INTERACTIONS BETWEEN INDIVIDUAL PLANT SPECIES AND SOIL NUTRIENT STATUS IN SHORTGRASS STEPPE[1]

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Abstract. The effect of plant community structure on nutrient cycling is fundamental to our understanding of ecosystem function. We examined the importance of plant species and plant cover (i.e., plant covered microsites vs. bare soil) on nutrient cycling in shortgrass steppe of northeastern Colorado. We tested the effects of both plant species and cover on soils in an area of undisturbed shortgrass steppe and an area that had undergone nitrogen and water additions from 1971 to 1974, resulting in significant shifts in plant species composition.

Soils under plants had consistently higher C and N mineralization rates and, in some cases, higher total and microbial C and N levels than soils without plant cover. Four native grasses, one sedge, and one 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 C mineralization and microbial biomass C than soil under the rhizomatous grass, *Agropyron smithii.* Also, the one introduced annual in the study, *Kochia scoparia,* had soils with less plant-induced heterogeneity and higher rates of C and N mineralization as well as higher levels of microbial biomass C than soils associated with the other species. This species was abundant only on plots that had received water and nitrogen for a 4-yr period that ended 20 yr ago, where it has persisted in the absence of resource additions for 20 yr, suggesting a positive feedback between plant 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. This result may be due to the semiarid nature of this grassland in which plant cover is discontinuous and 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 of these properties indicates that consideration of structural attributes, particularly plant cover patterns, is critical to estimates of ecosystem function in shortgrass steppe.

Key words: carbon; disturbance; functional groups; island of fertility; nitrogen; nutrient cycling; plant–soil feedback; shortgrass steppe; soil heterogeneity.

INTRODUCTION

Individual plant characteristics, such as life-span, 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 tall-grass 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 drier shrub and grassland ecosystems, individual plants concentrate biomass in soils beneath their canopies, forming "islands of soil fertility" (e.g., 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.

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 semiarid 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 life-span), 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 semiarid to arid areas with discontinuous plant cover, relating plant canopy presence to properties of the soil beneath the canopy. In our system, the shortgrass steppe of northeastern Colorado, we have both discontinuous plant cover and a mix of plant life-forms and species, allowing for both plant presence as well as plant life-form and tissue chemistry to have important effects on soils. Our system is characterized by the dominant C_4 bunchgrass, *Bouteloua gracilis,* with a mix of other grasses, forbs, and shrubs, and a significant amount of bare ground between individual plants. In investigating the importance of individual plants to nutrient cycling in the shortgrass steppe, it is necessary to consider both plant canopy presence and tissue chemical characteristics to completely address the issue.

Our primary objective in this study was to examine the influence of individual plants of several species on the local pattern of carbon and nitrogen cycling in the soil of shortgrass steppe. We were 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. We 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, we expected plant production and allocation measures to reflect the amount of material available for decomposition and nutrient release. We expected plant life-span 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 life-form should also affect the spatial pattern of biomass on the landscape, with bunchgrasses forming more concentrated locations of biomass than rhizomatous grasses. Thus, we expected both plant life-span and life-form 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 to 1974, which may have significantly changed these plant–soil relationships. The addition of these resources changed species composition dramatically, and some of the changes have persisted to the present, 20 yr after the resource addition ceased. We think this persistent response may represent an example of 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 with 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, we 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

TABLE 1. Plant species characteristics and relative percentage basal cover of plant species and bare ground in 1991 on plots in shortgrass steppe receiving additional nitrogen (N), additional water (W), both additional nitrogen and water (NW), or nothing (Control) from 1970 to 1974.

Species	Phenology*	Life-span 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 scoparia	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.

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. and 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 1970s (Lauenroth et al. 1978). The experiment consisted of a factorial combination of four treatments with two replicates: control (no resource addition), water (W), nitrogen (N) and nitrogen plus water (NW) additions. The eight cells of the design were contiguous plots of area 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 et al. 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 to 707 mm (Lauenroth et al. 1978). Nitrogen fertilizer (330 g/kg 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^- and NH_4^+). This resulted in addition of 100–150 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 (Dodd and Lauenroth 1978, Lauenroth

et al. 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 (Dodd and Lauenroth 1978, Lauenroth et al. 1978, Lauenroth and Dodd 1979) which has persisted, with some fluctuations in species relative abundance, into the present (Milchunas et al. 1990, Milchunas and Lauenroth 1995).

Tissue sampling and analyses

We sampled plant tissue and soils under plants of five species on each of the historical treatment plots (Table 1). These species were selected because they represented the majority of the biomass on the plots and because they represented a variety of life-forms. The species were: Bouteloua gracilis (H.B.K.) Lag. ex Griffiths, a perennial C_4 bunchgrass; Aristida longiseta Steud., a perennial C_4 bunchgrass; Stipa comata Trin. and Rupr., a perennial C_3 bunchgrass; Agropyron smithii Rydb., a perennial C_3 rhizomatous grass; and Artemisia frigida, 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 1).

Aboveground biomass and cover estimates were obtained for each target species by randomly locating six rectangular quadrats of area 0.1 m² along transects in each replicate of the historical treatment plots. We estimated percentage 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 his-

torical treatment plot, and individual plants were chosen along the transect in a stratified, random manner at 16 locations. Root cores from two individual plants at each of the 16 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° and weighed. The roots and stem bases were milled to pass through no. 40 (0.5 mm) mesh and subsamples were ashed at 550°C.

Total percentage carbon and nitrogen were determined on both aboveground and belowground plant tissue using a nitrogen/carbon analyzer (Carlo-Erba, Fison Instruments, Saddlebrook, New Jersey). 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 $\times$ 10 cm deep soil cores. Samples from between plants were taken on bare ground ≥ 10 cm 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. We took "under-plant" and "between-plant" cores from a total of four 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 $\times$ species $\times$ position combination. Soil samples were placed in coolers immediately and were transported to a laboratory refrigerator within 7 h after collection. All fresh soil analyses were performed within 3 d after collection.

Fresh soils were sieved to separate plant material and fragments >2 mm in diameter. The soils were then weighed, mixed, and divided into subsamples for four 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 mol/L 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 no. 40 paper. The extracts were refrigerated until analyzed for nitrate and ammonium on a Lachat (Milwaukee, Wisconsin) 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

mol/L 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° for 30 d. 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 mol/L 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, 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 mol/L K_2SO_4 for 30 min on a 200 rpm orbital shaker and filtered through Whatman no. 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 min, 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° 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 subplot factor and position (under-plant vs. between-plant) as the sub-subplot factor (Table 2). We used the GLM procedure in SAS (SAS Institute 1985) to perform a 3-way analysis of variance (ANOVA) on the data. We used transformed data when necessary to satisfy the assumptions of the ANOVA. When ANOVA indicated a significant effect, we tested differences between means with techniques specific to split-split plot designs (Gomez and Gomez 1984), and the Scheffe procedure. We 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., the N and NW vs. the control and W plots). In the statistical analyses of soil variables, we 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 subplot factor. We used planned contrasts to

TABLE 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 plus water additions from 1970 to 1974), species (both under and between plants of five different species), position (under vs. between plants) and factor interactions on soil response variables expressed on an area basis.*

	Factors											
	Treatment		Species		Position		Trt. × species		Trt. × position		Species × position	
Response	F	P	F	P	F	P	F	P	F	P	F	P
Soil carbon	4.49	0.1246	0.98	0.4459	12.55	0.0020	0.83	0.6202	15.21	0.0001	1.26	0.3172
Soil nitrogen	2.31	0.2551	1.15	0.3683	1.28	0.2721	1.05	0.4533	8.99	0.0006	0.93	0.4665
Carbon mineralization rate	1.51	0.3720	9.53	0.0004	119	0.0001	1.35	0.2847	5.30	0.0075	2.13	0.1153
Nitrogen mineralization rate	93.48	0.0018	1.86	0.1666	30.92	0.0001	0.57	0.8385	3.09	0.0505	0.14	0.9660
Microbial biomass C	9.79	0.0466	1.32	0.3051	3.12	0.0928	2.71	0.0325	0.80	0.5065	0.17	0.9495
Microbial biomass N	0.78	0.5788	4.26	0.0155	37.38	0.0001	0.46	0.9093	2.99	0.0553	0.25	0.9079

* The soil variable means are illustrated for species and positions for the control plots in Fig. 1 and for the nitrogen plus water plots in Fig. 4. Also, means for the historical treatments and positions are shown in Fig. 6.

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 subplot 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 subplot factor. We used planned contrasts to compare the effects of the annual *K. 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, we sampled only one of the historical treatment replicates, due to time constraints on root washing and sorting. We considered the historical treatment as the whole plot factor and the species as the subplot factor in a split plot design. In this case, we had no replication of the historical treatment, so we cannot make statistical inferences about the effects of historical treatment on belowground mass and tissue chemistry. However, we spatially replicated as much as possible by sampling 32 individuals across each entire historical treatment plot (1 ha area), so our inferences about historical treatment are unlikely to be affected by errors from local plot effects.

Ecosystem-level estimates

To estimate the impact of individual plants and species on larger scale ecosystem properties, we 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

TABLE 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 plus water additions from 1970 to 1974), plant species (five different species), and their interaction on plant biomass characteristics.*

	Factor					
	Historical treatment		Species		Historical treatment × species	
Response	F	P	F	P	F	P
Aboveground biomass (g/m²)	96.06	0.0018	44.94	0.0001	11.17	0.0001
Belowground biomass (g/m²)	6.59	0.0003	37.28	0.0001	6.92	0.0001
Root : Shoot	11.20	0.0001	77.25	0.0001	3.56	0.0001
Root C:N	23.74	0.0001	7.53	0.0001	0.30	0.9869
Leaf C:N	41.26	0.0001	47.76	0.0001	3.73	0.0001
Root lignin : N	2.94	0.0765	3.10	0.0274	⋯	⋯

* Fig. 2 shows the species means for plant biomass characteristics only on the control plots and Fig. 3 shows the species means for the nitrogen plus water plots. The means for plant biomass characteristics for the historical treatment plots are shown in Fig. 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.

TABLE 4. Results of a 2-way ANOVA showing the significance of the effects of historical treatment (T; treatments were control, nitrogen, water or nitrogen plus water additions from 1970 to 1974) and the estimate (E) method used to scale up local measurements of soil properties to the plot scale.*

Response	Factor	df	MS	F	P
Total soil carbon	T	3	33 610	14.86	0.0002
	E	2	5203	2.30	0.1426
	$T \times E$	6	5726	2.53	0.0805
	Error	12	2261		
Total soil nitrogen	T	3	515	5.47	0.0133
	E	2	5.7	0.06	0.9414
	$T \times E$	6	33.8	0.36	0.8911
	Error	12	94		
C mineralization	T	3	0.300	5.78	0.0111
	E	2	0.589	11.31	0.0017
	$T \times E$	6	0.030	0.058	0.7388
	Error	12	0.052		
N mineralization	T	3	0.002	10.78	0.0010
	E	2	0.001	7.29	0.0085
	$T \times E$	6	0.001	0.88	0.5353
	Error	12	0.0001		
Microbial biomass C	T	3	14.35	4.53	0.0240
	E	2	1.38	0.44	0.6566
	$T \times E$	6	0.99	0.31	0.9176
	Error	12	3.17		
Microbial biomass N	T	3	0.007	0.32	0.8137
	E	2	0.007	0.32	0.7347
	$T \times E$	6	0.001	0.03	0.9998
	Error	12	0.023		

* 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 Methods for an explanation of how each estimate was calculated.

and bare ground in the historical treatment area (Table 1). We obtained the estimates of plant species cover using our own cover data and data from another study (D. Milchunas, *personal communication*), that provided an estimate of the relative cover of bare ground on each treatment plot. We standardized percentage basal cover estimates for the five species (seven in the NW historical treatment plots) plus bare ground to 100%. We neglected the other species in the estimates since the five to seven sampled species represent >80% of plant cover in the plots (D. Milchunas, *personal communication*).

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-plant 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-plant 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, for bare as well as for plant-covered areas. Thus, we think 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-plant 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 percentage cover of that species, and the average between-plant soil property, multiplied by percentage 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. We used a 2-way ANOVA to see if historical treatment or estimate method significantly affected the results (Table 4).
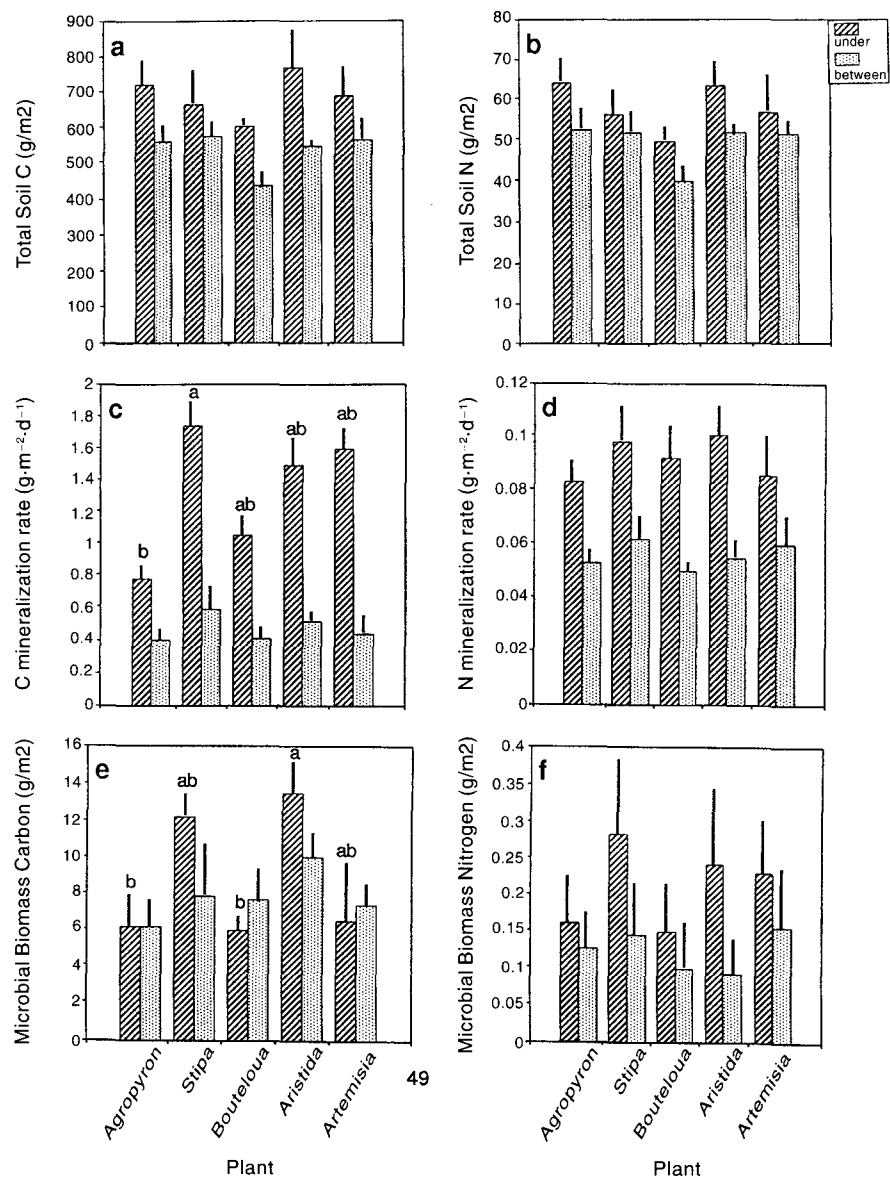
FIG. 1.   Total soil carbon (a), total soil nitrogen (b), carbon mineralization rate (c), potential nitrogen mineralization rate (d), microbial biomass carbon (e), and microbial biomass nitrogen (f) in soils from under and between plants of the species *Agropyron smithii, Stipa comata, Bouteloua gracilis, Aristida longiseta,* and *Artemisia frigida* on control plots (unfertilized and unwatered) of a historical treatment area in shortgrass steppe. The vertical line on each bar indicates 1 SE. The small letters indicate cases where significant differences ($P < 0.05$) existed among species in soil properties under their canopies.

RESULTS

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). Therefore, we will restrict our presentation of the effects of the five native, shortgrass species on soils to only the soils in the unaltered shortgrass steppe (Fig. 1). The five native short-

grass species did not differ from one another in their effects on total soil pools of carbon or nitrogen in soils beneath their canopies (Fig. 1a, b). Species did differ in their effects on C mineralization; the bunchgrass, *Stipa comata,* had significantly higher C mineralization rates in soils under its canopy than did the rhizomatous grass, *Agropyron smithii* (Fig. 1c). Also, soils under the bunchgrasses, *S. comata, Aristida longiseta,* and *Bouteloua gracilis,* collectively, had significantly higher carbon mineralization rates than did the soils under *A. smithii* (Fig. 1c). Species identity had no effect on
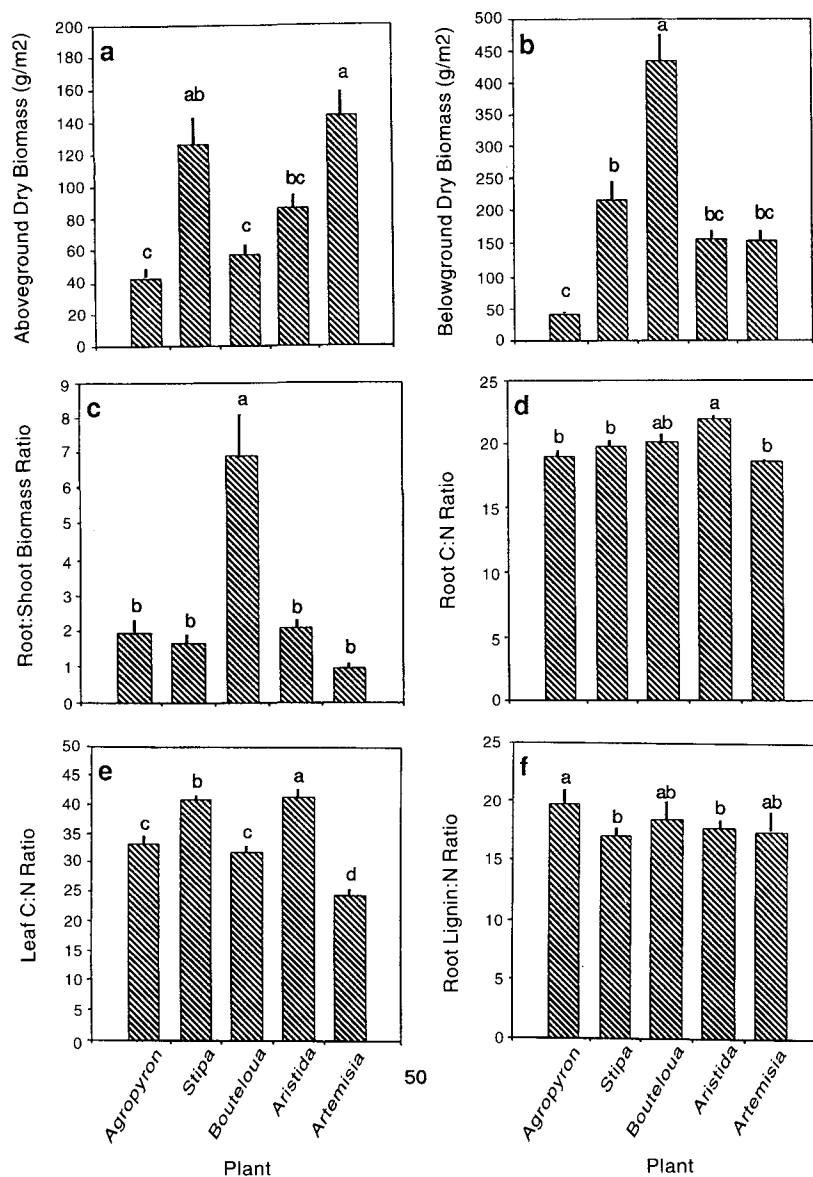
FIG. 2. Aboveground dry biomass (a), belowground dry biomass (b), root : shoot biomass ratio (c), root carbon : nitrogen ratio (d), leaf carbon : nitrogen ratio (e), and root lignin : nitrogen ratio (f) of *Agropyron smithii, Stipa comata, Bouteloua gracilis, Aristida longiseta,* and *Artemisia frigida* on 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 ($P \geq 0.05$).

potential nitrogen mineralization rate or microbial biomass nitrogen (Fig. 1d, f). Microbial biomass carbon showed a response similar to carbon mineralization rates; soils under *A. smithii* had one of the lowest levels (Fig. 1e).

The quantity and quality of biomass differed substantially among the five species (Table 3, Fig. 2). The shrub, *Artemisia frigida,* had significantly more aboveground biomass than the grass species, with the exception of *S. comata* (Fig. 2a). The tall bunchgrass, *S. comata,* had the most aboveground biomass among the

grasses. The dominant grass species of the shortgrass steppe, *B. gracilis,* had significantly more total belowground biomass than the other species (Fig. 2b). All of the bunchgrasses and the shrub had more belowground biomass than the rhizomatous grass, *A. smithii* (Fig. 2b). *B. gracilis* had much higher root to shoot ratios than the other species, which did not differ significantly from one another (Fig. 2c). Plant species also differed in tissue quality, or carbon : nitrogen and lignin : nitrogen ratios of above- and belowground tissue (Table 3). *A. 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 *B. gracilis* (Fig. 2d, e). *A. smithii* had significantly higher root lignin : nitrogen ratios than two of the other four species (Fig. 2f).

Plant position (under plants vs. between plants) exerted a strong and consistent effect on pool sizes and turnover rates of soil carbon and nitrogen in unaltered shortgrass steppe (Table 2, Fig. 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. 1). Although species × position was not statistically significant for all the historical treatment plots, in the control plots the contrast in the between-plant and under-plant positions was greater for bunchgrasses than for non-bunchgrasses.

NW treatment plots

The historical NW plots had very different relative abundances of species than the historically unaltered control plots (Table 1). In the NW plots, much of the plant cover was 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 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 (Figs. 2 and 3). However, there were some exceptions, and these contributed to the significant historical treatment × species interaction in the ANOVA for plant characteristics (Table 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 *B. gracilis* was less than or similar to that of the other five native species (Figs. 2b and 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 (Figs. 2a and 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 (Figs. 2 and 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, we compared the influence of the two invasive species, *K. scoparia* and *C. eleocharis,* to the influence of the other five species on plant and soil characteristics, all on the NW plots (Figs. 3 and 4). *K. scoparia* had significantly more aboveground biomass than the other species on the NW plots and both *K. scoparia* and *C. eleocharis* had significantly more belowground biomass per square metre than the other species (Fig. 3a, b). *C. eleocharis* had significantly higher root to shoot ratios than most other species (Fig.

3c). Both of these invasive species had lower belowground carbon to nitrogen ratios than the other species, except *A. smithii* (Fig. 3d), and both had significantly lower belowground lignin : nitrogen ratios than *A. smithii* and *B. gracilis* (Fig. 3f). Neither invasive species had significantly different effects on total soil carbon or nitrogen in soil beneath their canopies than the other species (Fig. 4a, b). However, soils associated with *K. scoparia* had significantly higher nitrogen mineralization rates, carbon mineralization rates and microbial biomass carbon than soils beneath the other species (Fig. 4c, d, e).

The effect of position on soils, i.e., the under-plant vs. between-plant soil pattern, was much less pronounced on the NW plots than on the control plots (Figs. 1 and 4). Also, *K. scoparia* 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. 4c, f).

Treatment plot comparisons

Historical resource addition significantly affected current aboveground plant biomass and tissue chemistry of the five species (Table 3). Total aboveground biomass was significantly higher on the N plots than on the other plots (Fig. 5a). Much of this increase in biomass on the N plots can be attributed to the very large and numerous individuals of the shrub, *Artemisia frigida,* on the N plots; this factor contributed to the significant historical treatment × species interaction effect on biomass (Table 3). Total belowground biomass of the five species was significantly lower on the NW plots than on control and N plots; the W plots had intermediate levels (Fig. 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. 5c). Carbon : nitrogen ratios of plant roots were significantly lower, and root lignin : nitrogen ratios tended to be lower than these values for the other plots (Fig. 5d, f). Carbon : nitrogen ratios of aboveground plant material were significantly lower on the NW plots than the other plots (Fig. 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 those that did not receive water, the control and N plots (Fig. 6a). Historical treatment also interacted with plant position to affect soil carbon and nitrogen (Table 2). More carbon and nitrogen was detected in soils under plants than in soils between plants on the control and N plots; this difference was not as striking or was absent in the plots that received water (Fig. 6a, b). Thus, 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.
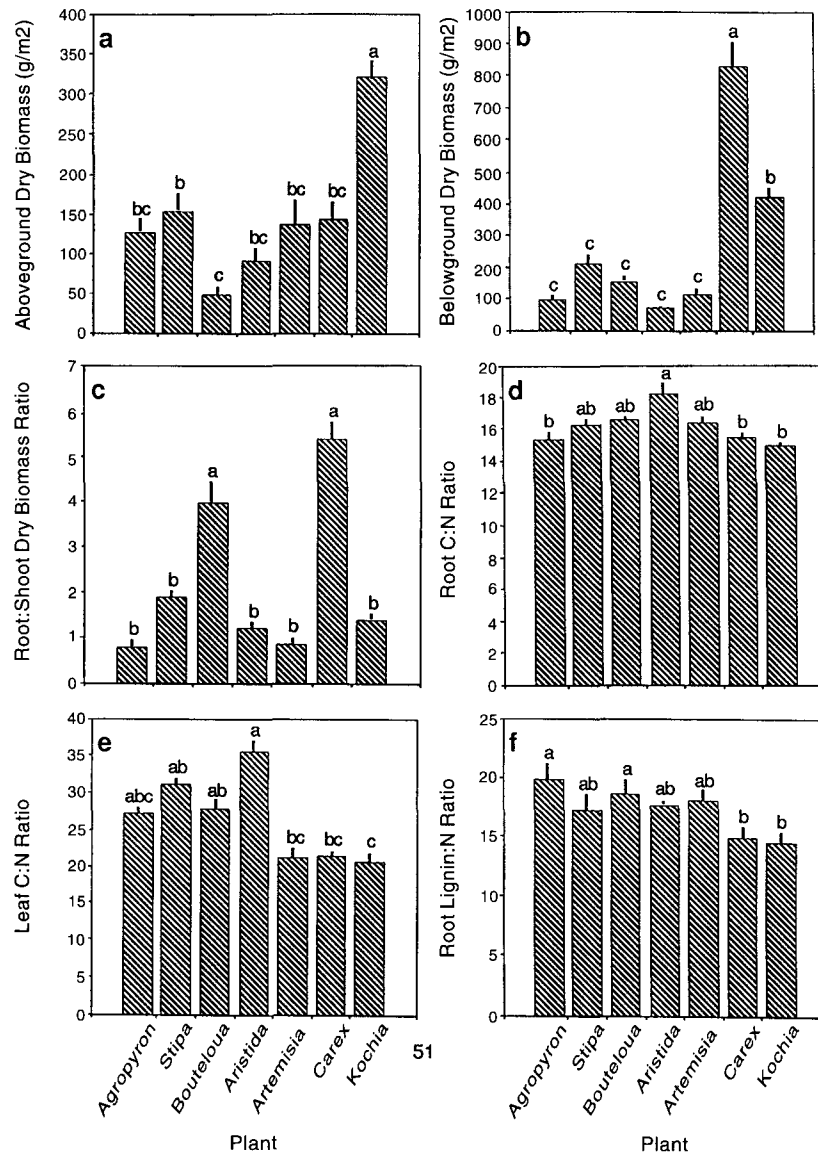
FIG. 3.   Aboveground dry biomass (a), belowground dry biomass (b), root : shoot biomass ratio (c), root carbon : nitrogen ratio (d), and aboveground biomass carbon : nitrogen ratio (e) of *Agropyron smithii, Stipa comata, Bouteloua gracilis, Aristida longiseta, Artemisia frigida, Carex eleocharis,* and *Kochia scoparia* on plots receiving nitrogen plus water from 1970 to 1974 on shortgrass steppe. The vertical line on each bar indicates 1 SE. Bars with the same letters are not significantly different ($P \geq 0.05$).

6c), but again interacted with plant presence (Table 2): the NW and W plots had significantly less of a contrast between positions in C mineralization than the other plots (Fig. 6c). Historical treatment affected nitrogen mineralization; the N and NW plots had higher rates of nitrogen mineralization than the control and W plots (Fig. 6d). As with total soil pool sizes and carbon mineralization rates, nitrogen mineralization rates were significantly higher in soils from under plants than from soils between plants, and the historical addition of water interacted with position (Table 2) to significantly decrease this contrast (Fig. 6d). No historical treatment

main effects were present in microbial biomass carbon or nitrogen (Table 2, Fig. 6e, f), but, again, there was less contrast in the W plots in the between-plant vs. under-plant levels of microbial biomass nitrogen.

Ecosystem level implications

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, Fig. 6), whereas soil properties expressed on a plot scale were, in most cases, significantly affected by historical treatment (Table 4).
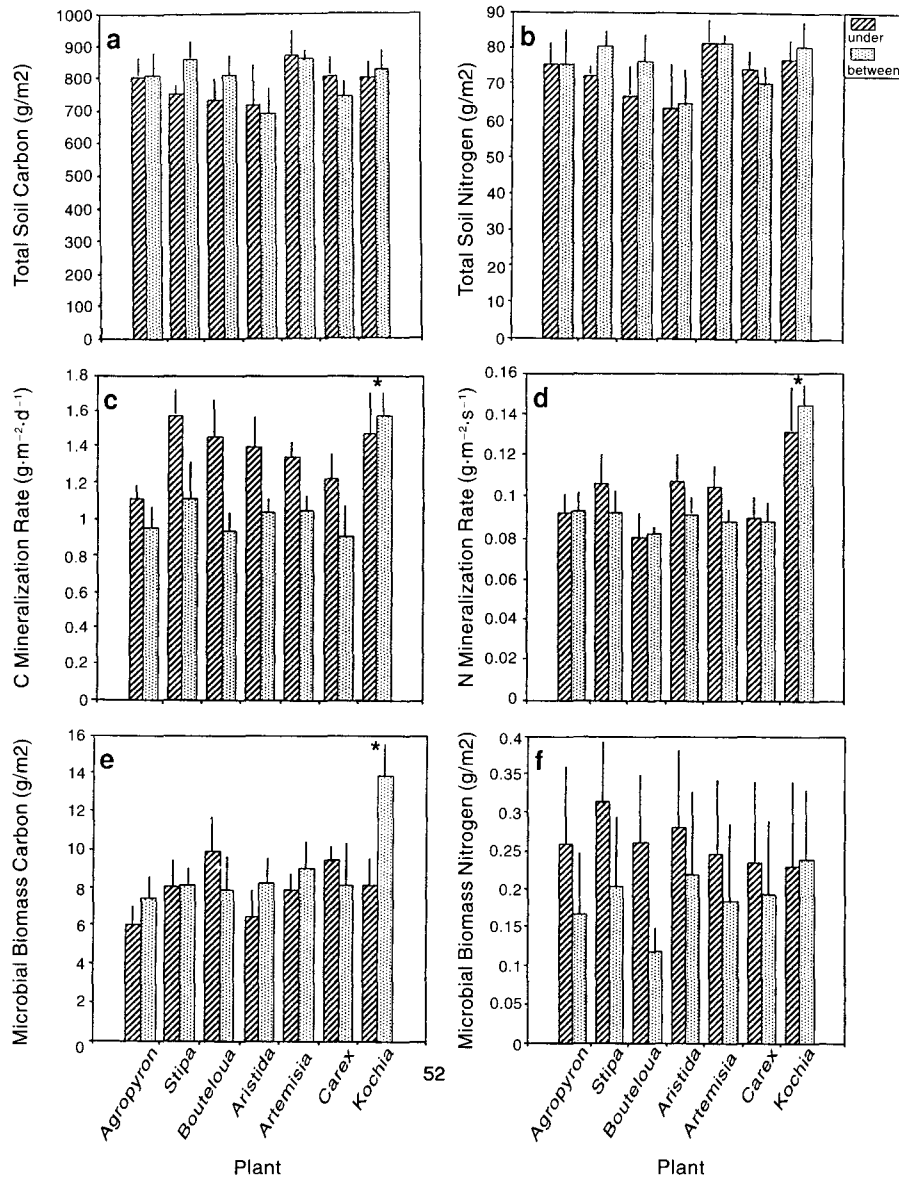
FIG. 4. Total soil carbon (a), total soil nitrogen (b), carbon mineralization rate (c), potential nitrogen mineralization rate (d), microbial biomass carbon (e), and microbial biomass nitrogen (f) in soils from under and between plants of seven species on plots in shortgrass steppe receiving nitrogen plus water from 1970 to 1974. The vertical line on each bar indicates 1 SE. Significant differences ($P < 0.05$) between soils associated with *Kochia scoparia* and soils under the other plant species are indicated with asterisks.

The NW plots had significantly more soil carbon and nitrogen on a plot basis than the control plots (Table 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 5). The N plots had higher rates of plot scale carbon mineralization than the control plots; the NW and the W plots were intermediate (Table 5). The NW plots had significantly higher plot scale microbial biomass carbon than the W plots, and the control and N plots were intermediate. Historical

treatment did not affect levels of microbial biomass nitrogen on a plot scale (Tables 4 and 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 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
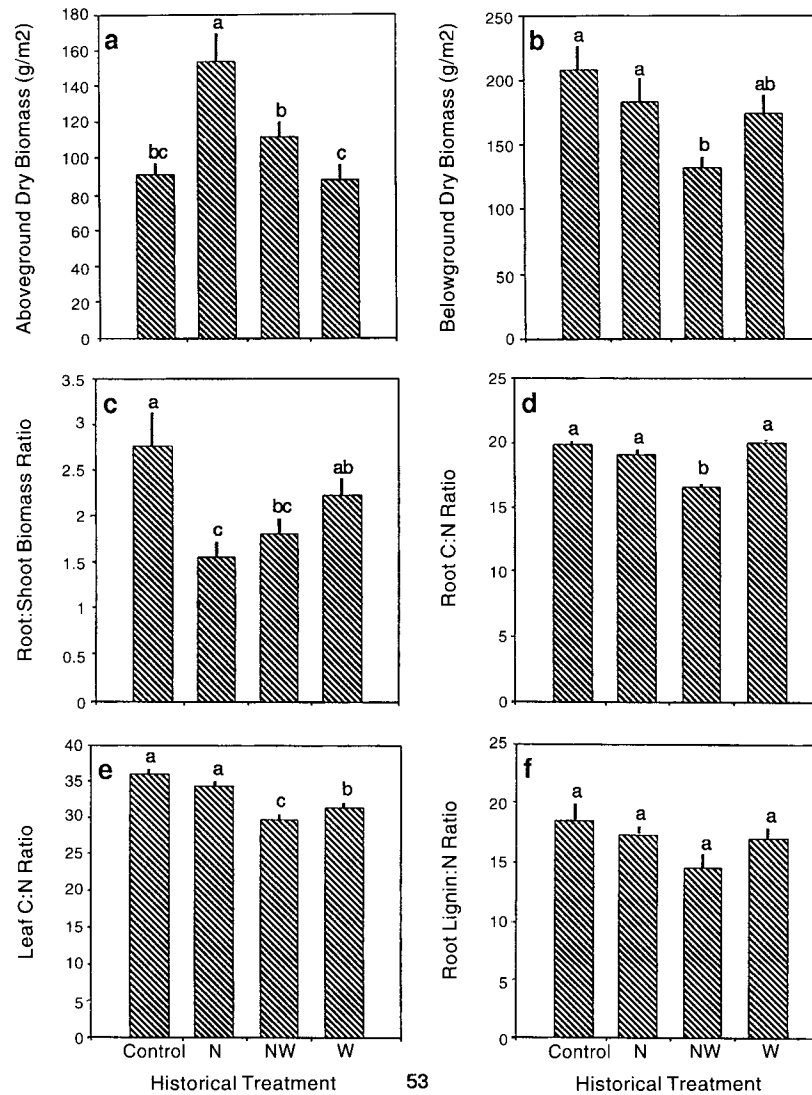
FIG. 5. Aboveground dry biomass (a), belowground dry biomass (b), root : shoot biomass ratio (c), root carbon : nitrogen ratio (d), leaf carbon : nitrogen ratio (e) and root lignin : nitrogen ratio (f) averaged across five plant species (only *Bouteloua gracilis* for root lignin : N) on plots in shortgrass steppe receiving nothing (Control), additional nitrogen (N), additional water (W), or both additional nitrogen and water (NW) from 1970 to 1974. The vertical line on each bar indicates 1 SE. Bars with the same letters are not significantly different ($P \geq 0.05$).

that considered only bare ground (Table 5). The three estimates did not result in different levels of microbial biomass carbon or nitrogen (Table 5).

DISCUSSION

Plant species and lifeform effects on soils

This study provided evidence that plant species, via tissue chemistry, biomass allocation, or life-span (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 nutrient cycling (see, for example, Chapin 1993, Mooney and Schulze 1993). Furthermore, the species (*Kochia scoparia*) most clearly different from the rest in terms of 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, and not the total, pools of carbon and nitrogen. This result is consistent with Wedin and Pas-
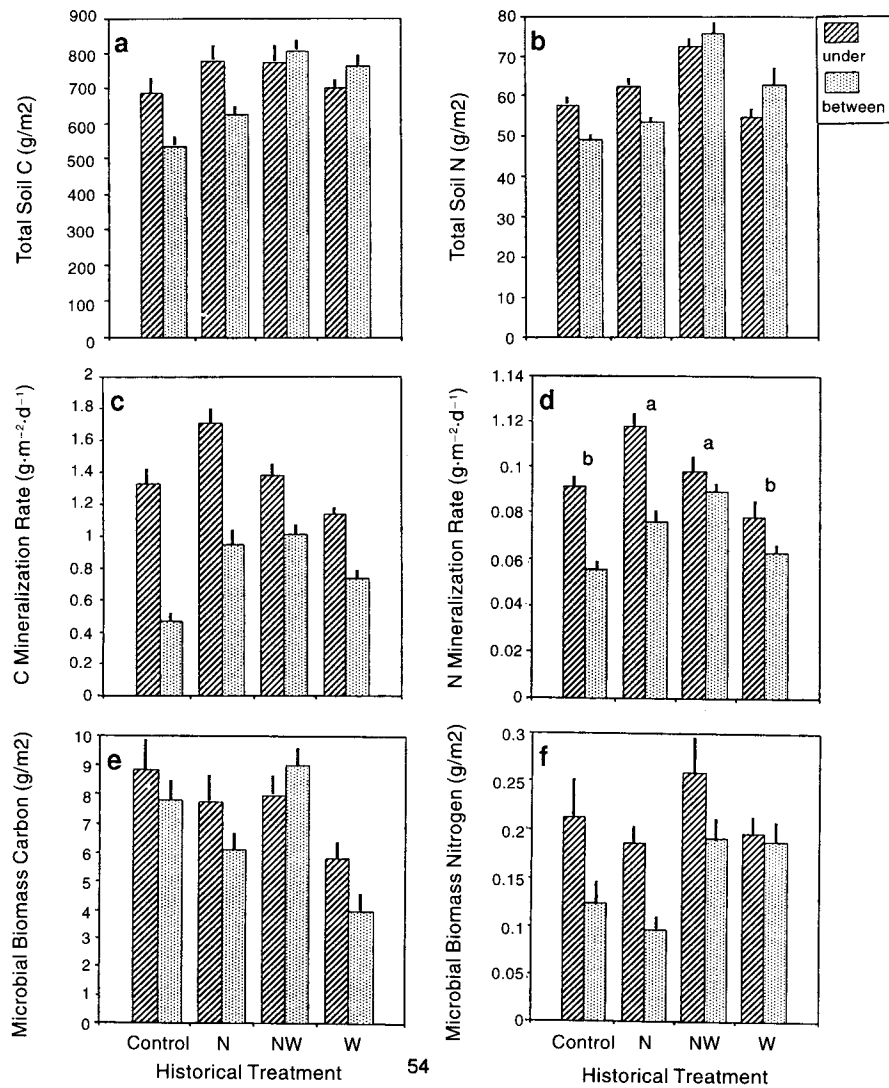
FIG. 6. Total soil carbon (a), total soil nitrogen (b), carbon mineralization rate (c), potential nitrogen mineralization rate (d), microbial biomass carbon (e), and microbial biomass nitrogen (f) in soils from under plants and between plants on plots in shortgrass steppe receiving nothing (Control), additional nitrogen (N), additional water (W), or both additional nitrogen and water (NW) from 1970 to 1974. Soils under and between five 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 ($P < 0.05$) existed in soil properties (averaged across both under- and between-plant positions) among historical treatments.

tor (1993), who found that species effects were more obvious in the labile portions than in the recalcitrant portions of soil nitrogen. The most responsive soil property seemed to be the indices 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 *A. 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, we 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, *K. 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

TABLE 5. Three estimates* of ecosystem 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 additional nitrogen (N), additional water (W), both additional nitrogen and water (NW), or nothing (Control) from 1970 to 1974. Data represent mean ± SE. Estimates with the same letter superscript are not significantly different ($P > 0.05$) when averaged over historical treatments. Historical treatments with the same letter are not significantly different ($P > 0.05$) when averaged over estimate.

	Historical treatment			
Estimate	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^{-1} d^{-1})			
	[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^{-1} d^{-1})			
	[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

* 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 Methods for an explanation of how each estimate was calculated.

species can have differential effects on both microbial immobilization and microbial release of nutrients. In our 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. *B. 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 *B. gracilis* soil and other species' soil with large amounts of fine root litter. In a root exudation study (Biondini et al. 1988), *B. gracilis* released more C and N from roots in sterile media than *A. smithii*; however, we 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-plant canopy vs. under-plant canopy differences in soil properties. *K. scoparia,* the only annual in the study, showed significantly less plant canopy-induced soil variation in carbon mineralization rates and microbial biomass nitrogen than did the perennial species. As an annual, *K. scoparia* plants presumably occupy microsites only briefly, with different microsites occupied each year. Also, bunchgrasses tended to have more of a contrast in soil properties in between-plant canopy vs. under-plant canopy positions than did the non-bunch life-forms. This difference could be explained by the spatial arrangement of stems. Bunchgrasses tend to have very localized points of biomass, in contrast to more diffuse or "stemmy" herbaceous

life-forms, 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 life-span of the plant, with the shorter-lived plant, *Bouteloua eriopoda,* having less between vs. under canopy difference in soils than the longer-lived plant, *B. gracilis.* In a study of the amount 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 than soil between plants. 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 semiarid areas (Charley and West 1975, 1977, Barth and Klemmedson 1978, Klopatek 1987, Burke et al. 1989, Bolton et al. 1990, 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 life-span. 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 semiarid grassland in southeastern 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 southwestern U.S. desert system, leads to ecosystem degradation and desertification. In our system, 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 1970s affected plant biomass and allocation in the early 1990s. 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 our data show the same pattern. Apparently, 20 yr 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, our 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 1970s 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 yr ago. Although current total pools of soil nitrogen were not detectably larger in the plots which received nitrogen from 1970 to 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 yr 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 yr ago), the abundance or productivity of *K. scoparia* did not drop to previous levels. Our data suggest that high nitrogen availability in soils beneath *K. scoparia* may be maintained in part by tissue chemistry favorable to microbial decomposition and release of nitrogen. The continued persistence of *K. scoparia,* 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, 1990, Vitousek et al. 1987).

Ecosystem level implications

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 semiarid grassland. In some cases (e.g., perennial vs. annual species) 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. We believe that in our semiarid 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 yr) and furthermore, these perturbations to soil resources may persist and be maintained through feedbacks between soil organic matter and plant species characteristics. In addition, we have 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.

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