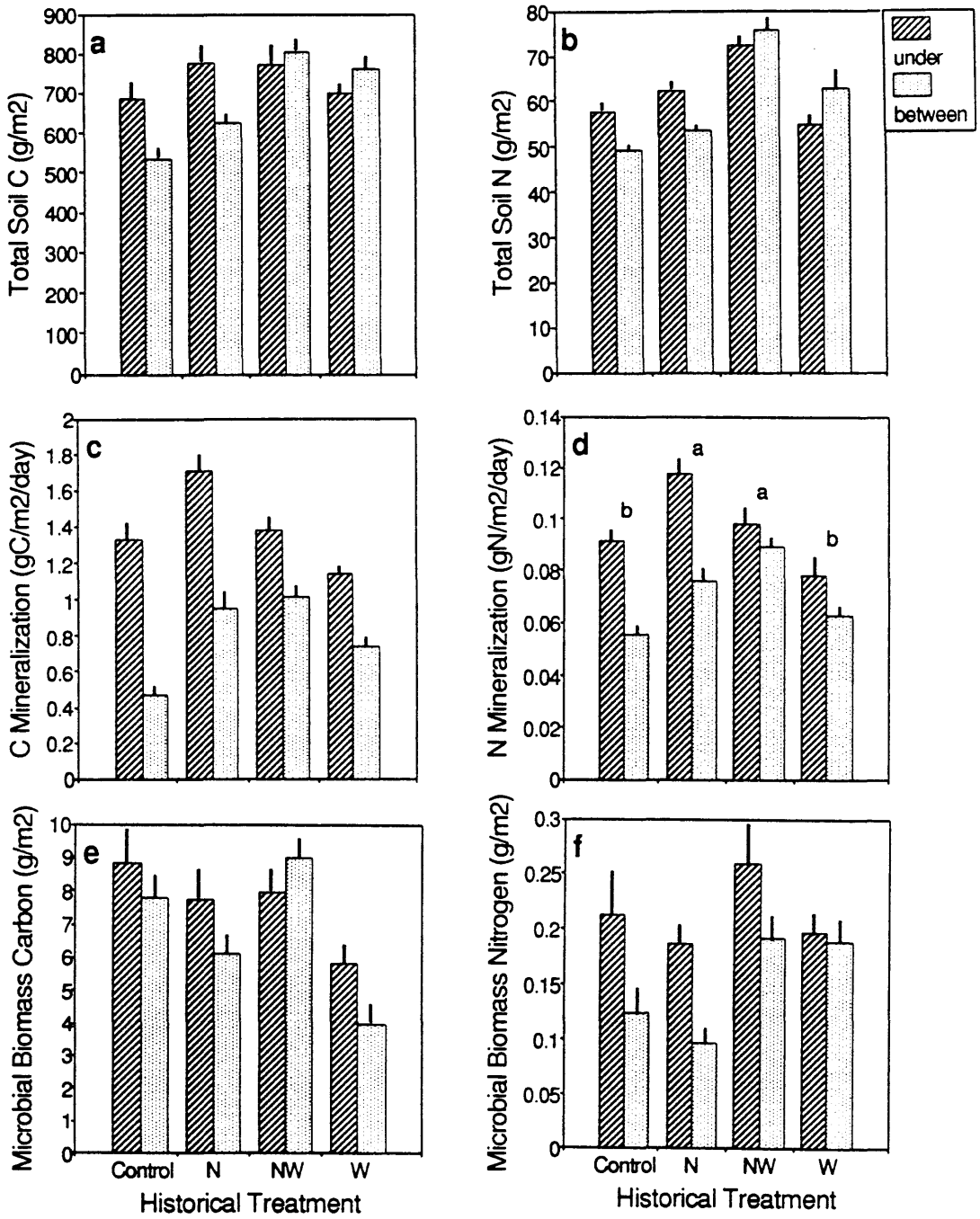

a
Aboveground Biomass (g/m2)
180
160
140
120
100
80
60
40
20
0
bc
a
b
c
b
Belowgroud Biomass (g/m2)
250
200
150
100
50
0
a
a
b
ab
c
Root/Shoot Biomass Ratio
3.5
3
2.5
2
1.5
1
0.5
0
a
c
bc
ab
d
Root C/N Ratio
25
20
15
10
5
0
a
a
b
a
e
Leaf C/N Ratio
40
35
30
25
20
15
10
5
0
a
a
c
b
Control
N
NW
W
Historical Treatment
f
Root Lignin/N Ratio
25
20
15
10
5
0
a
a
a
a
Control
N
NW
W
Historical Treatment

Figure 2.6. Total soil carbon (**a**), current total soil nitrogen (**b**), carbon mineralization rate (**c**), potential nitrogen mineralization rate (**d**), microbial biomass carbon (**e**), and microbial biomass nitrogen (**f**) in soils from under plants and between plants on plots in shortgrass steppe receiving no addition (Control), nitrogen addition (N), water addition (W), or both nitrogen and water addition (NW) from 1971-1974. Soils under and between 5 plant species were sampled; these data are averaged across plant species. The vertical line on each bar indicates 1 SE. Letters indicate situations where significant differences ($p<.05$) existed in soil properties (averaged across both under and between plant positions) among historical treatments.


a
Total Soil C (g/m2)
900
800
700
600
500
400
300
200
100
0
b
Total Soil N (g/m2)
80
70
60
50
40
30
20
10
0
under
between
c
C Mineralization (gC/m2/day)
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
d
N Mineralization (gN/m2/day)
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
a
a
b
b
e
Microbial Biomass Carbon (g/m2)
10
9
8
7
6
5
4
3
2
1
0
Control
N
NW
W
Historical Treatment
f
Microbial Biomass Nitrogen (g/m2)
0.3
0.25
0.2
0.15
0.1
0.05
0
Control
N
NW
W
Historical Treatment

III. PLANT EFFECTS ON SOIL NUTRIENT DYNAMICS ACROSS A PRECIPITATION GRADIENT IN GREAT PLAINS GRASSLANDS

ABSTRACT

The central grassland region of the U.S. encompasses major gradients in temperature and precipitation that determine the distribution of plant lifeforms, which in turn may influence key ecosystem processes such as nutrient cycling and soil organic matter dynamics. One such gradient is the 3x increase in precipitation from the eastern Colorado shortgrass-steppe, in the rain shadow of the Rocky Mountains, to the tallgrass prairie in eastern Kansas. I investigated the relative roles of plant species and plant cover in influencing soil C and N cycling in three sites along this gradient.

Plant cover (ie. the presence or absence of an individual plant) was relatively more important than plant species in explaining variability in soil properties at the dry site, the Central Plains Experimental Range in northeastern Colorado. However, plant species explained relatively more of the variability in soil properties than did plant cover at the two wetter sites, Hays and Konza, in central and eastern Kansas. The wettest sites had more continuous plant cover, resulting in less plant cover-induced variation in soil C and N, than did the dry site. Also, plant species at the wettest sites had higher and more

variable levels of tissue C:N than plant species at the dry site, both as a result of within species changes and changes in species composition. Aboveground tissue C:N was better correlated with net nitrogen mineralization rates at the wet sites than the dry site. The wettest sites had higher levels of total soil C and N and higher ratios of C:N than did the dry site.

These results indicate that the relative importance of plant cover patterns and plant species to soil C and N cycling varies over this gradient of increasing precipitation, with plant cover being most important at the dry end and plant species being most important at the wet end. The feedbacks between water availability and species composition and physiology over this regional gradient appear to be important in determining patterns in plant-soil relationships.

INTRODUCTION

A large body of work has focused on the effects of plant tissue chemical composition on decomposition and nutrient cycling. In general, high tissue C/N or lignin/N ratios are correlated with slow rates of decomposition and low rates of nitrogen mineralization (Fogel and Cromack 1977, Melillo et al. 1982, Stump and Binkley 1990). Some studies have focused on the relative importance of plant tissue chemical composition in the face of other, potentially interacting or overriding, environmental influences on decomposition and nutrient release. Meetemyer (1978, 1984) showed that tissue chemistry causing resistance to decay (i.e. high lignin values) had a much more pronounced inhibitory effect on

decomposition under moist environmental conditions than under drier conditions. Nadelhoffer et al. (1991), in a study of decomposition rates in soils from different Alaskan arctic ecosystems, found that substrate quality affected laboratory decomposition rates more than temperature. Pastor and Post (1986), using a simulation modeling approach, demonstrated that interactions between plant species characteristics such as tissue chemistry and abiotic environmental variables are important for predicting the dynamics of forest ecosystems.

The climatic gradients that create regional patterns in decomposition and nutrient cycling are also associated with variation in plant species composition. For example, the Central Grasslands region of the United States encompasses major gradients in temperature and precipitation that control the distribution of plant lifeforms (Borchert 1950, Weaver and Albertson 1956). Precipitation ranges from 300 mm/y in the west, in the rainshadow of the Rocky Mountains, to over 1000 mm/y in the east, and aboveground net primary production generally increases from west to east (Sala et al. 1988). Shortgrasses are dominant in the western part of the region while tallgrasses dominate in the eastern portion. Complex interactions among precipitation, temperature, and plant species composition likely determine decomposition and nutrient cycling patterns along regional gradients such as those in the Central Grasslands of the United States.

The relative importance of limiting resources (ie. water and nutrients) to plant production is likely to change as precipitation changes, and plant

responses to these limitations may affect patterns in nutrient cycling. One important pattern associated with increased precipitation is relatively less limitation of plant production by water and more limitation by nutrients, particularly nitrogen; this pattern may be manifest in an inverse correlation between plant water use efficiency and nitrogen use efficiency (Field et al. 1983). Plants growing under higher precipitation, all other factors being equal, will have higher nutrient use efficiencies and perhaps higher C/N ratios (Chapin 1980, Vitousek 1982) than plants growing in lower precipitation areas. Another possible outcome of increased precipitation is increased interspecies variability in tissue C/N ratios. This increased variability in plant C/N ratios might occur under mesic conditions because resources in addition to water (i.e. light, nitrogen) can limit plant growth at certain temporal and spatial scales, and plants may evolve a variety of different strategies manifested by a variety of C/N ratios to cope with different sets of limitations (Chapin et al. 1987). In semi-arid shortgrass-steppe, water is the primary limitation on plant production (Lauenroth et al. 1978), whereas in mesic tallgrass prairie, plants are limited by water as well as light and nutrients (Knapp and Seastedt 1986, Schimel et al. 1991, Seastedt et al. 1991). These results suggest that along a precipitation gradient from semi-arid shortgrass steppe to mesic tallgrass prairie, plant C/N ratios increase and become more variable, both within and among species. Thus, the opportunity for plant species-level control (via tissue quality) over decomposition and nutrient cycling rates may increase with precipitation.

Another important plant characteristic that varies with precipitation and is important to soil processes is plant cover patterns. Patterns of plant cover in dry grasslands tend to have an important horizontal dimension, whereas more mesic ecosystems have vertical as well as horizontal dimensions, resulting in multi-layer cover structures. In arid to semi-arid areas, patterns of plant-covered microsites vs. bare-ground microsites are a major determinant of soil nutrient patterns (Charley and West 1977, Burke 1989, Burke et al. 1989, Bolton et al. 1990, Schlesinger et al. 1990, Hook et al. 1991). This pattern is attributed to the acquisition of resources by plants from a large rooting radius, and the deposition of those resources as aboveground and belowground litter in a smaller radius beneath the plant. Among grasslands, semi-arid shortgrass-steppe has much more spatially discontinuous and patchy aboveground plant cover than mesic tallgrass prairie. Thus, heterogeneity in soil resources in tallgrass prairie is less likely to be controlled by spatial patterns in total biomass and litter accumulation. In shortgrass steppe, however, I expect plant-interspace location, or plant cover patterns, to be primary determinants of patterns in soil nutrient processes.

My objective in this study was to investigate the importance of plant species identity and cover patterns to soil C and N cycling along a precipitation gradient in the central Great Plains. I hypothesized that plant species identity would be relatively more important in the wettest site (tallgrass prairie), and

plant cover patterns would be relatively more important in the driest site (shortgrass-steppe).

METHODS

Site Descriptions

I sampled three sites arrayed along a precipitation gradient in the central Great Plains. The western-most, driest site was the Central Plains Experimental Range (CPER), located in north-central Colorado, approximately 60 km northeast of Fort Collins (40°49' N, 107°46' W). The CPER is administered by the Agricultural Research Service of the United States Department of Agriculture and is a member of the Long-term Ecological Research network, sponsored by the National Science Foundation (Franklin et al. 1990). Long-term annual precipitation at the CPER is 322 mm and mean monthly temperatures range from -3°C in January to 22°C in July (Parton and Greenland 1987), with an annual mean of 8.7°C. The vegetation of the area is typical of shortgrass steppe and is dominated by the perennial bunchgrass, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths (Milchunas et al. 1989). Other common species include the perennial grass, *Buchloë dactyloides* (Nutt.) Engelm.; the half-shrubs, *Gutierrezia sarothrae* (Pursh) Britt. & Rusby and *Artemisia frigida* Willd.; the forb, *Sphaeralcea coccinea* (Pursh) Rydb.; and the succulent, *Opuntia polyacantha* Haw. All plant nomenclature follows the Great Plains Flora Association (1986).

The intermediate precipitation site was located in west-central Kansas, near Hays (38°52' N, 99°23' W). This site has an average annual precipitation of 588 mm and an average annual temperature of 11.9°C (Hulett and Tomanek 1969, 1974). The vegetation consists of a mixture of short-, mid- and tallgrasses, such as *Bouteloua gracilis*, *Buchloe dactyloides*, *Bouteloua curtipendula* (Michx.) Kunth, *Andropogon gerardii* Vitman, and *Andropogon scoparius* Michx.

The eastern-most, wettest site was Konza Prairie Research Natural Area. This site is located in the Flint Hills of eastern Kansas, near Manhattan (39°05' N, 96°35' W), and is also a member of the Long-term Ecological Research network (Franklin et al. 1990). Annual precipitation is 835 mm and temperature ranges from a January average of -3°C to a July average of 27°C, with an annual mean of 12.8°C (Bark 1987). The vegetation is dominated by tallgrasses, especially *Andropogon gerardii*, *A. scoparius*, *Sorgastrum nutans* (L.) Nash and *Panicum virgatum* (L.) (Gibson and Hulbert 1987).

Species

I sampled plant tissue and soils associated with 5-6 different species at each site, and two species (*Bouteloua gracilis* and *Agropygon smithii* Rydb.) at all sites (Table 3.1). I chose species that were common at each site and that represented a variety of lifeforms. At CPER I sampled *Bouteloua gracilis*, a C_4 bunch grass; *Aristida longiseta* Steud., a C_4 bunch grass; *Stipa comata* Trin. &

Rupr., a C_3 bunch grass; *Agropyron smithii* Rydb., a C_3 rhizomatous grass; and *Artemisia frigida* Willd., a half-shrub; *Opuntia polyacantha* Haw., a succulent; *Psoralea tenuiflora* Pursh, a forb N-fixer; and *Gutierrezia sarothrae*, a half-shrub. At Hays I sampled *Agropyron smithii*; *Bouteloua gracilis*; *Andropogon gerardii*, a C_4, rhizomatous tall grass; *Andropogon scoparius*, a C_4 bunchgrass; *Aristida longiseta*; *Bouteloua curtipendula*, a C_4 rhizomatous grass; *Bromus japonicus*, an annual grass; and *Yucca glauca*, a scleropholous shrub. At Konza, I sampled *Agropyron smithii*; *Bouteloua gracilis*; *Andropogon gerardii*; *Andropogon scoparius*; *Bouteloua curtipendula*; *Sorgastrum nutans* (L.) Nash, a C_4 rhizomatous tall grass; *Sporobolus asper* (Michx.) Kunth, a C_4 bunchgrass; *Vernonia baldwinii* Torr., a forb; and *Ceanothus herbaceous* Raf. var. *pubescens* (T. & G.) Shinners, a shrub.

Soil and Plant Sampling and Analyses

I sampled plants and soils in two areas, or "blocks" at each site. The blocks represented areas with differing management strategies. At CPER and Hays, one block was grazed and one ungrazed, and at Konza one block was burned frequently (yearly) and one block was burned every 4 years. Since only one replicate of each block was sampled at each site, statistical inferences about management strategy are limited; however, I was interested primarily in testing the generality of the other factors across these different locations and management regimes.

I sampled soils directly under plants of each species and in adjacent openings between plants by taking 5 cm diameter, 5 cm deep soil cores. Samples from between plants were taken in openings at least 15 cm in diameter, at least 7-10 cm away from the target plant and neighboring plant canopies . Samples from under plants were taken at the location where a stem or a group of stems emerged from the soil. I took "under" and "between" cores from a total of 4 plants of each species in each block. Cores from two plants were composited for the analysis. Soil cores were placed in coolers immediately and were kept cool until microbially-mediated processes were measured (no more than 7 days).

Fresh soils were sieved to separate plant material and fragments greater than 2 mm in diameter. The soils were then weighed, mixed and subsampled for 4 analyses: water content, initial inorganic N, incubations to determine potential net N and C mineralization, and microbial biomass C. A 10 g subsample was extracted with 50 ml of 2 N KCl for 30 min on an orbital shaker to measure initial inorganic N. The extracts were allowed to settle for 10 min and then filtered through Whatman #40 paper. The extracts were refrigerated until analyzed for nitrate and ammonium on a Lachat autoanalyzer (EPA 1979).

For the soil incubation, a 20 g subsample from each composite sample was placed in a small beaker, brought to field capacity with deionized water and placed in a closed mason jar with 20 mls of deionized water in the bottom to

maintain a saturated atmosphere (Schimel 1986). Five mls of 2 N NaOH in a small vial were added to serve as a base trap for CO_2 respired by soil microbes (Schimel 1986). The samples were incubated at 25°C for 30 days, and then extracted with KCl, filtered and analyzed for nitrate and ammonium as described above. The base trap was titrated with 1 N HCl to determine the amount of CO_2 (Snyder and Trofymow 1984) released during incubation, or the potential C mineralization. Potential net N mineralization was calculated as the difference between initial and final inorganic N of the soil.

The chloroform fumigation-extraction procedure (Powlson and Jenkinson 1976 and Brookes et al. 1985) was used to estimate microbial biomass. A 10 g subsample of fresh, sieved soil was extracted with 50 ml of 0.5 M K_2SO_4 for 30 min on a 200 rpm orbital shaker and filtered through Whatman #40 paper. Another 10 g subsample of soil was fumigated with chloroform for 18 h, vented for 5 h, and extracted and filtered as described above. The control and fumigated soil extracts were frozen until they could be analyzed. Samples were thawed in warm water, agitated for 10 minutes and allowed to settle overnight before analysis the following day. Microbial biomass carbon was obtained by a wet oxidation diffusion procedure (Snyder and Trofymow 1984) performed on the extracts. The air-dried soil samples were ground and dried at 55°C before total carbon and nitrogen contents were measured using a Carlo-Erba automated combustion analyzer.

Aboveground standing dead tissue was collected from each species at

the end of the growing season. The tissue was dried, ground and analyzed for lignin using a modified Van Soest (1963) procedure (Waldern 1971). The tissue was also analyzed for total C and N using a Carlo-Erba automated combustion analyzer.

Statistical Analyses

Data were analyzed using ANOVA (SAS Institute 1989) and the Scheffe or the LSD procedure (depending on the power of the F test) to separate means. I tested the effects of blocks, species and position (under and between plants) and their interactions on soil variables at each of the three sites separately, since not all species were common to all sites. The design was a split-split plot, and F tests were constructed accordingly. Block was treated as the whole plot factor, species as the split factor and position as the split-split factor. I used contrast statements to compare the effects of species of different lifeforms or growth forms on soil properties. In order to test for possible species*site effects on soils, I used data from only the two species common to all three sites. In this case the design was again a split-split plot, with site and block as the whole-plot factors, species as the split factor and position as the split-split factor. I used a 2-way ANOVA for the effects of site, species and their interaction on plant tissue chemistry. Only data for the two species common to all three sites were used in this analysis.

RESULTS

Effects of plants on soil properties

Both plant species and position had significant effects on soils at all three sites, with plant position having particularly strong effects at the driest site, CPER (Fig. 3.1 and 3.2, Table 3.2). Also at CPER, position explained relatively more variability in soil properties than did plant species (Fig. 3.3). Soils under plants at CPER had significantly higher pool sizes and turnover rates of soil C and N than did soils from between plants (Fig. 3.1 and 3.2). Plant position interacted with species (Table 3.2), in that the under vs. between contrast in C and N mineralization rates was more pronounced for the shrubs *Gutierrezia sarothrae* and *Artemisia frigida* than for the other species. Species and lifeforms also significantly affected C and N mineralization (Table 3.2), with the two shrub species having significantly higher rates of C and N mineralization than did the grasses. The effects of species on total soil C and N were inconsistent across blocks (Table 3.2). The C_3 grasses, *Agropyron smithii* and *Stipa comata* had significantly higher levels of nitrogen and microbial biomass carbon in their soil than did the C_4 grasses at CPER (Table 3.2).

The effects of plant position at Hays (Table 3.3) were not as strong or consistent across all soil properties as they were at CPER (Table 3.2), and explained relatively less variation in soil properties than at CPER (Fig. 3.3). However, rates of C and N mineralization were again significantly higher under than between plants at Hays (Table 3.3, Fig. 3.2). These position effects were

consistent among blocks, but interacted with species (Table 3.3), primarily because soils associated with the annual grass, *Bromus japonicus*, had less under vs. between soil contrast than did soils of the perennial species. Species affected total pools and turnover rates of soil C and N, and in the case of total soil C and N interacted with block (Table 3.3). The cool-season grass, *Agropyron smithii*, had significantly higher rates of nitrogen mineralization and lower C:N mineralization than did the warm-season grasses at Hays (Table 3.3). Also, the annual *Bromus japonicus* had significantly lower soil C, higher rates of N mineralization and lower C:N mineralization rates in its soils than did soils of the perennial species (Table 3.3). The C_4 bunchgrass, *Andropogon scoparius* had significantly higher total soil C, higher soil C:N, lower N mineralization rates, higher C:N mineralization rates, and higher microbial biomass C than did most of the other species at Hays (Table 3.3). Soils from the grazed block had higher total soil C and N and higher rates of C and N mineralization than soil from the ungrazed block. The species*block interaction at Hays was mainly due to the fact that *Bromus japonicus* and *Yucca glauca* had similar soils on the two blocks while the other species' soils generally had higher soil C and N on the grazed block.

Like soil properties at Hays, variability in soil properties at Konza were explained more, in general, by plant species than plant position (Fig. 3.3). However, plant position had significant effects on soil properties at Konza, with soils under plants having higher soil C:N, microbial biomass C, and higher C

and N mineralization rates than soil from between plants (Table 3.4). Plant species significantly affected total C, C:N and N mineralization at Konza. Many of these effects were due to *Agropyron smithii*, which had lower soil C and N, lower C:N, and higher rates of C and N mineralization than did the warm season grasses (Table 3.4). Also the rhizomatous grasses, *A. smithii* and *Bouteloua curtipendula* had lower soil C:N ratios, higher N mineralization rates and microbial biomass C than did the bunch grasses (Table 3.4). The tall grasses, *Andropogon gerardii*, *Sorgastrum nutans*, and *Sporobolus asper*, had significantly higher total soil C and N in their soils than did the mid- and short grasses. *Andropogon scoparius* and *Sporobolus asper* had significantly higher total soil C:N and, along with *Agropyron smithii*, had higher rates of C mineralization in their soils than the other species. Also, *Andropogon scoparius* had significantly lower rates of net N mineralization than the other species. Block had strong effects on soils, with the soils from the 4-year burn having higher pool sizes and turnover rates of C and N than soils from the annually burned block (Table 3.4). In some cases, block interacted with species to influence soils (Table 3.4). These interactions were largely due to *Agropyron smithii*, which had bigger differences between its soils on the two blocks than did the other species.

Overall, plant properties explained substantial amounts of variation in soil properties (Fig. 3.3). The soil property that seemed to be most sensitive to plant species and cover pattern was the rate of C mineralization, while N

turnover was less sensitive and total pool sizes of soil C and N were least sensitive.

Effects of site on plant and soil properties

Plant tissue chemistry and soil nutrient properties varied significantly among sites across the precipitation gradient. Plant tissue from both *Agropyron smithii* and *Bouteloua gracilis* (the only two species sampled at all sites) at CPER had significantly higher nitrogen concentrations and lower C:N and lignin:N ratios than tissue from both Hays and Konza (Table 3.5, Table 3.6). This change in plant tissue chemistry across the sites also occurred because different plant species were sampled at Hays and Konza then CPER, and these species tended to have higher C:N ratios than the plant species sampled at CPER (Table 3.6). Thus, the change in tissue chemistry across the sites occurred as a result of 1) statistically significant within species (*Bouteloua gracilis* and *Agropyron smithii*) changes and 2) changes in species composition.

Total pools of soil carbon and nitrogen were highest at Hays, intermediate at Konza, and lowest at CPER (Fig. 3.1a and 3.2b). CPER also had the lowest total soil C:N ratios (Fig. 3.1c). The effects of site on total soil C and N interacted with block (Table 3.7); this was primarily the result of larger differences in soils between the blocks (burned annually and burned every 4 years) at Konza and in some cases, Hays, than blocks at CPER (grazed and ungrazed). Labile pools of soil carbon and nitrogen, indexed by potential mineralization rates, were not different among sites (for carbon, Fig. 3.2) or

were higher at CPER than at Hays and Konza (Fig. 3.2). It is important to note, however, that mineralization rates were measured in the laboratory under optimal temperature and moisture conditions. The laboratory-imposed release from field moisture constraints on mineralization rates was likely greater for CPER than for Hay and Konza. The ratio of C:N mineralized was significantly higher at Hays and Konza than at CPER (Table 3.7). The amount of carbon in microbial biomass was also higher at Hays and Konza than at CPER (Table 3.7, Fig. 3.3c).

Plant species had significant effects on soils at all three sites and in some cases their effects were dependent on site. In comparing the two species that occurred at all three sites, I found that *Agropyron smithii* had higher rates of C and N mineralization and microbial biomass carbon than *Bouteloua gracilis* when averaged over all sites (Table 3.7). However this result was primarily due to the large differences between the two at Konza; differences in soil properties between the two species at CPER and Hays were much less than at Konza, and this result gave rise to significant site*species interaction effects (Table 3.7).

Tissue chemistry (aboveground C:N ratios) at Hays and Konza was more closely correlated with potential net nitrogen mineralization than was tissue chemistry at CPER (Fig. 3.4). Also, the tissue chemistry of species was much more variable among species at Hays and Konza than among species at CPER (Table 3.6).

DISCUSSION

The relationship between ecosystem structure and function is a recurrent theme in ecosystem ecology research and a recent manifestation of this issue is interest in the relationship between plant community characteristics and ecosystem function (e.g. Mooney and Schulze 1993, Chapin 1993). I hypothesized that two aspects of vegetation structure, plant cover patterns and species composition, would vary in relative influence on soil carbon and nitrogen properties across a precipitation gradient in the Central Grasslands. Discontinuities in plant cover patterns are an often overlooked but important component of vegetation structure, particularly in grassland or savanna systems. Plant cover showed a distinct pattern in importance, with plant cover strongly affecting soil carbon and nitrogen at the dry site, CPER, and plant cover having much less of an effect at the wetter sites, Hays and Konza. The enhancement of soil nutrients under plant canopies vs. canopy interspaces is a well-documented occurrence in arid areas and it was not surprising that data from the driest site showed this pattern. However, I was interested in how and where this plant-induced soil heterogeneity dissipates or becomes overwhelmed by other factors. The data suggest that plant biomass, and associated soil organic matter, become more spatially continuous between grassland sites as mean annual precipitation increases from 322 mm to 588 mm. The decreasing importance of plant cover along this dry to wet gradient is likely due to more continuous above- and belowground plant cover at Konza and Hays than at

CPER. The plant interspaces at CPER have much less root biomass (Hook et al. 1994) than positions under plant canopies, whereas roots are likely much more continuous in the soil at Hays and Konza.

Although plant species had significant effects on soil properties at all sites, the relative amount of variation in soil properties explained by plant species increased from CPER to Konza. Also, significantly more difference existed in soil properties among the two species, *Agropyron smithii*, and *Bouteloua gracilis* at Konza than at CPER. A potential explanation for increasing species importance is that tissue quality, measured on aboveground plant parts at the end of the growing season, was generally lower (higher C/N ratios) and more variable among species at Hays and Konza than at CPER. Thus, plant tissue quality may have been a more important factor determining soil properties at the wet than the dry sites. Furthermore, these data suggest that aboveground plant C:N ratio explains more variation in potential nitrogen mineralization at Hays and Konza than at CPER.

The inverse relationship between precipitation and tissue quality shown in the data is used in the ecosystem simulation model of grassland soil organic matter, CENTURY (Parton et al. 1987). The tissue quality-precipitation relationship in CENTURY was based on unpublished tissue quality data collected during the US-IBP Grassland Biome project. The proximate cause of this relationship could be the change from an herbaceous plant community (high quality tissue) to a community with more woody plants (low quality tissue) as

precipitation increases. However, the data suggest that even among herbaceous plants, and within species, higher precipitation could result in lower tissue quality, presumably because of tradeoffs between water use efficiency and nutrient use efficiency (Field et al. 1983, Lajtha and Whitford 1989). This tradeoff could occur because plants under high precipitation are able to keep stomata open longer than plants at the dry sites, thereby capturing more carbon per amount of N-rich photosynthetic machinery. This interpretation is consistent with Vitousek et al. (1994), who observed higher substrate quality in native Hawaiian trees growing on dry sites than trees of the same species growing on wet sites. Overall, this study suggests that some aspects of plant species characteristics, such as tissue quality, are not conservative in these grassland species. Thus, the driving variable, precipitation, could potentially override intrinsic species differences in tissue quality to affect soil organic matter dynamics. Also, since precipitation appears to exert large controls on species distribution in these ecosystems, the two factors, species composition and water availability, appear to be closely linked with strong feedbacks in their effects on soil organic matter dynamics.

Species composition had significant effects on soil properties at each site, and in some cases, these effects could be attributed to lifeform or tissue chemistry characteristics. At CPER, the two shrub species had higher rates of C and N mineralization in their soils than did the grasses. The shrubs did not have particularly high tissue quality, so this result may be due to the high

quantity of litter deposited under the shrub canopy relative to the grass canopies. Also, the shrubs at CPER had more plant-interspace heterogeneity in their soils than did the other plant species, a result consistent with work in desert grasslands showing more heterogeneity associated with shrubs than grasses (Schlesinger et al. 1990), although work in Great Basin grasslands has shown more soil heterogeneity associated with bunchgrasses than shrubs (Jackson and Caldwell 1993).

At Hays, plant-induced soil heterogeneity was significantly less for soils associated with the annual, *Bromus japonicus*, than for the perennial species. Also at Hays, the C_3 grass, *Agropyron smithii*, had higher rates of potential net N mineralization and lower C:N mineralization rates than the C_4 grasses. *Agropyron smithii* also had higher tissue quality than some of the C_4 species at Hays, which may explain the high N turnover rates in associated soils. *Bromus japonicus* also differed significantly in several soil properties from the other species at Hays. The presence of this annual species may reflect a recent soil disturbance (eg. Platt 1975), and so the soil properties in the *B. japonicus* soils may reflect the effects of the disturbance more than the effects of this particular species.

At Konza, soils associated with *Agropyron smithii* differed from soils associated with other species in many cases. These effects may be explained in part by the fairly high quality tissue of *A. smithii* relative to the other species. Also, *A. smithii* tends to grow on fairly fine-textured soils at Konza, so the

possibility exists that the differences observed were the result of *A. smithii* colonizing unique soil locations rather than direct effects of *A. smithii* on soils. Also at Konza, *Andropogon scoparius* had significantly higher C mineralization rates, lower N mineralization rates and (along with *Sporobolus asper*) higher total soil C:N than most of the other species. *Andropogon scoparius* and *Sporobolus asper* are both very productive bunchgrasses and soils under their canopies likely have a large amount of organic matter. This large amount of organic matter in the soil probably led to high microbial activity (thus high C mineralization rates) and immobilization of N into microbial biomass, resulting in low net nitrogen mineralization rates. Like *Andropogon scoparius* at Konza, *Andropogon scoparius* at Hays also had low rates of net N mineralization, high soil C:N, and high C:N mineralization rates, as well as high microbial biomass C, all indicators of high microbial activity, possibly as a result of plentiful substrate.

The increase in total soil pool sizes of carbon and nitrogen with increasing precipitation is consistent with other observations of soil organic matter patterns over temperature and precipitation gradients (Parton et al. 1987, Burke et al. 1989). This pattern can be attributed to changes in production, decomposition, or physical soil characteristics such as texture. In this case, decomposition would likely be greater at the wet sites (Meetemyer 1978) and production is greater (Sala et al 1988); therefore greater soil pools of carbon and nitrogen are likely caused by greater plant production at the wetter sites.

An alternative, or complementary, explanation for the increase in soil carbon and nitrogen at the wet sites is that of soil texture changes; soils in the dry site tend to be coarser-textured than soils in the wet site.

One interesting, albeit not statistically replicated, result was that management treatment (forming the two blocks at each site) had much more of an effect on soil properties at Konza and Hays than at CPER. This result is consistent with other studies that have found burning or grazing management in sub-humid grasslands to have very strong effects on soil carbon dynamics (Seastedt et al. 1994). This study also suggests that management strategies that disrupt plant cover will have much more of an effect on soil properties at CPER than at Hays and Konza, whereas management strategies that involve the establishment of different plant species will have more of an effect at Hays and Konza than at CPER.

This study emphasizes that plant community structure can have important consequences for soil carbon and nitrogen dynamics. Furthermore, the importance of two particular elements of vegetation structure, plant species composition vs. plant cover, for soil processes shifts over a gradient in precipitation. The observed pattern in soil carbon and nitrogen processes over this precipitation gradient is likely a result of complex interactions between abiotic variables such as precipitation and soil texture and biotic variables such as plant and microbial physiology and community composition.

LITERATURE CITED

Bolton, H, J.L. Smith, and R.E. Wildung. 1990. Nitrogen mineralization potential of shrub-steppe soils with different disturbance histories. Soil Science Society of America Journal. 54: 887-891.

Borchert, J.R. 1950. The climate of the central North American grassland. Annals of the Association of American Geographers. 40: 1-39.

Brookes, P.C., A. Landman, G. Pruden, and D.S. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology and Biochemistry 17: 837-842.

Burke, I.C., W.A. Reiners, and D.S. Schimel. 1989. Organic matter turnover in a sagebrush steppe landscape. Biogeochemistry 7:11-31.

Burke, I.C. 1989. Control of N mineralization in a sagebrush steppe landscape. Ecology 70(4): 1115-1126.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233-260.

Chapin, F.S., A.J. Bloom, C.B. Field, and R.H. Waring. 1987. Plant responses to multiple environmental factors. Bioscience 37: 49-57.

Chapin, F.S. 1993. Functional role of growth forms in ecosystem and global processes. *in* J.R. Ehleringer and C.B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, London.

Charley, J.L., and N.E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. Journal of Ecology 63: 945-963.

EPA. 1979. Methods for chemical analysis of water and wastes. EPA-600/4-79-020, March 1979, U.S. Environmental Protection Agency. U.S. Government Printing Office, Washington, D.C.

Field, C., J. Merino, and H.A. Mooney. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia 60: 384-389.

Fogel, R. and K. Cromack. 1977. The effects of habitat and substrate quality on

Douglas-fir litter decomposition in western Oregon. Canadian Journal of Botany 55: 1632-1640.

Franklin, J.F., C.S. Bledsoe, and J.T. Callahan. 1990. Contributions of the Long-Term Ecological research program. Bioscience 40: 509-523.

Gibson, D.J., and L.C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72: 175-185.

Great Plains Flora Association. 1986. Flora of the Great Plains. Univ. Press of Kansas, Lawrence, Kansas, USA.

Hook, P.B., I.C. Burke, and W.K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. Plant and Soil 138: 247-256.

Hook, P.B., W.K. Lauenroth, and I.C. Burke. Spatial patterns of roots in a semiarid grassland: abundance of canopy openings and regeneration gaps. Journal of Ecology: in press.

Hulett, G.K. and G.W. Tomanek. 1969. Remnant prairies on the shallow limy range site in North Central Kansas. Journal of Range Management 22: 19-23.

Jackson, R.B. and M.M. Caldwell. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. Journal of Ecology 81: 683-692.

Knapp, A.K. and T.R. Seastedt. 1986. Detritus accumulation limits the productivity of tallgrass prairie. Bioscience 36: 662-668.

Lajtha, K. and W.G. Whitford. 1989. The effects of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. Oecologia 80: 341-348.

Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978, The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36: 211-222.

Meetemyer, V. 1978. Macroclimatic and lignin control of litter decomposition rates. Ecology 59: 465-472.

Meetemyer, V. 1984. The geography of organic decomposition rates. Annals of the Association of American Geographers 74: 551-560.

Melillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621-626.

Milchunas, D.G., W.K. Lauenroth, P.L. Chapman, and M.K. Kazempour. 1990. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80: 11-23.

Mooney, H.A., and E. Schulze. 1993. Biodiversity and ecosystem function. Springer Verlag. New York. 525 p.

Nadelhoffer, K.J., A.E. Giblin, G.R. Shaver, and J.A. Laundre. 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology 72: 242-253.

Parton, W.J., and D. Greenland. 1987. Central Plains Experimental Range Site, Colorado. Pages 23-27 *in* D. Greenland, editor. The climates of the long-term ecological research sites. Occasional Paper No. 44, Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, USA.

Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51: 1173-1179.

Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycle. Biogeochemistry 2: 3-27.

Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs 45: 285-305.

Powlson D.S., and D.S. Jenkinson. 1976. The effects of biocidal treatments on metabolism in soil-II. Gamma irradiation, autoclaving, air-drying and fumigation. Soil Biology and Biochemistry 8: 179-188.

Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary production of the Central Grassland region of the United States. Ecology 69: 40-45.

SAS Institute. 1989. SAS Statistics, Version 6.08. SAS Institute, Cary, N.C.

Seastedt, T.R., J.M. Briggs, and D.G. Gibson. 1991. Controls of nitrogen limitations in tallgrass prairie. Oecologia 87:72-79.

Seastedt, T.R., C.C. Coxwell, D.S. Ojima, and W.J. Parton. 1994. Controls of plant and soil carbon in a semihumid temperate grassland. Ecological Applications 4: 344-353.

Schimel, D.S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry 2:345-357.

Schimel, D.S., T.G.F. Kittel, A.K. Knapp, T.R. Seastedt, W.J. Parton and V.B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. Ecology 72: 672-684.

Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.G. Whitford. 1990. Biological feedbacks in global desertification. Science 247: 1043-1047.

Snyder, J.D., and J.A. Trofymow. 1984. A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil samples. Communications in Soil Science and Plant Analysis. 15: 587-597.

Stump, L.M., and D. Binkley. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Canadian Journal of Forest Research 23: 492-502.

Van Soest P.F. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. Journal of the Association of Official Analytical Chemists 46: 829-835.

Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. American Naturalists 119: 553-572.

Vitousek, P.M., D.R. Turner, W.J. Parton, and R.L. Sanford. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms and models. Ecology 75: 418-429.

Waldern, D.E. 1971. A rapid micro-digestion procedure for neutral and acid detergent fiber. Canadian Journal of Animal Science 51: 67-69.

Weaver, J.E. and F.W. Albertson. 1956. Grasslands of the Great Plains. Johnsen Publishing Co., Lincoln, NE. 395 p.

Table 3.1. Sites and plant species sampled. All species are perennial except where otherwise noted.

Central Plains Experimental Range (NE Colorado)

Bouteloua gracilis	warm season*, short bunch grass
Aristida longiseta	warm season, mid-length bunch grass
Stipa comata	cool season, mid-length bunch grass
Agropyron smithii	cool season, mid-length rhizomatous grass
Artemisia frigida	half-shrub
Opuntia polyacantha	succulent
Psoralea tenuiflora	forb, symbiotic nitrogen-fixer
Gutierrezia sarothrae	half-shrub

Fort Hays State University College Farm, Hays, KS

Agropyron smithii	cool season, mid-length rhizomatous grass
Bouteloua gracilis	warm season, short bunchgrass
Andropogon gerardii	warm season, tall rhizomatous grass
Andropogon scoparius	warm season, mid-length bunchgrass
Aristida longiseta	warm season, mid-length bunchgrass
Bouteloua curtipendula	warm season, mid-length rhizomatous grass
Bromus japonicus	annual mid-length grass
Yucca glauca	sclerophylous shrub

Konza Prairie Research Natural Area, Manhattan, KS

Agropyron smithii	cool season, mid-length, rhizomatous grass
Bouteloua gracilis	warm season, short, bunch grass
Andropogon gerardii	warm season, tall, rhizomatous grass
Andropogon scoparius	warm season, mid-length, bunchgrass
Bouteloua curtipendula	warm season, mid-length, rhizomatous grass
Sorgastrum nutans	warm season, tall, rhizomatous grass
Sporobolus asper	warm season, tall bunchgrass
Vernonia baldwinii	forb
Ceanothus herbaceous	shrub

*Warm or cool season refers to the season during which most growth and activity takes place. Warm season plants generally have the C_4 photosynthetic pathway and cool season plants have the C_3 pathway.

Table 3.2. F values from a 3-way ANOVA table (using a split-split plot design structure) for the effects of species (see list of species in Table 3.1), block (grazed and ungrazed) and position (under plant canopy or between plant canopy) on soil properties at the CPER. The effects of species have been treated separately, and grouped according to life- or growth form.

Factor	Total Soil C	Total Soil N	Total Soil C:N	C Mineralization	N Mineralization	C:N Mineralization	Microbial Biomass C
Block	0.18	0.15	0.77	1.36	4.76	0.43	52.31*
Species	2.78*	3.81*	1.76	5.06**	3.28*	0.88	1.51
Species*Block	5.76**	4.06*	3.41*	0.69	0.35	0.51	2.20
Position	39.05***	20.67***	31.30***	294.75***	145.72***	77.93***	20.17***
Position*Block	6.43*	5.37*	2.23	0.16	3.17	4.27	1.08
Position*Species	1.18	0.86	0.97	6.28**	5.47**	3.80*	1.38
Position*Species*Block	3.23	1.92	1.54	1.77	1.00	1.40	1.38
Rhizomatous vs.bunch grasses	0.21	1.10	0.18	0.11	0.29	1.05	3.17
Cool- vs. Warm season grasses	4.41	11.79**	0.62	4.25	4.59	0.63	8.45*
Shrubs vs. grasses	0.96	2.33	0.03	24.36***	9.10**	0.29	0.20

* p<.0500
** p<.0100
*** p<.0010

Table 3.3. F values from a 3-way ANOVA table (using a split-split plot design structure) for the effects of species (see list of species in Table 3.1), block (grazed and ungrazed) and position (under plant canopy or between plant canopy) on soil properties at Hays. The effects of species have been treated separately, and grouped according to life- or growth form.

Factor	Total Soil C	Total Soil N	Total Soil C:N	C Mineralization	N Mineralization	C:N Mineralization	Microbial Biomass C
Block	253.42**	83.40*	1.32	1403.91***	51.45*	1.41	0.05
Species	3.40*	1.24	5.60**	1.07	2.76*	3.44*	3.26*
Species*Block	2.83*	3.76*	2.52	0.71	0.68	1.57	1.90
Position	1.08	1.63	0.17	32.48***	4.55*	6.41*	0.20
Position*Block	0.37	0.34	0.01	0.11	0.01	2.99	1.31
Position*Species	1.83	1.40	2.61	2.97*	1.14	2.82*	3.40*
Position*Species*Block	0.53	0.36	1.52	0.36	0.49	2.46	2.02
Rhizomatous vs. bunch grasses	2.39	0.49	3.71	3.32	0.85	2.90	0.46
Cool- vs. Warm season grasses	3.17	1.34	2.99	0.41	14.5**	11.89**	0.69
Shrub vs. grasses	0.03	0.26	0.72	0.01	0.63	1.18	0.04
Annual vs. Perennial	6.01*	3.91	3.35	0.61	10.44**	5.47*	0.28

* p<.0500
** p<.0100
*** p<.0010

Table 3.4. F values from a 3-way ANOVA table (using a split-split plot design structure) for the effects of species (see list of species in Table 3.1), block (burned annually and every four years) and position (under plant canopy or between plant canopy) on soil properties at Konza. The effects of species have been treated separately, and grouped according to life- or growth form.

Factor	Total Soil C	Total Soil N	Total Soil C:N	C Mineralization	N Mineralization	C:N Mineralization	Microbial Biomass C
Block	243.88**	215.08**	10.59	3.18	1.48	3.86	26.09*
Species	2.83*	2.30	4.73**	2.70	10.44***	2.18	1.62
Species*Block	1.52	2.18	0.79	2.80*	4.52**	1.09	4.66**
Position	0.41	0.00	7.03*	25.57***	15.88**	21.75***	12.03**
Position*Block	0.84	1.20	0.19	2.67	0.04	3.46	1.14
Position*Species	0.80	1.14	1.04	1.88	10.04***	8.87***	3.14*
Position*Species*Block	0.36	0.51	0.22	0.92	1.45	2.74	1.66
Rhizomatous vs. bunch grasses	1.77	0.21	9.17**	0.88	7.30*	0.61	5.09*
Cool- vs. Warm Season grasses	15.43**	10.31**	19.50***	9.59**	64.07***	2.14	1.81
Forb/Shrub vs. grasses	2.81	2.64	0.59	0.49	0.00	0.97	2.77
Tall vs. Mid/Short grasses	5.88*	5.18*	2.47	0.89	1.34	0.02	0.98

* p<.0500
** p<.0100
*** p<.0010

Table 3.5. Results of a two-way ANOVA, showing F Values for the effects of species (*Bouteloua gracilis* and *Agropyron smithii*), site (CPER, Hays and Konza) and their interaction on nitrogen concentration, lignin concentration, C:N or lignin:N of aboveground standing dead tissue.

Factor	Nitrogen	Lignin	Carbon:Nitrogen	Lignin:Nitrogen
Site	44.93***	2.37	19.64***	11.21***
Species	1.76	1.74	3.26	0.01
Species*Site	0.84	1.48	0.84	0.08

* p<.0500
** p<.0100
*** p<.0010

Table 3.6. Nitrogen (% of dry weight), lignin (% of dry weight), carbon:nitrogen and lignin:nitrogen in aboveground standing dead tissue (only leaves from shrubs) collected from plants of species at three sites. Means of 4 samples are shown with 1 SE in parentheses. Where no SE is shown, the samples were composited before the analyses.

Site and Species		Nitrogen	Lignin	Carbon: Nitrogen	Lignin: Nitrogen
CPER					
	Agropyron smithii	1.4 (.09)	6.9 (.2)	34 (2.3)	4.8 (0.3)
	Artemisia frigida	2.1 (.06)	7.9 (.4)	23 (0.8)	3.7 (0.3)
	Aristida longiseta	1.1 (.03)	7.4 (.2)	40 (1.2)	6.9 (0.5)
	Bouteloua gracilis	1.3 (.06)	6.8 (.1)	32 (1.3)	4.8 (0.3)
	Gutierrezia sarothrae	1.2	16.0	40	13.7
	Opuntia polyacantha	0.6	8.0	72	13.3
	Psoralea tenuiflora	1.4	10.0	31	7.2
	Stipa comata	1.1 (.01)	8.6 (.2)	40 (0.3)	7.5 (0.2)
Hays					
	Agropyron smithii	0.7 (.05)	7.2 (0.3)	63 (4.1)	10.6 (1.1)
	Andropogon gerardii	0.4 (.03)	13.4 (5.5)	123 (8.0)	38.3 (17.4)
	Andropogon scoparius	0.4 (.03)	8.1 (1.5)	115 (8.8)	21.1 (4.3)
	Aristida longiseta	0.8 (.03)	7.1 (0.3)	53 (2.3)	9.2 (0.7)
	Bouteloua curtipendula	0.6 (.05)	8.5 (0.4)	69 (5.2)	14.4 (0.5)
	Bouteloua gracilis	0.9 (.04)	9.5 (0.4)	47 (2.4)	11.0 (0.6)
	Bromus japonicus	0.8 (.12)	17.9 (5.3)	53 (9.8)	21.4 (3.3)
	Yucca glauca	1.3 (.07)	7.6 (0.7)	36 (1.7)	6.0 (0.2)
Konza					
	Agropyron smithii	0.7 (.07)	6.9 (1.1)	67 (6.1)	10.4 (1.8)
	Andropogon gerardii	0.5 (.13)	9.8 (2.7)	106 (23.6)	25.3 (12.1)
	Andropogon scoparius	0.5 (.03)	7.3 (1.5)	82 (4.9)	13.8 (3.2)
	Bouteloua curtipendula	0.6 (.03)	9.0 (0.6)	64 (4.6)	14.4 (0.8)
	Bouteloua gracilis	0.8 (.12)	7.1 (1.2)	61 (12.9)	9.8 (1.9)
	Sorgastrum nutans	0.4 (.04)	6.4 (0.8)	103 (9.9)	15.7 (3.6)
	Sporobolus asper	0.6 (.01)	6.1 (0.2)	71 (1.0)	9.8 (0.2)
	Vernonia baldwinii	1.0 (.02)	19.1 (3.4)	47 (0.4)	19.1 (3.7)
	Ceanothus herbaceous	1.5 (.06)	8.7 (0.8)	32 (1.1)	6.0 (0.8)

Table 3.7. F values from a four-way ANOVA table (using a split-split plot design) showing the effects of site (CPER, Hays or Konza), block (either an unburned/ungrazed block or a burned/grazed block) species (*Agropyron smithii* or *Bouteloua gracilis*) and position (under plant canopy or between plant canopy) and their interactions on soil properties.

Factor	Total Soil C	Total Soil N	Total Soil C:N	C Mineralization	N Mineralization	C:N Mineralization	Microbial Biomass C
Site	62.95**	128.46***	3.19	3.46	5.68*	9.55*	14.22**
Block	24.49**	25.22**	5.70	7.57*	5.55	1.90	9.13*
Site*Block	10.02*	12.12**	1.56	1.61	1.96	1.51	0.14
Species	2.26	1.28	0.75	7.88*	25.48**	2.52	26.68**
Species*Site	7.26*	5.94*	1.74	1.73	5.75*	1.13	2.83
Species*Block	1.59	3.00	0.06	3.88	14.17**	0.88	0.32
Species*Site*Block	5.99*	4.72	1.77	3.24	8.14*	0.19	0.48
Position	4.20	1.68	6.15*	22.06***	27.84***	16.84**	5.77*
Position*Site	2.29	1.03	3.70	0.86	5.27*	2.87	2.22
Position*Block	4.61	3.68	1.72	.23	0.59	1.36	0.96
Position*Species	0.00	0.05	0.53	1.43	21.69***	12.21**	4.40
Position*Site*Block	1.88	1.02	2.11	0.76	1.03	2.41	0.14
Position*Site*Species	0.14	0.13	0.95	1.60	3.45	0.82	0.91
Position*Site*Sp.*Block	0.98	0.31	1.63	1.04	2.18	2.40	0.08

* p<.0500; ** p<.0100; *** p<.0010

Figure 3.1. Total soil carbon (a.), total soil nitrogen (b.), and soil C:N ratio (c.) in soil collected from under and between plants of 8-9 species at each of three sites: Central Plains Experimental Range (CPER) in northeastern Colorado, the Fort Hays State University College Farm near Hays in west-central Kansas, and Konza Prairie Research Natural Area near Manhattan in eastern Kansas. The vertical lines on each bar indicate 1 SE of the mean.

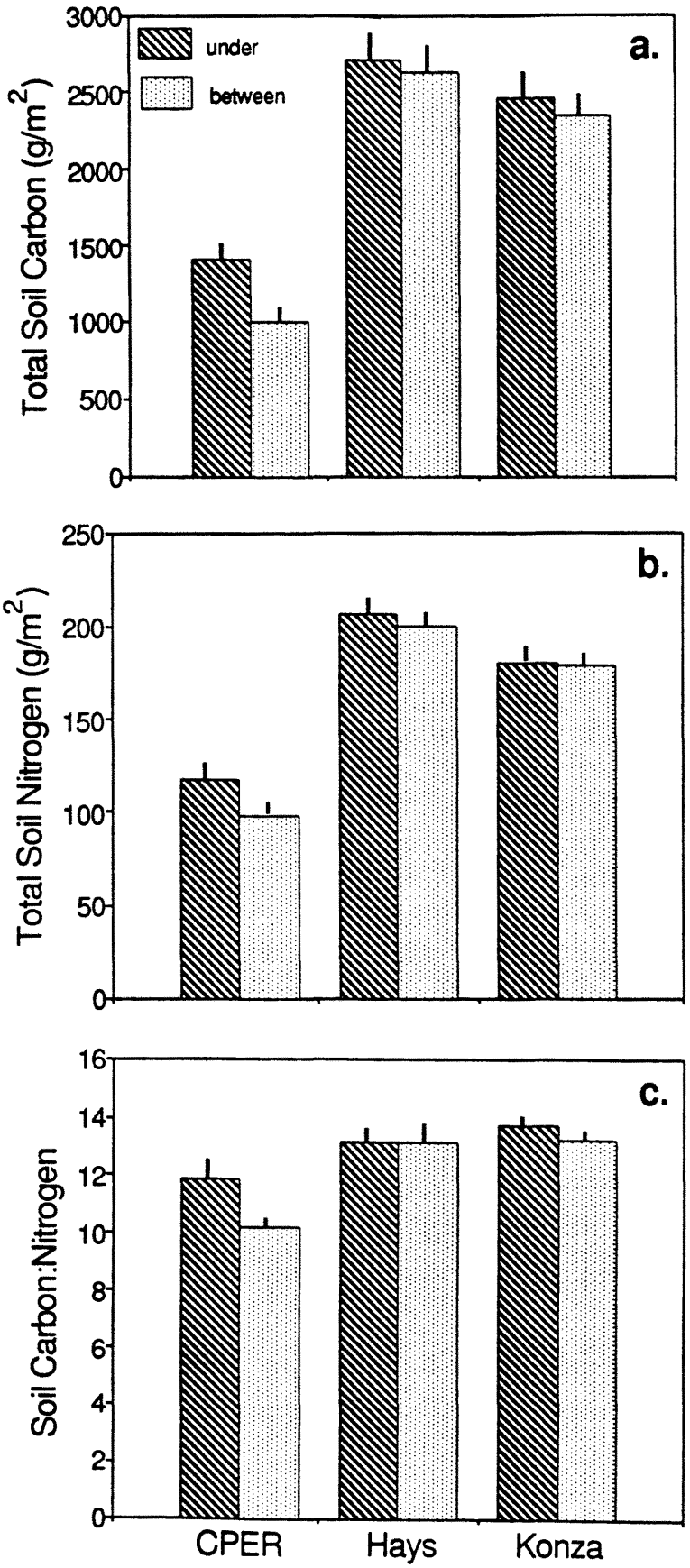

a.
under
between
Total Soil Carbon (g/m2)
3000
2500
2000
1500
1000
500
0
b.
Total Soil Nitrogen (g/m2)
250
200
150
100
50
0
c.
Soil Carbon:Nitrogen
16
14
12
10
8
6
4
2
0
CPER
Hays
Konza

Figure 3.2. Carbon mineralization rates (a.), potential net nitrogen mineralization rates (b.) and microbial biomass carbon (c.) in soils collected from under and between plants of 8-9 species at each of three sites: Central Plains Experimental Range (CPER) in northeastern Colorado, the Fort Hays State University College Farm near Hays in west-central Kansas, and Konza Prairie Research Natural Area near Manhattan in eastern Kansas. The vertical lines on each bar indicate 1 SE of the mean.

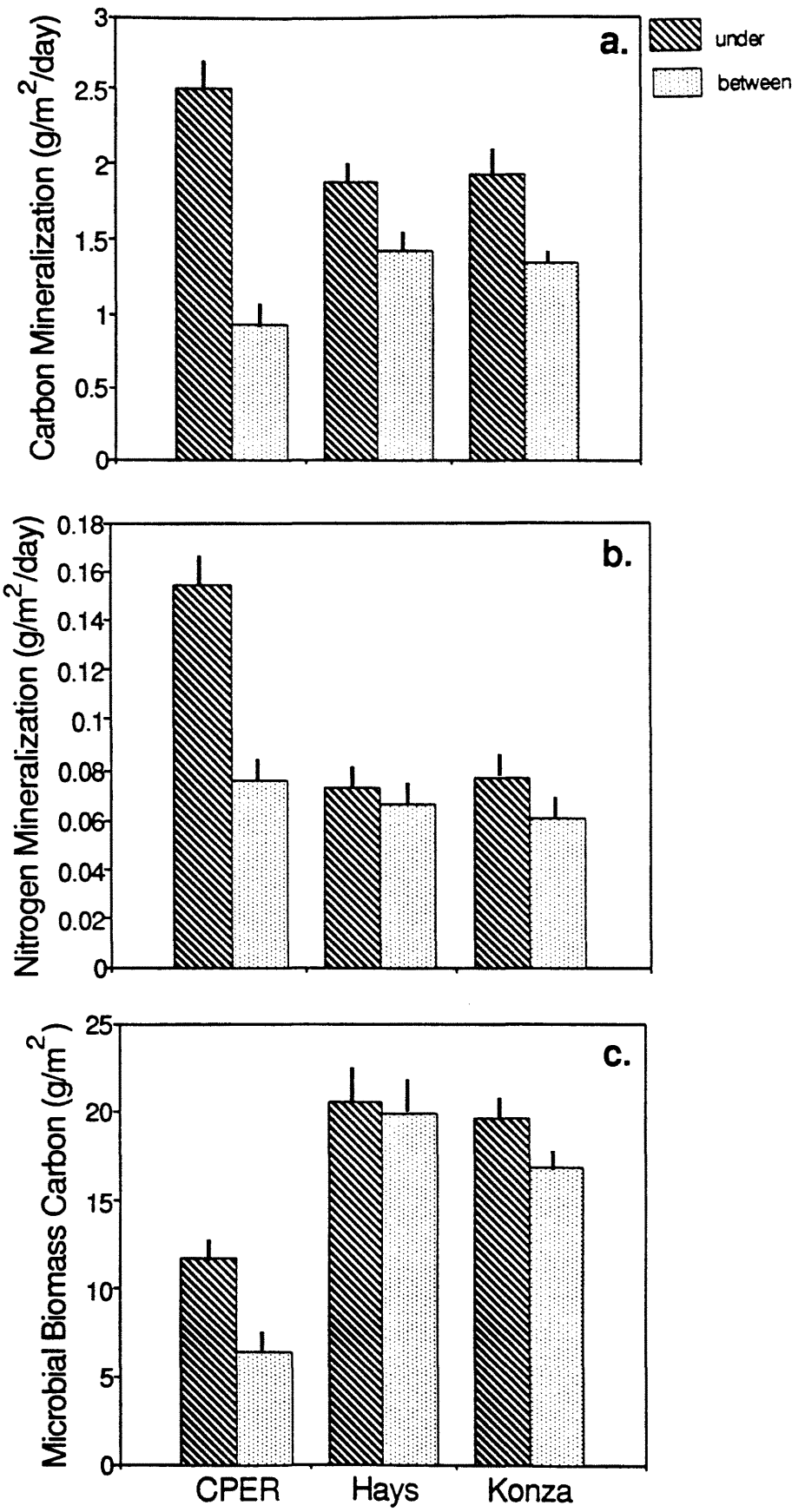
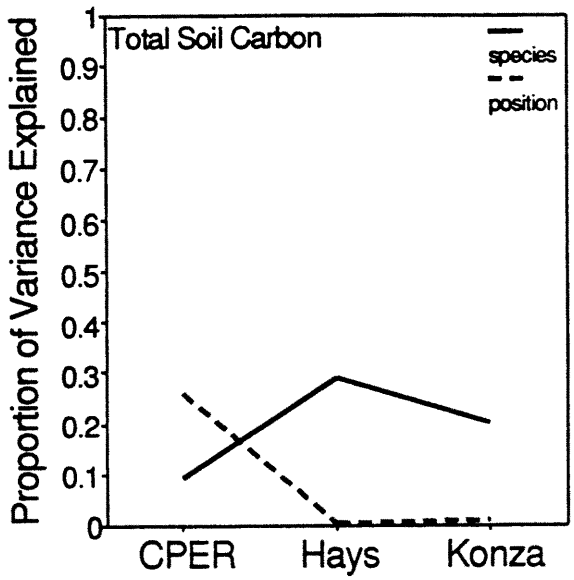
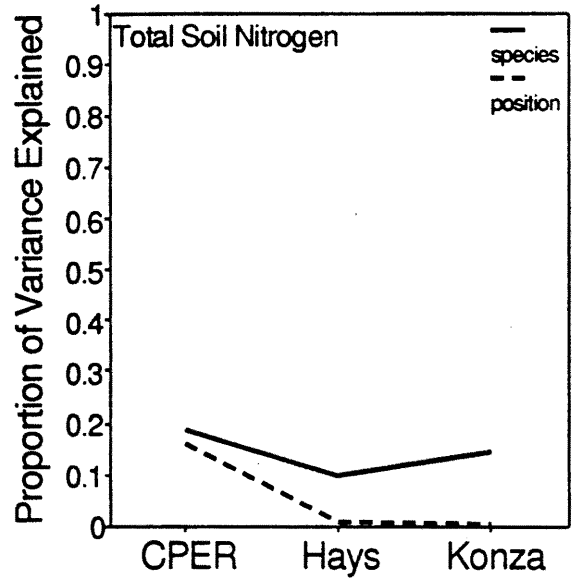
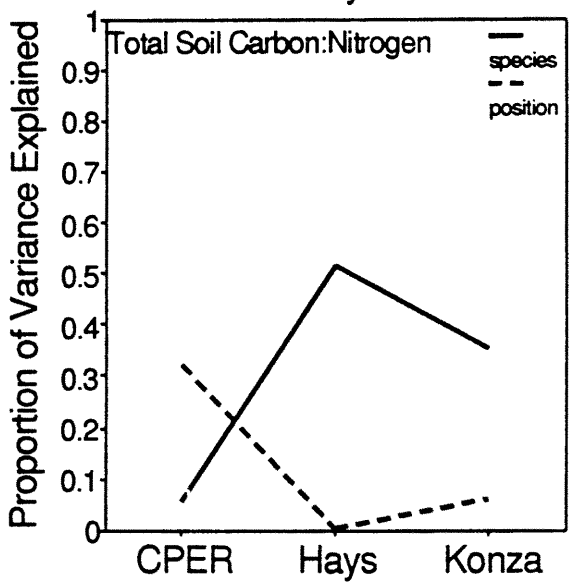
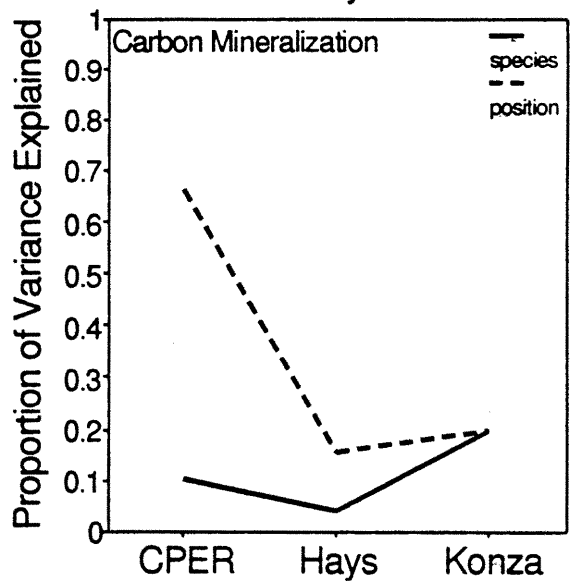

a.
under
between
Carbon Mineralization (g/m2/day)
3
2.5
2
1.5
1
0.5
0
b.
Nitrogen Mineralization (g/m2/day)
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
c.
Microbial Biomass Carbon (g/m2)
25
20
15
10
5
0
CPER
Hays
Konza

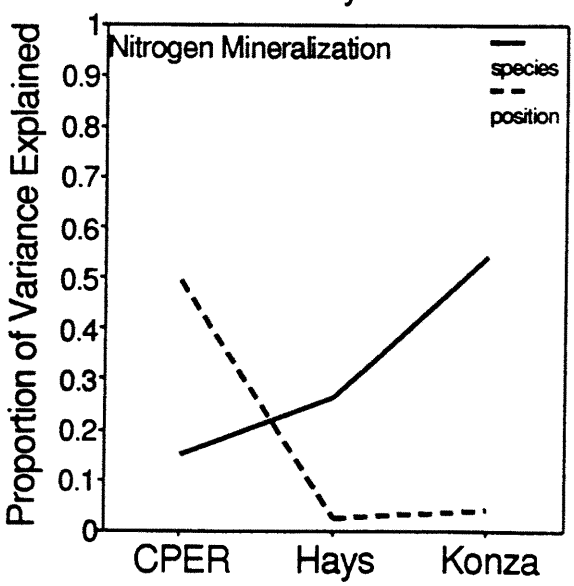
Figure 3.3. Amount of variation explained by plant presence and plant species for various soil properties at three sites: Central Plains Experimental Range (CPER) in northeastern Colorado, the Fort Hays State University College Farm near Hays in west-central Kansas, and Konza Prairie Research Natural Area near Manhattan in eastern Kansas. The y axis is the proportion of the total sum of squares accounted for by the species and position factors from an analyses of variance conducted for each site that included the effects of block, species, position and their interactions.


Total Soil Carbon
species
position
Proportion of Variance Explained
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
CPER
Hays
Konza


Total Soil Nitrogen
species
position
Proportion of Variance Explained
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
CPER
Hays
Konza


Total Soil Carbon:Nitrogen
species
position
Proportion of Variance Explained
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
CPER
Hays
Konza


Carbon Mineralization
species
position
Proportion of Variance Explained
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
CPER
Hays
Konza


Nitrogen Mineralization
species
position
Proportion of Variance Explained
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
CPER
Hays
Konza

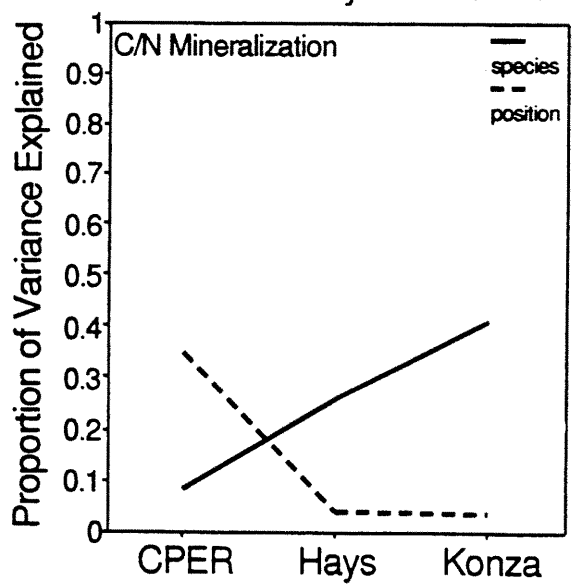
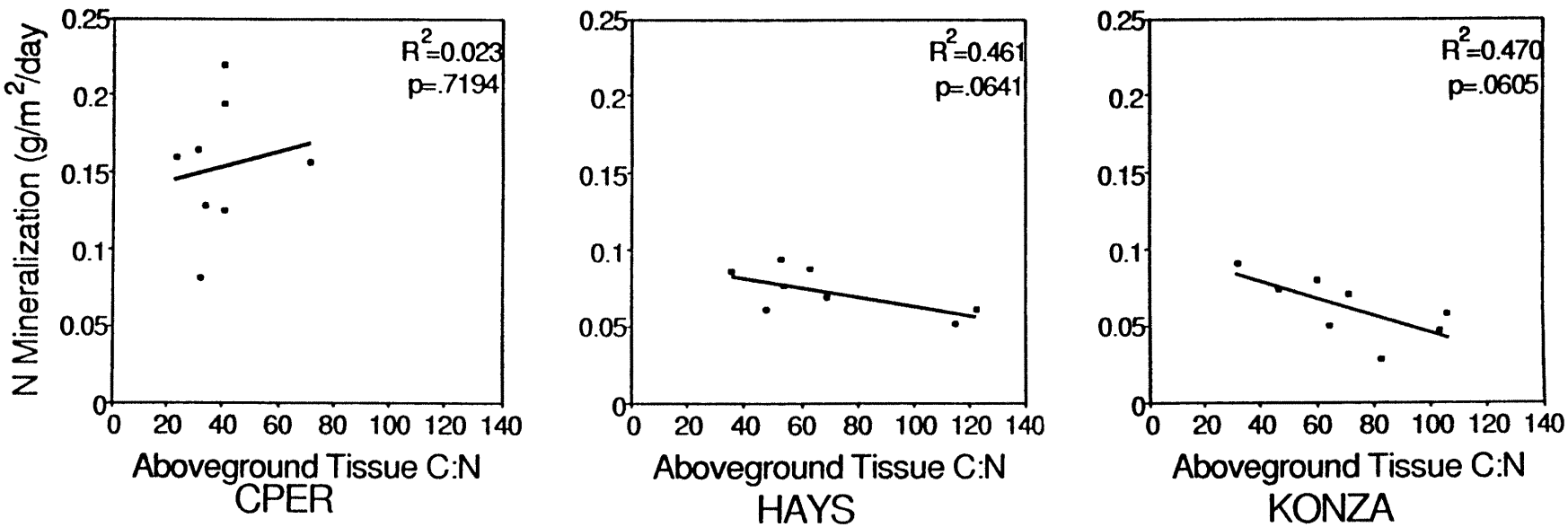

C/N Mineralization
species
position
Proportion of Variance Explained
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
CPER
Hays
Konza

Figure 3.4. The relationship between potential net nitrogen mineralization rates in soils collected under the canopy of 8 plant species and the aboveground, standing dead tissue carbon:nitrogen ratio of the species at each of three sites in the central Great Plains: Central Plains Experimental Range (CPER) in northeastern Colorado, the Fort Hays State University College Farm near Hays in west-central Kansas, and Konza Prairie Research Natural Area near Manhattan in eastern Kansas.


N Mineralization (g/m2/day
0.25
0.2
0.15
0.1
0.05
0
0 20 40 60 80 100 120 140
R2=0.023
p=.7194
Aboveground Tissue C:N
CPER
R2=0.461
p=.0641
Aboveground Tissue C:N
HAYS
R2=0.470
p=.0605
Aboveground Tissue C:N
KONZA

IV. THE INFLUENCE OF TWO SPECIES OF *BOUTELOUA* ON SOIL PROCESSES IN DESERT- AND SHORTGRASS-STEPPE GRASSLANDS

ABSTRACT

Plant-induced soil heterogeneity is an important feature of arid and semi-arid ecosystems, and changes in this soil heterogeneity are associated with disturbances and ecosystem stability. I tested the relative roles of biotic, ie. plant species, and abiotic factors in plant-induced soil properties in desert- and shortgrass-steppe grasslands. Two species were used, *Bouteloua eriopoda* and *Bouteloua gracilis*, that are both warm-season, perennial bunchgrasses but with different lifespan and dispersal characteristics and responses to grazing. I sampled these species and associated soils at three sites, capturing the extremes and the shared sites in the geographical distribution of the two species. I sampled soils and plants of 1) *B. eriopoda* in southern New Mexico (Jornada Experimental Range), at the northern border of the Chihuahuan Desert 2) *B. eriopoda* and *B. gracilis* in both pure and mixed stands in central New Mexico (Sevilleta) and 3) *B. gracilis* at the Central Plains Experimental Range (CPER) in shortgrass-steppe in northeastern Colorado.

Total soil carbon increased from the warmest site, Jornada, to the coolest site, CPER, probably as a result of decreases in decomposition rates. Soils

under plants had generally higher pool sizes, particularly labile pools, of carbon and nitrogen than did soils between plants in all three systems. This plant-induced soil heterogeneity was larger at Sevilleta than at either Jornada or CPER for soil carbon. Sevilleta also had the largest bare ground cover, so erosional processes between plants may have contributed to the under plant vs. between plant contrast in soil carbon at this site to a greater degree than at the other sites. Within Sevilleta, the two species growing together in mixed stands did not differ from one another in their effects on soils. However, soils associated with species growing in pure stands differed from soils associated with their conspecifics growing in mixed stands at Sevilleta. This result may have been due to differing successional age between stands. Since *B. eriopoda* may be shorter-lived and recruit more frequently than *B. gracilis*, the *B. gracilis* stands may be the oldest, resulting in higher rates of soil carbon and nitrogen cycling in the pure *B. gracilis* stands than in the other stands.

Individual plants affected soil nitrogen and carbon dynamics at all three sites. Also, the abiotic factors varying with site interacted with the biological factors associated with *B. eriopoda* and *B. gracilis* to significantly influence soil properties. In particular, abiotic factors that determine lifespan, productivity and erosional characteristics are all important in determining patterns in plant-soil heterogeneity in these desert- and shortgrass-steppe grasslands.

INTRODUCTION

Numerous studies have found that plant-induced soil heterogeneity is an important feature of arid and semi-arid ecosystems (e.g. Charley and West 1975, Schlesinger 1990) and may be related to low precipitation and plant cover (Vinton 1994). In desert systems, this heterogeneity has been interpreted in relation to vegetation change and system stability, in that the change from a grass-dominated to a shrub-dominated system is associated with increasing soil heterogeneity, desertification and ecosystem instability (Schlesinger et al. 1990). In semi-arid shortgrass-steppe of North America, however, plant-induced soil heterogeneity has been interpreted as a feature of the native, stable shortgrass-steppe ecosystem (Hook et al. 1991). The disruption of this soil heterogeneity (ie. increased spatial evenness in soil properties) in shortgrass-steppe has been associated with highly disturbed areas, due to chronic fertilizer and water additions (Vinton 1994) or cultivation (Burke et al. submitted).

The two dominant grasses in both central North American desert and semi-arid grassland systems, *Bouteloua eriopoda* and *Bouteloua gracilis*, are closely related taxonomically and they are both C_4 (warm season), perennial bunchgrasses. Given that desert- and semi-arid grasslands share many features, including similar plant species and discontinuous plant cover, how can the consequences of plant-induced soil heterogeneity be so different for these ecosystems? One possibility is that these seemingly similar plant species have biological differences that are critical in influencing soil processes. In addition

to these biological effects of the dominant grass species, desert and shortgrass steppe grasslands could have abiotic differences that are important in influencing soil processes.

The two species have different life-history attributes and responses to grazing. In a simulation analysis, Lauenroth et al. (in press) recently suggested that these differences may be responsible for the differences in small-scale soil heterogeneity in desert- vs. shortgrass-steppe grassland. The estimated *B. eriopoda* ramet lifespan is 28 years whereas the estimated maximum lifespan for *B. gracilis* is 400 years. Also, *B. eriopoda* is stoloniferous, and recruits more frequently from seed than does *B. gracilis*, in which tillers spread through belowground node activation. Thus the initial lack of soil heterogeneity in desert-grasslands (before shrub invasion), could be due to the high recruitment and turnover of *B. eriopoda* on the landscape, and system instability could be caused by its inability to tolerate grazing. Conversely the heterogeneity associated with short-grass steppe vegetation could be caused by the relative long-lived, *B. gracilis* plants occupying specific locations and thus increasing plant-interplant soil heterogeneity. Also, *B. gracilis* is very persistent under grazing pressure (Milchunas et al. 1988), which also adds to system stability. *B. eriopoda* and *B. gracilis* could have also have different inherent production, allocation or tissue chemistry characteristics that influence the soil properties under, relative to between, their canopies. Numerous studies have shown that plant species can have important effects on soil nutrient dynamics (Pastor and

Post 1986, Aerts and Berendse 1989, Wedin and Tilman 1990, Johnson and Damman 1991), and the effects can in some cases be attributed to plant growth form characteristics, such as tissue chemistry or biomass allocation.

Alternatively, the differences in the consequences of plant-induced soil properties between desert and shortgrass-steppe grasslands could be caused by climatic or disturbance-regime differences between the two systems. For example, wind erosion of soil between plants could be higher in shortgrass-steppe than in desert-grassland, thereby increasing plant-interspace soil heterogeneity. Also, increased water availability in the shortgrass-steppe vs. the desert grassland may result in higher productivity of the grasses, thereby increasing soil organic matter under, relative to between, plant canopies. Grazing regime, by influencing the productivity and lifespan of the plants, could also influence soil-plant relationships.

I investigated the effects of the two plant species, *Bouteloua eriopoda* and *Bouteloua gracilis*, over a gradient from desert- to shortgrass-steppe grassland, on soil carbon and nitrogen cycling. I was interested in separating site (abiotic) effects and disturbance history effects from biological, species effects on soils in these *B. eriopoda* and *B. gracilis* ecosystems. I was also interested in what aspects of soils, labile vs. total pools, are most likely affected by species attributes and whether allocation and tissue chemistry characteristics of the plant species could explain the soil patterns. I sampled soils and plants of 1) *B. eriopoda* in southern New Mexico (Jornada Experimental Range), at the

northern border of the Chihuahuan Desert 2) *B. eriopoda* and *B. gracilis* in both pure and mixed stands in central New Mexico (Sevilleta) and 3) *B. gracilis* at the Central Plains Experimental Range (CPER) in shortgrass-steppe in northeastern Colorado (Fig. 4.1). This sampling strategy of capturing the extremes and the shared sites in the geographical distribution of both species allowed us to separate the effects of site (e.g. precipitation, temperature, disturbance history) from the effects of plant species biology on soils. Comparisons of plant-soil patterns among *B. eriopoda* from Jornada vs. Sevilleta allowed us to test the effects of site on soil carbon and nitrogen dynamics. Similarly I compared patterns from *B. gracilis* plants from Colorado vs. Sevilleta to test the effects of site. I compared plants of both species at pure and mixed stands at Sevilleta to test the effects of species and disturbance history on soils.

METHODS

Site Descriptions

I sampled two sites in New Mexico and one site in Colorado (Fig. 4.1). These sites are either desert or shortgrass-steppe grasslands and they represent areas with varying dominance of two short bunchgrass *Bouteloua* species. Of the two species, one site has primarily *B. eriopoda*, one site has a mix of both *B. eriopoda* and *B. gracilis* and one site has only *B. gracilis*. All sites are members of the NSF-sponsored Long-term Ecological Research

(LTER) network (Franklin et al. 1990). The southernmost site was the Jornada LTER, located 37 km north of Las Cruces, New Mexico (32°30'N and 106°45'W) in the northern Chihuahuan desert. Average annual precipitation is 229 mm, with 52 percent occurring during the summer (Van Cleve and Martin 1991). The vegetation of Jornada is dominated by shrubs, particularly *Prosopis glandulosa* and *Larrea tridentata*, and grasses including *Hilaria mutica*, *Scleropogon brevifolius*, and some *B. eriopoda*. The vegetation at Jornada has undergone large changes in the past century, with extensive areas of *B. eriopoda* replaced by shrub communities (Buffington and Herbel 1965, Schlesinger et al. 1990).

The other New Mexico site was the Sevilleta LTER (34°13N and 106°30'W), located 75 km south of Albuquerque. Average annual precipitation is 280 mm, with large, but variable summer thunderstorms often accounting for over half of the annual moisture (Van Cleve and Martin 1991). Mean monthly temperatures range from +2.5°C to 27°C. The Sevilleta spans the Rio Grande River basin and has several major vegetation types, including grasslands, shrub-steppe, Chihuahuan Desert, interior chaparral and montane coniferous forests (Van Cleve and Martin 1991). I sampled plants in areas dominated by grasslands, particularly *B. eriopoda* and *B. gracilis.*

The Colorado site was the Central Plains Experimental Range (CPER), located in north-central Colorado, approximately 60 km northeast of Fort Collins (40°49' N, 107°46' W). The CPER is administered by the Agricultural Research Service of the United States Department of Agriculture. Mean annual

precipitation at the CPER is 322 mm and mean monthly temperatures range from -3°C in January to 22°C in July (Parton and Greenland 1987), with an annual mean of 8.7°C. The vegetation of the area is typical of shortgrass steppe and is dominated by the perennial bunchgrass, *B. gracilis* (H.B.K.) Lag. ex Griffiths (Milchunas et al. 1989). Other common species include the perennial grass, *Buchloë dactyloides* (Nutt.) Engelm.; the half-shrubs, *Gutierrezia sarothrae* (Pursh) Britt. & Rusby and *Artemisia frigida* Willd.; the forb, *Sphaeralcea coccinea* (Pursh) Rydb.; and the succulent, *Opuntia polyacantha* Haw. All plant nomenclature follows the Great Plains Flora Association (1986).

Soil and Plant Sampling and Analyses

I sampled *B. eriopoda* plants and soils in two grazing exclosures at Jornada. At Sevilleta, I sampled plants and soils in two replications of three areas: those dominated by only *B. eriopoda*, only *B. gracilis*, or in areas with a mix of both species. At CPER, I sampled *B. gracilis* plants and soils in exclosures. The CPER data were collected as part of another study, but collection procedures and laboratory analyses were the same as those used for the two other sites. I sampled soils directly under plants of each species and in adjacent openings between plants by taking 5 cm diameter, 5 cm deep soil cores. At Jornada and at the mixed stands at Sevilleta, I took 10 cm deep cores and divided them into a 0-5 cm portion and a 5-10 cm portion. Samples

from between plants were taken at least 7-10 cm away from the target plant and neighboring plant canopies in openings at least 15 cm in diameter. Samples from under plants were taken at the location where a stem or a group of stems emerged from the soil. I took "under" and "between" cores from a total of 5 plants of each species in each area of each site. At the Jornada and at the mixed stands at Sevilleta, I removed soil cores 10 cm in depth and each core was divided into a 0-5 cm and a 5-10 cm portion for the analysis. Soil cores were placed in coolers immediately and were kept cool until microbially-mediated processes were measured.

Fresh soils were sieved to separate plant material and fragments greater than 2 mm in diameter. The soils were then weighed, mixed and subsampled for 3 analyses: water content, initial inorganic N, and incubations to determine potential net N and C mineralization. A 10 g subsample was extracted with 50 ml of 2 N KCl for 30 min on an orbital shaker to measure initial inorganic N. The extracts were allowed to settle for 10 min and were filtered through Whatman #40 paper. The extracts were refrigerated until analyzed for nitrate and ammonium on a Latchet autoanalyzer (EPA 1979).

For the soil incubation, a 20 g subsample from each composite sample was placed in a small beaker, brought to field capacity with deionized water and placed in a closed mason jar with 20 mls of deionized water in the bottom to maintain a saturated atmosphere (Schimel 1986). Three mls of 2 N NaOH in a small vial was added to the jar to serve as a base trap for CO_2 respired by

soil microbes (Schimel 1986). The samples were incubated at 25°C for 28 days. At the end of the incubation, soils were extracted with KCl, filtered and analyzed for nitrate and ammonium as described above. The base trap was titrated with 1 N HCl to determine the amount of CO_2 (Snyder and Trofymow 1984) released during incubation, or the potential C mineralization . Potential net N mineralization was calculated as the difference between initial and final inorganic N of the soil. Air-dried soil samples were ground and dried at 55°C before total carbon and nitrogen contents were measured using a Carlo-Erba automated combustion analyzer.

Aboveground standing dead tissue was collected from each plant species at the time when soils were sampled. Large roots were sieved (2 mm sieve size) from the soil samples, dried at 55°C and weighed. All tissue was dried, ground and analyzed for total C and N using a Carlo-Erba automated combustion analyzer.

Statistical Analyses

Data were analyzed with ANOVA (SAS Institute 1989) using a significant probability level of ≤ 0.05 and the LSD or the Scheffe procedure for comparing means. The soil variables from one depth (0-5 cm) were analyzed in a split plot design, with site and species as the whole plot factor and position (under or between plants) as the split factor. Because not all species were present at all sites, I used five separate ANOVAs: 1) *B. eriopoda* sites at Jornada and

Sevilleta (*B. eriopoda* in both pure and mixed stands), 2) *B. gracilis* sites at CPER and Sevilleta (*B. gracilis* in both pure and mixed stands), 3) mixed stands of *B. eriopoda* and *B. gracilis* at Sevilleta 4) mixed and pure stands of *B. eriopoda* at Sevilleta and 5) mixed and pure stands of *B. gracilis* at Sevilleta. This strategy allowed us to test site effects while holding species constant and test species effects while holding site constant. I used these ANOVAs to compare soil properties associated with *B. eriopoda* at Jornada vs. Sevilleta and soil properties associated with *B. gracilis* at CPER vs. Sevilleta. At Sevilleta, I compared the two species within the mixed stands; I also made comparisons between pure and mixed stands for each species.

I used a split-block design to test the effects of depth on soil properties among these sites and species. The site and species combination was the whole plot factor, and position and depth were the split-block factor. The two soil depths were taken only at the Jornada and at the mixed stands at Sevilleta. I focused on the Jornada vs. Sevilleta site comparison, as well as the species comparison within Sevilleta.

RESULTS

Effects of species and sites on soil properties

Plant presence had strong effects on soil C and N, particularly the labile portions, with soil under plants generally having higher pool sizes and turnover rates of C and N than soil between plants (Fig. 4.2-4.5). However, the

magnitude of this effect was significantly affected by site. In soils associated with only *B. eriopoda*, the under vs. between plant contrast in soils was higher at Sevilleta than at Jornada for C and N mineralization (Fig. 4.2). Also the contrast was significantly larger for *B. gracilis* at CPER than *B. gracilis* at Sevilleta for total soil C and N (Fig. 4.3). However, for C and N mineralization rates, the under vs. between contrast was significantly larger for *B. gracilis* at Sevilleta than CPER (Fig. 4.2). No significant differences in the degree of plant-associated soil heterogeneity existed in comparisons at Sevilleta of 1) *B. eriopoda* vs. *B. gracilis* in mixed sites or 2) plants of either species in thier mixed vs. pure stands. (Fig. 4.2 and 4.3).

Soils associated with *B. eriopoda* at Sevilleta had significantly greater total C, C:N and nitrogen mineralization rates than did soils associated with *B. eriopoda* at Jornada (Fig. 4.2 and 4.3). Also, soils associated with *B. gracilis* at CPER had significantly higher total C, total N, C:N, C mineralization rates, N mineralization rates and C:N mineralization than did soils associated with *B. gracilis* at Sevilleta (Fig. 4.2 and 4.3). *B. eriopoda* and *B. gracilis* growing together at mixed sites at Sevilleta did not have significantly different effects on soil properties. However, the plants growing in pure stands had significantly different associated soils than those plant growing in the mixed stands. *B. eriopoda* in pure stands at Sevilleta had significantly more total C and higher soil C:N than *B. eriopoda* in mixed stands (Fig. 4.3). Also, *B. gracilis* in the pure stands had more total soil C and N, higher rates of C and N mineralization,

and higher C:N mineralization (Fig. 4.2 and 4.3) than did *B. gracilis* in the mixed stands.

Total pool sizes of soil C and N did not vary as much with depth or plant position, as C and N turnover rates, which were significantly affected by depth and plant position (Fig. 4.4 and 4.5). Soil in the 0-5 cm layer under plants had significantly higher C and N mineralization rates than did soil from the 0-5 cm layer between plants. The surface soil layer (0-5 cm) had a much greater proportion of C and N turnover activity than did the deeper (5-15 cm) soil layer (Fig. 4.5). The decrease in C and N turnover with depth was much more pronounced in the soils from under plants than the soil between plants (Fig. 4.5). In contrast, total pool sizes of C and N were more evenly distributed among the shallow and deep soil layers, and more consistent with plant position, ie. soils under plants had similar amounts of total C and N as soils between plants (Fig. 4.4). No significant differences in depth- or plant position-induced soil patterns existed between the two species at Sevilleta. *B. eriopoda* from Jornada had more of a under vs. between canopy contrast in C and N mineralization than did *B. eriopoda* from Sevilleta (Fig. 4.5 and 4.2).

Plant Biomass and Tissue Chemistry

Plant roots of both species were concentrated in the 0-5 cm layer and were much less abundant in the 5-10 cm layer (Fig. 4.6). *B. eriopoda* had significantly more of its roots in the 0-5 cm layer than did *B. gracilis* at Sevilleta,

whereas the two species had similar amounts of roots in the 5-10 cm soil layer (Fig. 4.6).

Root N concentration and C:N ratios were consistent among the plant species at Jornada and Sevilleta (Table 4.1). Root N concentration was significantly higher and C:N ratios were lower for *B. gracilis* at CPER than both *B. eriopoda* and *B. gracilis* at Jornada and Sevilleta. Aboveground N concentrations were significantly higher, and C:N ratio lower, for *B. gracilis*, both at Sevilleta and CPER, than for *B. eriopoda* at Jornada and Sevilleta (Table 4.1).

DISCUSSION

These data emphasize the importance of abiotic factors varying across sites, and their interaction with plant species factors in influencing soil properties. The largest differences in soil C and N properties occurred between sites, rather than between different plant species or communities within a site. Soils associated with *B. eriopoda* at Jornada had less soil C than soils associated with *B. eriopoda* at Sevilleta, and similarly, soils associated with *B. gracilis* at Sevilleta had lower soil C than soil associated with *B. gracilis* at CPER. Thus, in soils associated with the same plant species, total C increased from the southern to the northern site. In addition, total soil N and turnover rates of C and N increased from Sevilleta to CPER.

Site-induced differences in soil carbon and nitrogen pool sizes likely arise

because of differences in inputs to and outputs from soil organic matter, ie. production and decomposition of plant material. Site differences in soil C and N could also arise because of soil texture differences (Burke et al. 1989a), but soil texture at the three sites was similar (Minnick, unpubl. data). Sala et al. (1988) showed that plant production increased with precipitation in the central grasslands of the U.S., but showed no effect of temperature. However, decomposition rates have been shown to be sensitive to temperature changes, with higher rates of microbial activity and thus higher organic matter decomposition rates with higher temperatures (Meetemyer 1978, Burke et al. 1989a). The higher mean annual temperature at Jornada than that at CPER, results in higher decomposition rates and thus lower soil C and N pools.

Plant-associated soil heterogeneity also differed between sites. *B. eriopoda* at Jornada had less of a contrast in between vs. under plant soil C and N turnover rates than did *B. eriopoda* at Sevilleta. *B. gracilis* at Sevilleta had less of a plant-associated contrast in total soil C and N but more contrast in C and N mineralization rates than did *B. gracilis* at CPER. Plant-induced spatial heterogeneity in soil properties is a well-established phenomena in arid and semi-arid areas (Charley and West, Burke et al. 1989b Schlesinger et al. 1990). This spatial heterogeneity is thought to arise from mainly two processes: 1) plants fixing carbon from the atmosphere, collecting N from the soil, and depositing it in a small radius around the plant and 2) the loss of soil C and N from barren areas between plants, because of wind or water erosion. Thus the

difference in soil properties under and between plants can be interpreted as either amount of organic matter a plant has concentrated beneath its canopy or the amount of material eroded from areas with no plant cover. Both processes are influenced by length of time a plant has occupied a certain location.

Since interspace areas are typically larger and thus may be more vulnerable to erosional losses in the most desert-like site, Jornada, I expected to find increased heterogeneity associated with *B. eriopoda* at Jornada over that at Sevilleta. However, percent cover of bare ground at the Jornada sites was lower than at the Sevilleta sites (46-47% at Jornada and 57-76% at Sevilleta) (Minnick, unpubl. data). The larger bare ground areas at Sevilleta may suffer more erosional losses of C and N, and thus have lower amounts of C and N available for mineralization, than the bare ground areas at Jornada. However, the increased plant-interspace heterogeneity at Sevilleta over Jornada mainly occurred as increases in mineralization rates under plants. Plants at Sevilleta may be more productive than those at Jornada, perhaps because of increased water availability. This would result in more organic matter available for microbial decomposition and thus higher C and N mineralization rates. Plant tissue quality is also an important regulator of microbial decomposition and nutrient mineralization. However, estimates of tissue quality (N concentration and C/N ratios) did not differ between *B. eriopoda* at Jornada vs. Sevilleta.

Plant-interspace heterogeneity in soils associated with *B. gracilis* plants was different between Sevilleta and CPER. Soils between plants at CPER had

higher pool sizes and turnover rates of soil C and N than soils between plants at Sevilleta. Soils under plants also had higher pool sizes, but not rates, at CPER than Sevilleta. This resulted in a significantly greater contrast in under vs. between plant total soil C and N at CPER than at Sevilleta. It seems unlikely that this pattern can be explained by increased losses between plants at CPER than Sevilleta. The percent of bare ground at the CPER sites is less than that at the Sevilleta sites (Minnick, upubl. data), so erosional losses at CPER are probably not any greater than those at Sevilleta. However, increased productivity or lifespan of the plants at CPER than plants at Sevilleta is a potential explanation.

I hypothesized that since *B. gracilis* is thought to be much longer-lived than *B. eriopoda* (Lauenroth et al. in press), that *B. gracilis* would have a much greater under vs. between plant contrast in soils than would *B. eriopoda*. This difference was found for total soil carbon in previous studies, using plants from different sites (Lauenroth et al. in press). When species within a site were compared, however, no significant difference was found in plant-associated soil heterogeneity between the two species. Also, no significant difference was found in soil properties (averaging over plant position) between the two species in mixed stands at Sevilleta. This lack of difference in soil properties between the two species indicates that these species, when present at the same site, could be grouped into the same functional type for soil carbon and nitrogen processes. Since soil properties, particularly labile C and N pools, are very

different under than between plants, it would be more important to estimate plant vs. bare ground cover, rather than the amount of plant cover of each species, to adequately characterize soil C and N properties in these ecosystems.

Plant cover is also very important in affecting the vertical pattern, as well as the horizontal pattern, of soil processes. Soils in the surface 5 cm had much higher rates of soil C and N turnover than soils in the 5-10 cm layer. This pattern was more prevalent in soils under plants than soils between plants. Plant roots of both species were also concentrated in the top 5 cm, and likely drive the pattern in soil C and N. Although *B. eriopoda* had relatively more roots in the top 5 cm of the soil than did *B. gracilis*, no effect of this difference on soil properties was present. *B. eriopoda* had more roots in this layer than did *B. gracilis*, however the *B. gracilis* litter (particularly aboveground) may decompose faster than the *B. eriopoda* litter. The higher C:N ratios of the *B. eriopoda* aboveground tissue than the aboveground tissue of *B. gracilis* would support this idea.

Significant differences in soil properties existed between the pure vs. mixed community types at Sevilleta. The original causes for the differences in abundance of the two species may provide some explanation for the current soil patterns. *B. eriopoda* is estimated to be shorter-lived and to have higher recruitment rates than *B. gracilis* (Lauenroth et al. in press). Also, some evidence suggests that *B. gracilis* is very resistant to grazing (Milchunas et al.

1988), whereas *B. eriopoda* may be sensitive to overgrazing. Sevilleta is currently not grazed by domestic livestock, but before the 1970's it was used for grazing. Assuming that a disturbance such as over-grazing resulted in plant death, followed by recruitment of first *B. eriopoda*, then pure *B. gracilis* stands would likely be the areas where plants have been present for the longest period of time. Thus the pure *B. gracilis* stands may be older than the pure *B. eriopoda* stands and the mixed stands at Sevilleta. This might explain the higher soil C and N turnover rates in the pure *B. gracilis* stands than in the other stands at Sevilleta. It is also possible that rainfall or other environmental factors varying between the pure and the mixed sites are controlling the relative success of the two species, and thus controlling the soil processes. The differences in between-site vs. within site soil patterns among *B. eriopoda* and *B. gracilis* indicated that both abiotic factors varying between sites, species biology within sites and the interaction between these factors

This study shows that individual plants can have substantial effects on soil nutrient cycling. However, plant species effects on ecosystem biogeochemistry must be evaluated in the context of site-based environmental variables varying over the the geographic range of the species. Plant species characteristics clearly interact with abiotic factors varying between sites to influence ecosystem function. The site factors that determine lifespan,

productivity and erosional characteristics are all important in determining patterns of plant-soil heterogeneity associated with *B. eriopoda* and *B. gracilis* in these desert- and shortgrass-steppe grasslands.

LITERATURE CITED

Aerts, R., and F. Berendse. 1989. Aboveground nutrient turnover and production of an evergreen and a deciduous species in a heathland ecosystem. Journal of Ecology 77: 343-356.

Buffington, L.C. and C.H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecological Monographs 35: 139-164.

Burke, I.C., C.M. Yonker, W.J. Parton, C.V. Cole, K. Flach, and D.S. Schimel. 1989a. Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils. Soil Science Society of America Journal 53: 800-805.

Burke, I.C., W.A. Reiners, and D.S. Schimel. 1989b. Organic matter turnover in a sagebrush steppe landscape. Biogeochemistry 7:11-31.

Charley, J.L., and N.E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. Journal of Ecology 63: 945-963.

Johnson, L.C. and A.W.H. Damman. 1991. Species-controlled Sphagnum decay on a South Swedish raised bog. Oikos 61: 234-242.

Lauenroth, W.K., D.P. Coffin, I.C. Burke, and R.A. Virginia. in press. Interactions between demographic and ecosystem processes: a challenge for functional types. *in* T.M. Smith, I.A. Woodward and H.H. Shugart, editors. Plant Functional Types. Cambridge University Press, Cambridge.

Milchunas, D.G., O.E. Sala, and W.K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 132: 87-106.

Milchunas, D.G., W.K. Lauenroth, P.L. Chapman, and M.K. Kazempour. 1989.

Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80: 11-23.

Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycle. Biogeochemistry 2: 3-27.

Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary production of the Central Grassland region of the United States. Ecology 69: 40-45.SAS Institute. 1989.

SAS Statistics, Version 6.08. SAS Institute, Cary, N.C.

Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.G. Whitford. 1990. Biological feedbacks in global desertification. Science 247: 1043-1047.

Van Cleve, K., and S. Martin. 1991. Long-term ecological research in the United States: a network of research sites, 1991. Sixth ed. LTER Publication Number 11. Long-term Ecological Research Network Office, University of Washington, College of Forest Resources, Seattle, Washington.

Vinton, M.A. 1994. The influence of individual plants on soil nutrient dynamics in the Central Grassland region of the United States. Dissertation. Colorado State University.

Wedin, D.A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84: 433-441.

Wedin, D.A., and J. Pastor. 1993. Nitrogen mineralization dynamics in grass monocultures. Oecologia 96: 186-192.

Wright, R.G. and G.M. Van Dyne. 1976. Environmental factors influencing semidesert grassland perennial grass demography. The Southwestern Naturalist 21: 259-274.

Table 4.1. Nitrogen concentration and carbon:nitrogen ratios in aboveground tissue and root tissue of *Bouteloua eriopoda* at the Jornada Experimental Range in southern New Mexico, *Bouteloua eriopoda* and *Bouteloua gracilis* in pure and mixed stands at the Sevilleta National Wildlife Refuge in central New Mexico, and *Bouteloua gracilis* at the Central Plains Experimental Range (CPER) in northeastern Colorado. All tissue was collected at the conclusion of the growing season. Aboveground values are means of 6-10 samples, while root values are means of 9-11 samples. Standard errors of the means are shown in parentheses.

Site	Species	Aboveground Tissue		Root Tissue	
		N (%)	C:N	N (%)	C:N
Jornada					
pure stand	*B. eriopoda*	0.82 (0.03)	54.4 (1.9)	0.55 (0.02)	50.4 (2.0)
Sevilleta					
pure stand	*B. eriopoda*	0.74 (0.04)	58.6 (2.9)	0.66 (0.03)	52.6 (2.3)
mixed stand	*B. eriopoda*	0.81 (0.05)	55.5 (3.0)	0.56 (0.02)	52.9 (1.3)
mixed stand	*B. gracilis*	0.97 (0.04)	44.5 (1.8)	0.53 (0.01)	52.1 (1.2)
pure stand	*B. gracilis*	0.93 (0.03)	43.2 (1.3)	0.65 (0.03)	48.9 (2.0)
CPER					
pure stand	*B. gracilis*	1.33 (0.04)	31.9 (0.9)	1.43 (.09)	20.1 (0.6)

Figure 4.1. Location of the plants and soils sampled. Sites were located in Colorado and New Mexico and include the Central Plains Experimental Range (CPER), the Sevilleta National Wildlife Refuge, and the Jornada Experimental Range. Of the two species of *Bouteloua*, Jornada has primarily *B. eriopoda*, Sevilleta has both *B. eriopoda* and *B. gracilis*, and CPER has only *B. gracilis*. Species of *Bouteloua* were sampled in pure stands as well as mixed stands at Sevilleta.

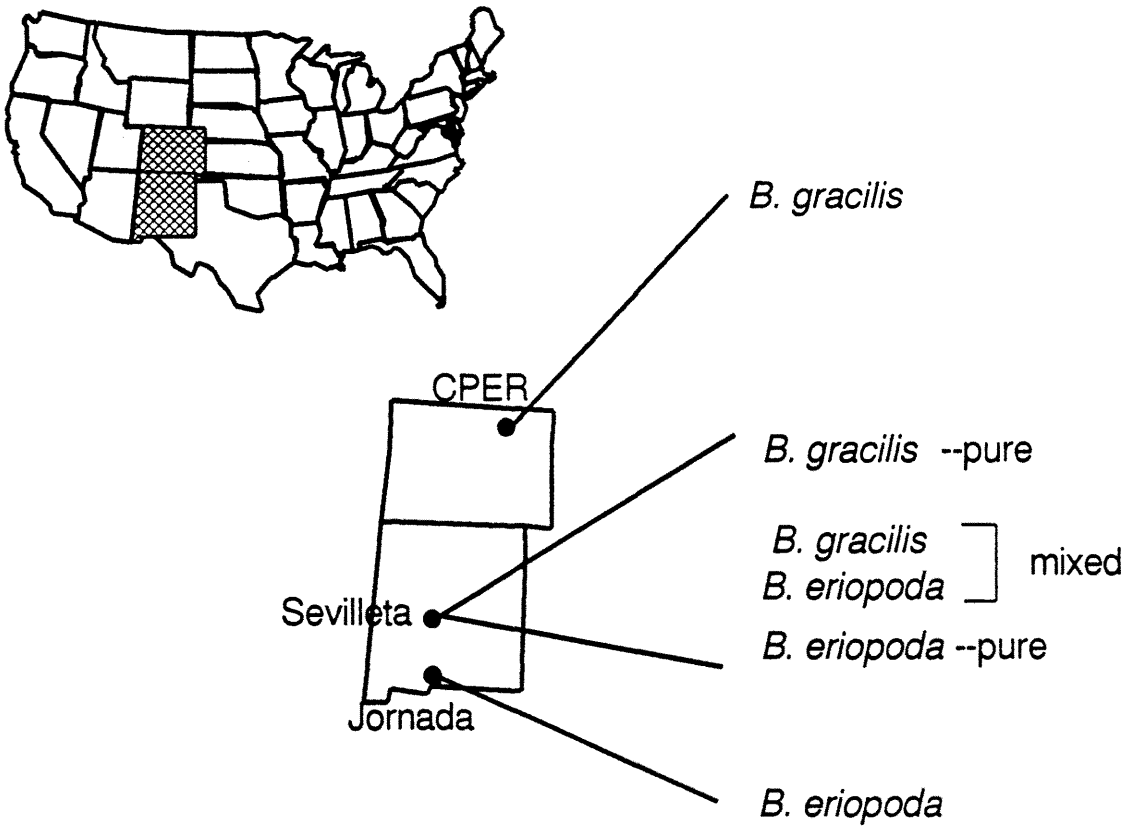

B. gracilis
CPER
B. gracilis --pure
B. gracilis
B. eriopoda
mixed
Sevilleta
B. eriopoda --pure
Jornada
B. eriopoda

Figure 4.2. Carbon mineralization rate, nitrogen mineralization rate, and carbon:nitrogen mineralization rate of soils sampled in the top 5 cm under and between the canopies of *Bouteloua eriopoda* (Be) at the Jornada Experimental Range in southern New Mexico, *Bouteloua eriopoda* and *Bouteloua gracilis* (Bg) in pure and mixed stands at the Sevilleta National Wildlife Refuge in central New Mexico, and *Bouteloua gracilis* at the Central Plains Experimental Range (CPER) in northeastern Colorado. The following statistical comparisons were made: 1) soils of *B. eriopoda* at Jornada vs. those of mixed and pure stands of *B. eriopoda* at Sevilleta (the first set of bars vs. the average of the second and third sets), 2) soils of *B. gracilis* at CPER vs. those of mixed and pure stands of *B. gracilis* at Sevilleta (the last bar set vs the average of the fourth and fifth sets) 3) soils of *B. eriopoda* in mixed stands at Sevilleta vs. *B. gracilis* in mixed stands at Sevilleta (the third set of bars vs. the fourth set of bars, (4) soils of mixed vs pure stands of *B. eriopoda* at Sevilleta (the second and third sets of bars), and 5) soils of mixed vs. pure stands of *B. gracilis* at Sevilleta (the third vs. fourth set of bars).

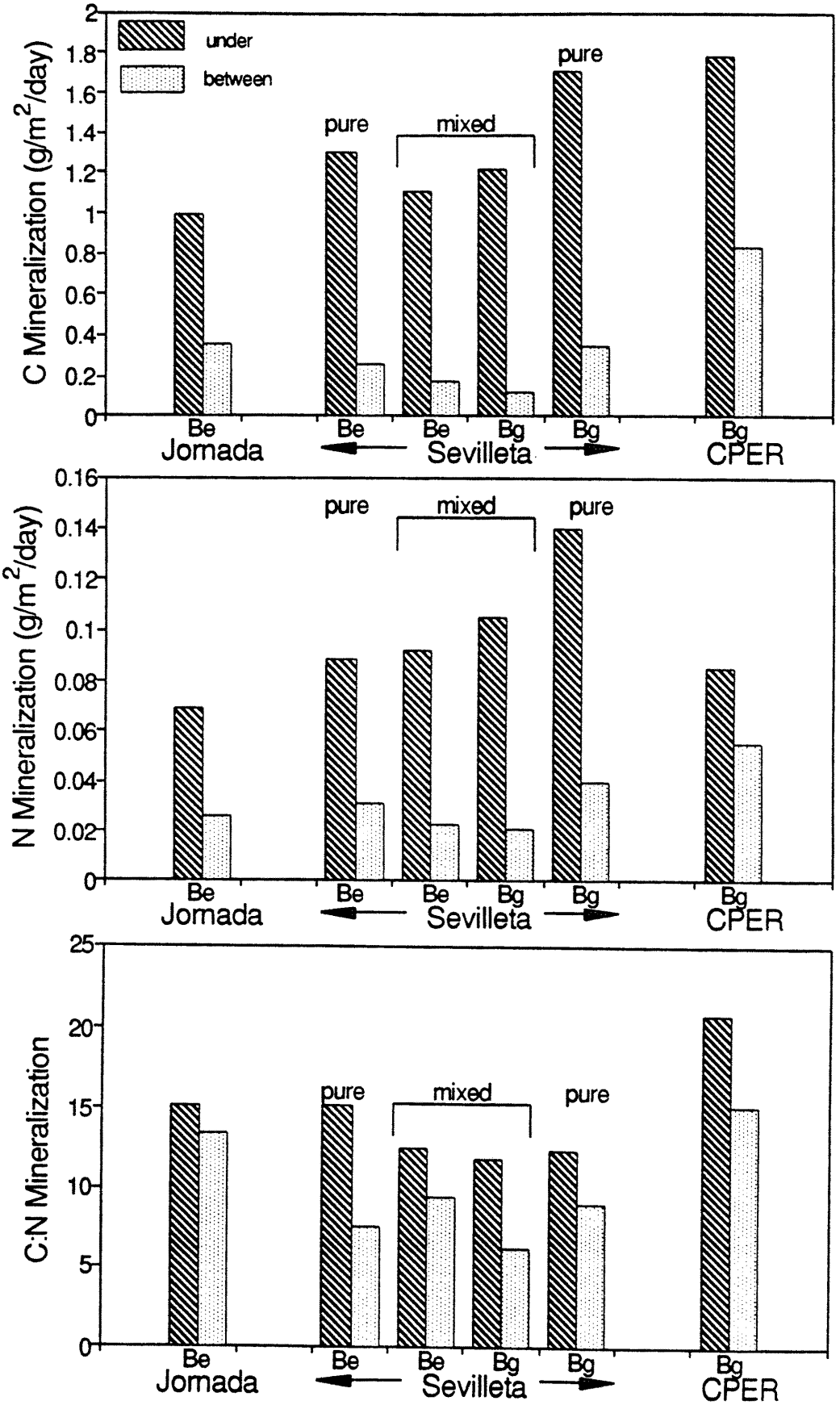

under
between
C Mineralization (g/m2/day)
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
pure
mixed
pure
Be
Be
Be
Bg
Bg
Bg
Jornada
Sevilleta
CPER
N Mineralization (g/m2/day)
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
pure
mixed
pure
Be
Be
Be
Bg
Bg
Bg
Jornada
Sevilleta
CPER
C:N Mineralization
25
20
15
10
5
0
pure
mixed
pure
Be
Be
Be
Bg
Bg
Bg
Jornada
Sevilleta
CPER

Figure 4.3. Total soil carbon, nitrogen and carbon:nitrogen ratio of soils sampled in the top 5 cm under and between the canopies of *Bouteloua eriopoda* (Be) at the Jornada Experimental Range in southern New Mexico, *Bouteloua eriopoda* and *Bouteloua gracilis* (Bg) in pure and mixed stands at the Sevilleta National Wildlife Refuge in central New Mexico, and *Bouteloua gracilis* at the Central Plains Experimental Range (CPER) in northeastern Colorado. The following statistical comparisons were made: 1) soils of *B. eriopoda* at Jornada vs. those of mixed and pure stands of *B. eriopoda* at Sevilleta (the first set of bars vs. the average of the second and third sets), 2) soils of *B. gracilis* at CPER vs. those of mixed and pure stands of *B. gracilis* at Sevilleta (the last bar set vs the average of the fourth and fifth sets) 3) soils of *B. eriopoda* in mixed stands at Sevilleta vs. *B. gracilis* in mixed stands at Sevilleta (the third set of bars vs. the fourth set of bars, (4) soils of mixed vs pure stands of *B. eriopoda* at Sevilleta (the second and third sets of bars), and 5) soils of mixed vs. pure stands of *B. gracilis* at Sevilleta (the third vs. fourth set of bars).

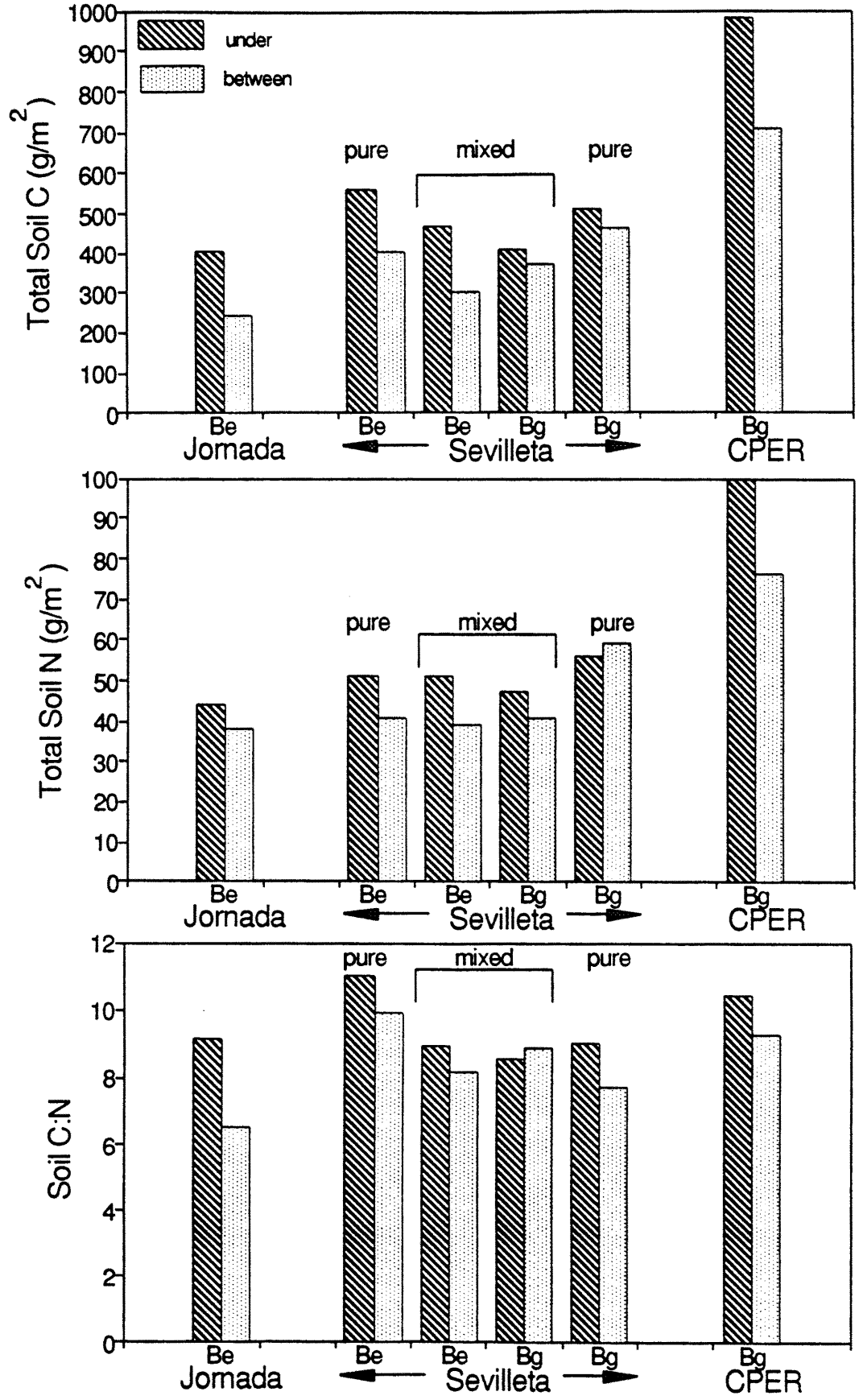

Total Soil C (g/m2)
1000
900
800
700
600
500
400
300
200
100
0
under
between
pure
mixed
pure
Be
Be
Be
Bg
Bg
Bg
Jornada
Sevilleta
CPER
Total Soil N (g/m2)
100
90
80
70
60
50
40
30
20
10
0
pure
mixed
pure
Be
Be
Be
Bg
Bg
Bg
Jornada
Sevilleta
CPER
Soil C:N
12
10
8
6
4
2
0
pure
mixed
pure
Be
Be
Be
Bg
Bg
Bg
Jornada
Sevilleta
CPER

Figure 4.4. Total soil carbon and nitrogen in the top 5 cm and the 5-10 cm layer of soils sampled under and between the canopies of *Bouteloua eriopoda* (Be) at the Jornada Experimental Range in southern New Mexico, *Bouteloua eriopoda* and *Bouteloua gracilis* (Bg) in mixed stands at the Sevilleta National Wildlife Refuge in central New Mexico. The following statistical comparisons were made: 1) soils of *B. eriopoda* at Jornada vs. *B. eriopoda* at Sevilleta (the first set of bars vs. the second set of bars) and 2) soils of *B. eriopoda* at Sevilleta vs. *B. gracilis* at Sevilleta (the second set of bars vs. the third set of bars).

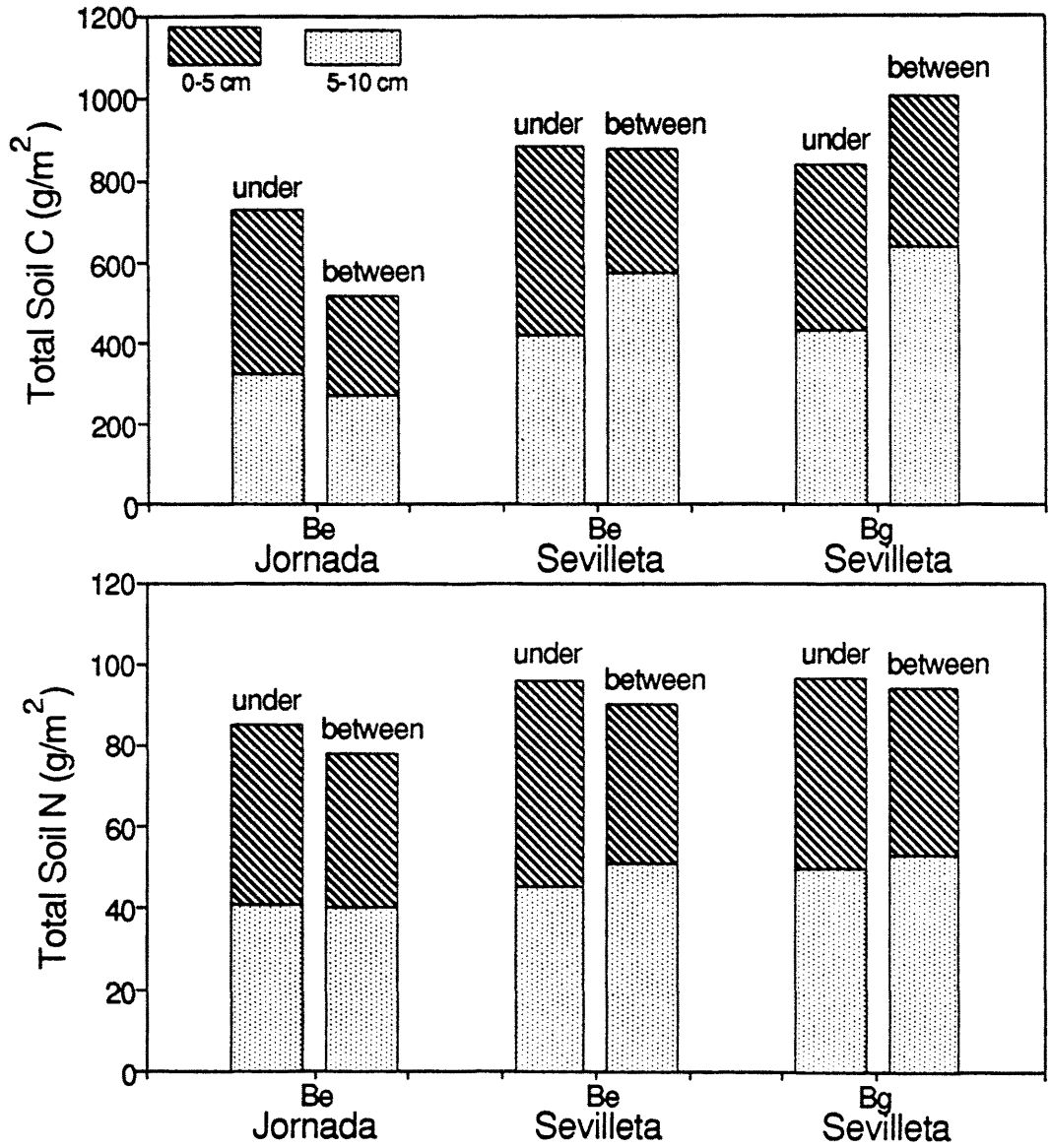

Total Soil C (g/m2)
1200
1000
800
600
400
200
0
0-5 cm
5-10 cm
under
between
under
between
under
between
Be
Jornada
Be
Sevilleta
Bg
Sevilleta
Total Soil N (g/m2)
120
100
80
60
40
20
0
under
between
under
between
under
between
Be
Jornada
Be
Sevilleta
Bg
Sevilleta

Figure 4.5. Carbon and nitrogen mineralization rates in the top 5 cm and the 5-10 cm layer of soils sampled under and between the canopies of *Bouteloua eriopoda* (Be) at the Jornada Experimental Range in southern New Mexico, *Bouteloua eriopoda* and *Bouteloua gracilis* (Bg) in mixed stands at the Sevilleta National Wildlife Refuge in central New Mexico. The following statistical comparisons were made: 1) soils of *B. eriopoda* at Jornada vs. *B. eriopoda* at Sevilleta (the first set of bars vs. the second set of bars) and 2) soils of *B. eriopoda* at Sevilleta vs. *B. gracilis* at Sevilleta (the second set of bars vs. the third set of bars).

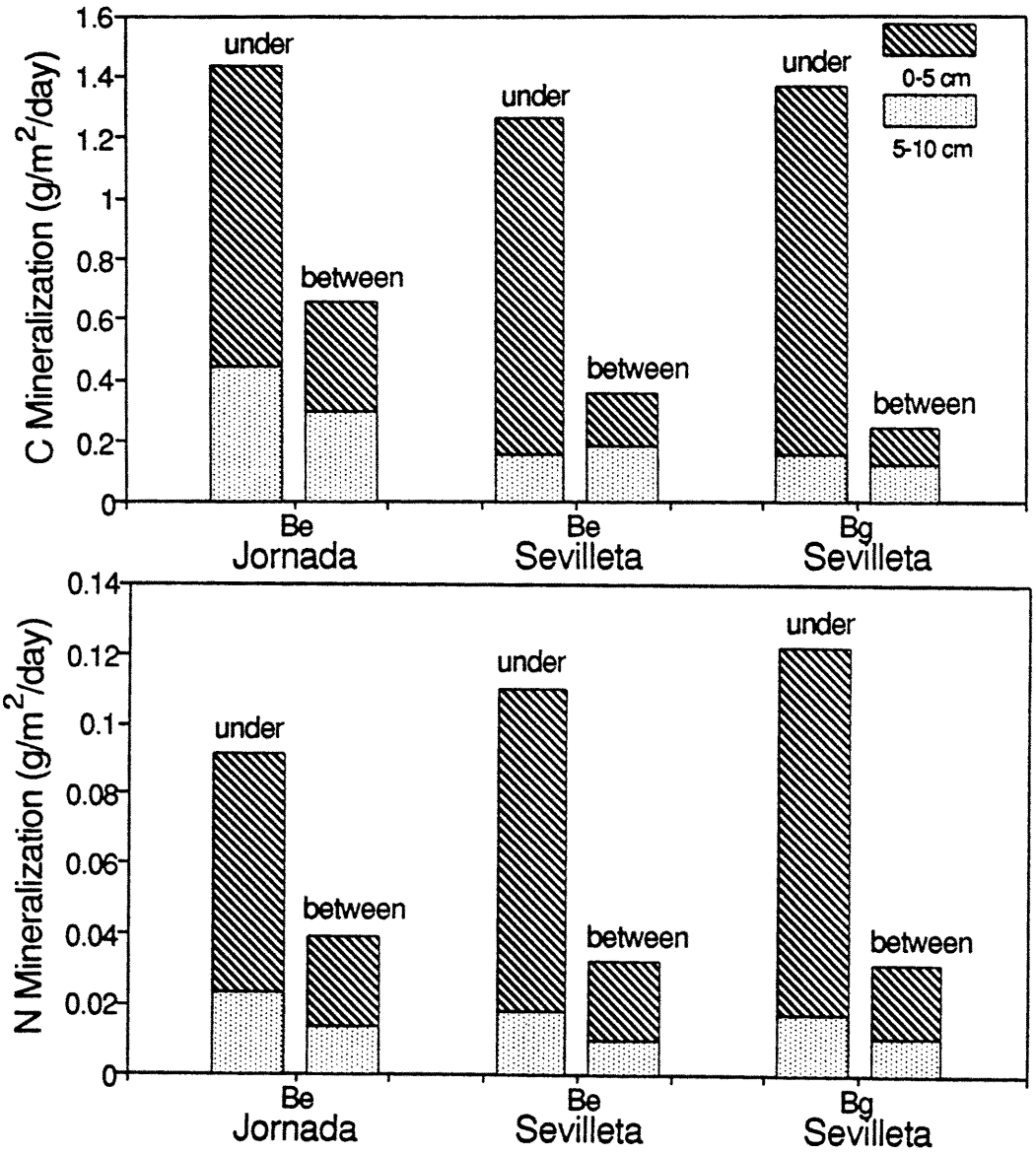
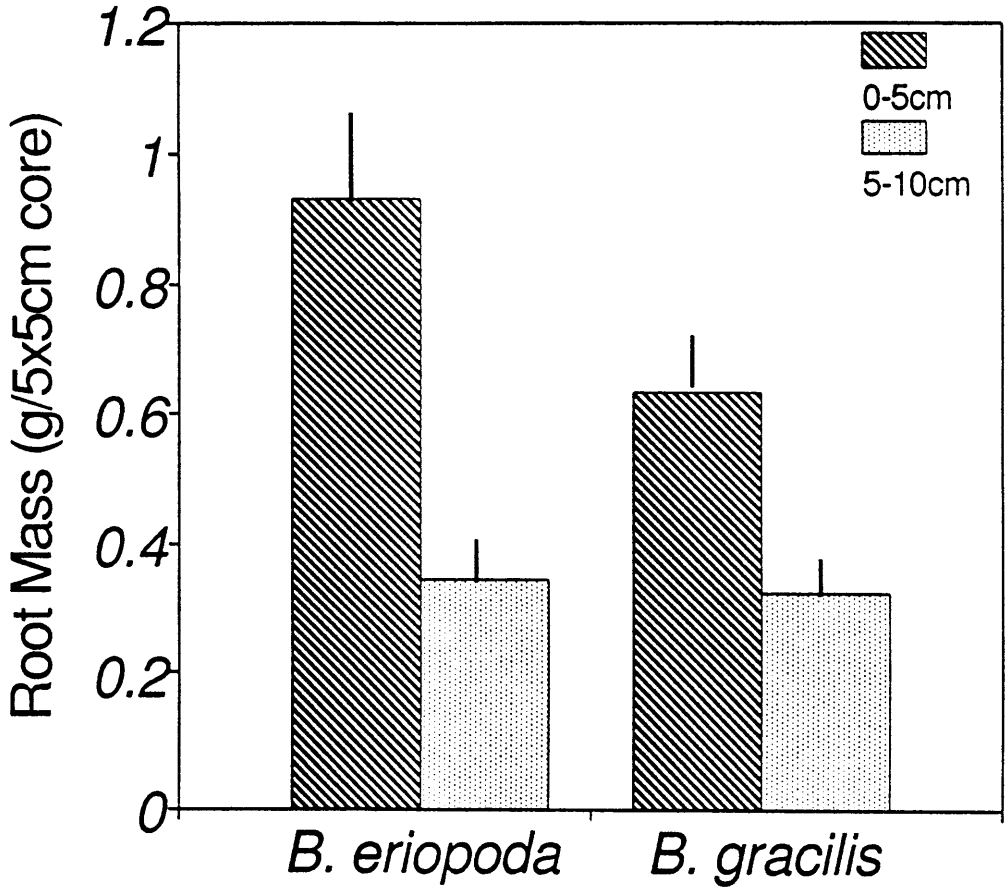

C Mineralization (g/m2/day)
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
under
between
under
between
under
between
0-5 cm
5-10 cm
Be
Jornada
Be
Sevilleta
Bg
Sevilleta
N Mineralization (g/m2/day)
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
under
between
under
between
under
between
Be
Jornada
Be
Sevilleta
Bg
Sevilleta

Figure 4.6. Root mass (g dry mass/core) in 0-5 cm and 5-10 cm soil layers from *Bouteloua eriopoda* and *Bouteloua gracilis* collected at mixed stands at Sevilleta National Wildlife Refuge in New Mexico. Values are not corrected for ash content. Values are means of 10 samples and the line above each bar represents one SE of the mean.


Root Mass (g/5x5cm core)
1.2
1
0.8
0.6
0.4
0.2
0
0-5cm
5-10cm
B. eriopoda
B. gracilis

V. CONCLUSION

The hypothesis that vegetation structure has important effects on ecosystem function was a central theme to my research. The results of these studies support this hypothesis in general, but also emphasize the relative importance of different aspects of vegetation structure, as well as that of other environmental factors, in influencing soil carbon and nitrogen dynamics in different ecosystems.

In arid and semi-arid ecosystems, plant cover patterns were very important in influencing soil nutrient dynamics. In some cases, plant species had lifeform of lifespan characteristics that afforded them with different effects on soil heterogeneity. Bunchgrasses tended to foster more soil heterogeneity than did other herbaceous lifeforms. In the second study, shrubs at the semi-arid site promoted more soil heterogeneity than did the grasses. Short-lived species, especially annuals, fostered less spatial heterogeneity in soil properties than longer-lived species. In the sub-humid grassland, plant cover, and associated soil properties, were much more spatially homogenous than in the dry grasslands. Thus, soil carbon and nitrogen properties between and under plants in the sub-humid grasslands were much more similar than those in arid and semi-arid areas. Although plants did not exert much control on the spatial

distribution of soil properties in the sub-humid grasslands, plant production (influenced by management) did appear to have a profound influence on soil properties.

These studies also provided evidence that local, plant-induced soil patterns were important at the ecosystem scale. Both variations in plant cover and variations in species composition caused variation in ecosystem-scale soil properties. In semi-arid sites, the presence of a plant, rather than the identity of the plant, had the largest effect on plot-scale estimates of soil properties.

The effects of plant cover, and its dependance on plant lifespan and dispersal characteristics, on soil properties may be important in determining ecosystem stability. The first study, as well as previous work by other researchers (Hook et al. 1991), shows that plant-induced soil heterogeneity is an important feature of native shortgrass-steppe. This study showed that this heterogeneity was disrupted by historical addition of soil resources, and subsequent invasion by an exotic species with an annual lifespan. Other studies have shown that plant-induced soil heterogeneity was disrupted by historical cultivation, and the development of soil heterogeneity may be viewed as an important stage in the recovery of formerly cultivated fields (Burke, et al. submitted).

In desert grasslands, plant-induced soil heterogeneity has been viewed as an unstable feature of the ecosystem, potentially leading to degradation (Schlesinger et al. 1990). The third study, by comparing plant-induced soil

heterogeneity among the dominant grasses in shortgrass steppe and desert grassland demonstrates that plant lifespan, and its interaction with disturbance history, may be involved in conferring soil heterogeneity in the two ecosystems. In particular, the longer-lived species, *Bouteloua gracilis*, in the oldest successional communities, imposed greater plant-induced soil heterogeneity than the shorter-lived species, *Bouteloua eriopoda*. Also, the abiotic site variables in desert- and shortgrass steppe ecosystems may confer different levels of plant production, thus influencing the net movement of carbon into soils beneath plant canopies. These abiotic site variables may also lead to different rates of erosion of soils between plants and thus influence soil properties in plant interspaces.

In these three studies, the plant species had quite different allocation or tissue chemistry characteristics in some cases, but these differences did not always translate into differences in carbon and nitrogen dynamics of associated soils. The soil carbon and nitrogen pools that were most affected by plants were the portions which turned over most often and probably those most associated with microbial activity. Some of the species effects on soil could be explained by some characteristics of the plants, e.g. tissue quality or biomass allocation. Also, some growth forms had differential effects on soils which could be attributed to their biomass allocation or tissue chemistry characteristics. Overall, the evidence that plant species could be aggregated into growth- or lifeforms to adequately describe their effects on ecosystem function (e.g.

Mooney and Schulze 1993, Chapin 1993) was inconclusive.

That the importance of vegetation structure to soil nutrient cycling is influenced by other factors may be best demonstrated by the changes in importance of vegetation structure to soil properties over environmental gradients. The second study demonstrated that the importance of plant cover patterns vs. plant species characteristics, varied over a gradient in precipitation. The importance of plant species to soil properties increased with precipitation, whereas the importance of plant cover patterns decreased with precipitation. The third study demonstrated that differences in site-based variables such as temperature, precipitation, and disturbance history, resulted in different levels of vegetation-induced soil heterogeneity. The site with the maximum potential for soil erosion between plants (indicated by percent cover of bare ground), as well as a relatively high capacity for plant productivity (indexed by mean annual precipitation), and thus carbon input to soils beneath plants, had the maximum amount of plant-induced soil heterogeneity.

Clearly, vegetation structure influenced an important element of ecosystem function, soil carbon and nitrogen dynamics, in these grassland ecosystems. Further work should seek to elucidate the interactions between these biotic effects on soil processes and the effects of important abiotic factors such as precipitation and temperature.

LITERATURE CITED

Burke, I.C., W.K. Lauenroth, and D.P. Coffin. submitted. Recovery of soil organic matter and N mineralization in semiarid grasslands. Ecological Applications, submitted.

Chapin, F.S. 1993. Functional role of growth forms in ecosystem and global processes. *in* J.R. Ehleringer and C.B. Field, editors. Scaling physiological processes: leaf to globe. Academic Press, London.

Hook, P.B., I.C. Burke, and W.K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. Plant and Soil 138: 247-256.

Mooney, H.A., and E. Schulze. 1993. Biodiversity and ecosystem function. Springer Verlag. New York. 525 p.

Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.G. Whitford. 1990. Biological feedbacks in global desertification. Science 247: 1043-1047.