*Plant and Soil* **191:** 147–156, 1997.
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# Does grazing mediate soil carbon and nitrogen accumulation beneath $C_4$, perennial grasses along an environmental gradient?

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Received 23 September 1996. Accepted in revised form 28 March 1997

*Key words:* environmental gradient, grazing, nutrient accumulation, plant-animal interactions, soil heterogeneity

## Abstract

An experiment was conducted to evaluate the influence of long-term (>25 yrs) grazing on soil organic carbon (SOC) and total soil nitrogen (N) accumulation beneath individual plants of three perennial grasses along an environmental gradient in the North American Great Plains. The zone of maximum SOC and N accumulation was restricted vertically to the upper soil depth (0-5 cm) and horizontally within the basal area occupied by individual caespitose grasses, which contributed to fine-scale patterning of soil heterogeneity. Long-term grazing mediated SOC and N accumulation in the tall-, mid- and shortgrass communities, but the responses were community specific. SOC and N were lower beneath *Schizachyrium scoparium* plants in long-term grazed sites of the tall- and midgrass communities, but higher beneath *Bouteloua gracilis* plants in the long-term grazed site of the shortgrass community. SOC, but not N, was greater in soils beneath compared to between *S. scoparium* plants in an abandoned field seeded in 1941, indicating that this caespitose grass accumulated SOC more rapidly than N. SOC and N were greater in the 0-5 cm soil depth beneath a caespitose grass (*S. scoparium*) compared to a rhizomatous grass (*Panicum virgatum*) in the tallgrass community, with no significant accumulation of either SOC or N beneath *P. virgatum* plants. Grazing appears to indirectly mediate nutrient accumulation beneath caespitose grasses along the environmental gradient by modifying the size class distribution of plants. Populations with a greater proportion of large plants have a greater potential for biomass incorporation into soils and may more effectively capture redistributed organic matter from between plant locations. Contrasting plant responses to grazing at various locations along the environmental gradient conform to the predictions of the generalized grazing model, as the selection pressures of grazing and aridity may have also influenced the ability of caespitose grasses to accumulate nutrients in soils beneath them by mediating grazing resistance, competitive ability and population structure.

## Introduction

Plant-induced soil heterogeneity has been documented for both arborescent and herbaceous species in diverse communities including woodlands (e.g. Zinke, 1962), savannas (e.g. Belsky et al., 1989), desert shrublands (e.g. Charley and West, 1975; Schlesinger et al., 1990) and semi-arid grasslands (e.g. Hook et al., 1991; Vinton and Burke, 1995). These 'islands of fertility' appear to result from nutrient accumulation mediated by both biological and physical processes (Coppinger et al., 1991; Schlesinger et al., 1996). Soil heterogeneity has numerous implications for vegetation dynamics (Hook et al., 1991; Vinton and Burke, 1995) and has been proposed as an indicator of desertifcation in arid and semi-arid environments (Schlesinger et al., 1996). Although 'islands of fertility' were initially documented with shrub species (Charley and West, 1975; Halvorson et al., 1994, 1995; Schlesinger et al., 1990), it has recently become clear that perennial grasses are also capable of accumulating nutrients in soils (e.g. Hook et al., 1991; Jackson and Caldwell, 1989, 1993a, b; Vinton and Burke, 1995). However, the pattern of soil heterogeneity induced by perennial grasses is a finer-scale

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than that associated with shrubs (Schlesinger et al., 1996).

Soil organic carbon (SOC) and total soil nitrogen (N) accumulation beneath several species of caespitose (syn. bunchgrass) grasses has been documented in both semi-arid and mesic environments (Hook et al., 1991; Rice et al., 1994; Vinton, 1994; Vinton and Burke, 1995). Caespitose grasses are characterized by the compact arrangement of a large number of tillers within a relatively small basal area and the absence of rhizomes and stolons (Briske, 1991). In contrast, rhizomatous and stoloniferous grasses have a more diffuse arrangement of tillers and generally greater plant basal area and have been shown to induce less soil heterogeneity compared to caespitose grasses in a shortgrass steppe (Vinton and Burke, 1995). However, the mechanisms and ecological consequences associated with the occurrence of fine-scale soil heterogeneity and the contrasting response between caespitose and rhizomatous grasses merit additional research emphasis. For example, does nutrient accumulation beneath individual plants extend to the zone of nutrient accumulation of neighboring plants, or is it restricted to the immediate proximity of each plant? What are the temporal requirements associated with the progression from coarse-scale to fine-scale soil heterogeneity in grasslands dominated by caespitose species? The available evidence suggests that decadal time periods are required for both SOC and N accumulation in soils beneath caespitose grasses (Burke et al., 1995).

Grazing has been documented to modify both the magnitude and distribution of SOC and N (e.g., Kieft, 1994; Milchunas and Lauenroth, 1993; Ruess and McNaughton, 1987), as well as the relative proportion of each of these resources at the plant community level. However, it is less clear how grazing may potentially modify nutrient accumulation beneath individual caespitose grasses. Long-term intensive grazing may decrease the input of organic matter into soils in the immediate vicinity of individual plants and eventually reduce nutrient concentrations beneath plants by limiting availability of photosynthetic and/or meristematic tissues necessary for growth (e.g. Briske and Richards, 1995). A reduction in organic matter input into soils beneath these plants may potentially diminish soil nutrient accumulation and alter their relative competitive ability. Consequently, grazing-induced degradation of caespitose grass populations may be partially mediated by a reduction of SOC and N in soils beneath plants.

An experiment was conducted to evaluate SOC and N accumulation in soils beneath plants of three $C_4$, perennial grasses along an east-west environmental gradient in the North American Great Plains. This gradient has previously been utilized to compare nutrient accumulation beneath contrasting grass growth forms (Vinton, 1994). We tested the hypotheses that: 1) the spatial distribution of SOC and N gradually diminished from the center of individual plants to areas between plants, 2) SOC and N are greater in soils beneath compared to between caespitose grasses in an abandoned field seeded in 1941, 3) SOC and N are greater in soils beneath caespitose compared to rhizomatous grasses in a mesic grassland, and 4) SOC and N are lower in soils beneath caespitose grasses in sites with a history of long-term grazing by domestic cattle compared to long-term ungrazed sites. These hypotheses were evaluated with dominant grasses in tallgrass (*Schizachyrium scoparium*, caespitose; *Panicum virgatum*, rhizomatous), midgrass (*S. scoparium*), and shortgrass (*B. gracilis*, caespitose) communities. Plants of each species were evaluated in both a long-term (> 25 yrs) grazed and ungrazed site within each of the three communities.

## Materials and methods

### *Site descriptions*

The tallgrass community site, Konza Prairie Research Natural Area, was located on a midslope topographical position in the Flint Hills of eastern Kansas, near Manhattan (39°05′ N, 96°35′ W). Vegetation is dominated by *Andropogon gerardii* Vitman, *Sorghastrum nutans* L., *S. scoparium*, and *P. virgatum* with a mean annual net primary productivity (ANPP) of 4,000 kg $ha^{-1}$. Annual mean precipitation is 835 mm and annual mean temperature is 12.8 °C (Bark, 1987). The midgrass community site was located on a midslope topographical position in west-central Kansas at Fort Hays State University (38°52′ N, 99°23′ W), where *S. scoparium*, *A. gerardii*, and *B. curtipendula* (Michx.) Kunth comprise the dominant species, and mean ANPP is 2,200 kg $ha^{-1}$. This location has an mean annual precipitation of 588 mm and annual mean temperature of 11.9 °C (Hulett and Tomanek, 1969). The shortgrass community site was located on a swale topographical position at the Central Plains Experimental Range (CPER) in north-central Colorado, approximately 60 km northeast of Fort Collins (40°49′ N, 107°46′ W).

Mean annual precipitation is 321 mm and mean annual temperature is 8.6 °C (Lauenroth and Sala, 1992). Vegetation is predominately (90% of basal area) *B. gracilis* (Milchunas et al., 1989), and mean ANPP is 1,000 kg $ha^{-1}$. Long-term ungrazed (since 1969, 1908 and 1939 for the tallgrass, midgrass and shortgrass sites, respectively) and nearby moderately grazed sites were sampled within each community.

*Sampling methods*

SOC and N directly beneath, between, and at the periphery of plants, within long-term grazed and ungrazed sites in each community, were determined by the collection of soil samples from ten pairs of equidistant plants in June 1994. The mean distance between plants in a pair was 20 cm at each community, and tiller number $plant^{-1}$ was counted for each plant pair. The relatively large plant basal areas of *S. scoparium* plants in grazed compared to ungrazed sites within the tallgrass community very likely resulted from the greater grazing avoidance associated with large compared to small plants (Ganskopp et al., 1992; Truscott and Currie, 1989). Additional soil samples were collected from ten pairs of rhizomatous *P. virgatum* plants in the tallgrass community and *S. scoparium* plants seeded on abandoned cropland in 1941 near Fort Hays State University (Riegel et al., 1963). These data provide a comparison between caespitose and rhizomatous grasses in the tallgrass community, and a temporal reference for the accumulation of SOC and N within soils beneath caespitose grasses, respectively.

Two soil cores (2 cm diameter×30 cm deep) were collected from five locations for each pair of plants and pooled to reduce sample variability. Locations included: 1) plant centers, 2) midpoint between plant peripheries, and 3) the periphery of both plants. Soil cores were divided into three depth increments (0-5, 5-15 and 15-30 cm) and large roots (>2 mm) were removed by passing the soil through a 2 mm sieve. These soils were dried at 60 °C for 5 days. Fine-earth soil bulk density was determined on ten additional soil cores (2×30 cm) taken directly beneath and between plants for each grazed and ungrazed site in the three communities. Soil passing a 2 mm sieve was dried at 105 °C for five days and weighed with soil volume calculated using the volume of a cylinder. Rock fragments (particle size > 2 mm) were dried and weighed and their volume was determined through water displacement (Vincent and Chadwick, 1994). Fine-earth soil bulk density was calculated by subtracting rock fragment weight and volume from total weight and core volume (Vincent and Chadwick, 1994).

Soil samples were ground with a ring pulverizer (Model TE250, Angstrom, Inc., Belleville, Michigan, USA) and analyzed for SOC (Niewenhuize et al., 1994) and N using a Carlo-Erba NA1500 (Fisons Instruments, Danvers, Massachusetts, USA) elemental analyzer. Average precision (standard deviation for triplicate samples) was 0.25 g $kg^{-1}$ for SOC and 0.025 g $kg^{-1}$ for N. Pool sizes of SOC and N in a cylinder directly beneath the basal area of individual plants were expressed on a tiller $plant^{-1}$ basis to allow comparisons among plants with similar basal areas, but varying numbers of tillers $plant^{-1}$. A cylinder directly beneath the basal area of individual plants was selected because this volume provided the least arbitrary approach for defining a resource volume directly accessible to the plant. Within this cylinder, SOC and N pools were calculated by multiplying pools (g $m^{-2}$) by the plant basal area ($cm^2$) and dividing the product by 10,000 for expression on a g $cm^{-2}$ basis, which is an appropriate scale for individual plant investigations. Division of this pool size by the number of tillers in a plant allowed expression of this pool size on a tiller $plant^{-1}$ basis. Logistic regression equations were developed to estimate spatial patterning of SOC and N among sample points within a soil core location.

*Statistical analyses*

The experiment was analyzed as a split-plot design with grazing and soil core location comprising the main factors and soil depth designated as the split factor. Communities were not replicated across the environmental gradient so analyses were performed separately for each community. The error term used to test main factors was the interaction of the main factors while the split factor and interactions were tested with the residual error (Steel and Torrie, 1980, p 377). Data from soil core locations beneath plants in each pair and the periphery locations were pooled leaving three soil core locations in each community (i.e. beneath plants, between plants, and plant periphery). Data were analyzed for each community using GLM procedures (SAS Institute Inc., 1988) and means were separated with Bonferroni t-tests when a factor was signifcant ($p<0.05$). Data collected from *S. scoparium* plant pairs in the seeded field were analyzed using t-tests with comparisons contrasting soil core locations beneath and between plants within a soil depth.

*Table 1.* Mean (± SE) values for soil attributes within three communities along an environmental gradient in the North American Great Plains. Letters indicate significant ($p<0.05$) differences among soil depths within a soil core location (GLM, $n=10$)

| Community | Depth (cm) | Soil pH | Bulk density (g cm$^{-3}$) |
|---|---|---|---|
| Tallgrass | 0-5 | $6.32\pm0.02^a$ | $0.91\pm0.02^a$ |
| | 5-15 | $6.16\pm0.03^b$ | $1.13\pm0.01^b$ |
| | 15-30 | $6.47\pm0.08^c$ | $1.22\pm0.01^c$ |
| Midgrass | 0-5 | $8.06\pm0.02^a$ | $0.92\pm0.02^a$ |
| | 5-15 | $8.21\pm0.02^b$ | $1.05\pm0.02^b$ |
| | 15-30 | $8.31\pm0.02^c$ | $1.09\pm0.03^b$ |
| Shortgrass | 0-5 | $8.10\pm0.09^a$ | $1.21\pm0.02^a$ |
| | 5-15 | $8.55\pm0.06^b$ | $1.23\pm0.02^a$ |
| | 15-30 | $8.63\pm0.04^b$ | $1.21\pm0.02^a$ |

## Results

### *Soil attributes and root biomass*

Soil bulk density and soil pH did not differ significantly beneath or between plants or within long-term grazed or ungrazed sites in any of the communities (data not shown). Soil bulk density increased with depth for all three communities (Table 1). Soil pH in the upper soil depth (0-5 cm) was significantly different compared to the lower soil depths in all three communities (Table 1).

Large root biomass was signifcantly greater in the 0-5 cm soil depth beneath compared to between plants of all species from both grazing histories (Table 2). Large root biomass in the 0-5 cm soil depth was signifcantly lower beneath *S. scoparium* plants in long-term grazed sites at both the tall- and midgrass communities, while no signifcant effect was associated with grazing history for *B. gracilis* plants in the shortgrass community. Large root biomass between plants exposed to the contrasting grazing histories did not differ significantly at any soil depth in any community.

### *Soil organic carbon and total nitrogen*

SOC and N within the 0-5 cm soil depth beneath caespitose grasses along the environmental gradient were highest for *S. scoparium* plants in the midgrass community and lowest for *B. gracilis* plants in the shortgrass community (Figures 1, 2). SOC and N at the plant periphery and between plant locations were not significantly different within any soil depth in any community (Figures 1, 2, 3).

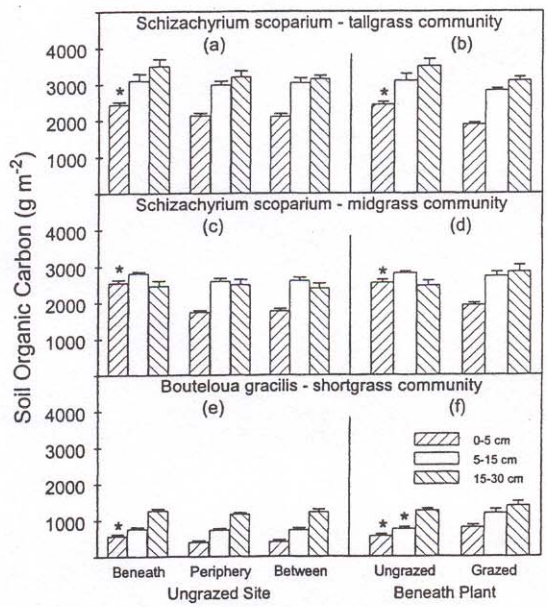


*Figure 1.* Pools (mean±SE) of soil organic carbon (g m$^{-2}$) in soils beneath, at the periphery and between dominant caespitose grasses in a long-term (>25 yrs) ungrazed site at each community (**a**, **c** and **e**), and beneath caespitose grasses only in long-term (>25 yrs) grazed and ungrazed communities along an environmental gradient in the North American Great Plains (**b**, **d** and **f**). Asterisks (*) indicate a significant ($p<0.05$) difference within a soil depth.

*Table 2.* Mean (±SE) values for large root (> 2 mm) biomass (g $cm^{-3}$) beneath and between caespitose grasses within three communities along an environmental gradient in the North American Great Plains. Letters indicate signifcant ($p<0.05$) differences between grazing histories within each soil depth for each species. Asterisks indicate significant differences ($p<0.05$) beneath and between plants within each soil depth in a grazing history for each species (GLM, $n=10$)

| | | | Large root biomass | |
|---|---|---|---|---|
| Species | Grazing history | Depth (cm) | Beneath plant | Between plant |
| *Schizachyrium scoparium*, tallgrass community | Ungrazed | 0-5 | 0.0766±0.0136[a]* | 0.0246±0.0047 |
| | | 5-15 | 0.0067±0.0020 | 0.0046±0.0011 |
| | | 15-30 | 0.0008±0.0002 | 0.0010±0.0003 |
| | Grazed | 0-5 | 0.0445±0.0086* | 0.0255±0.0075 |
| | | 5-15 | 0.0038±0.0006 | 0.0042±0.0005 |
| | | 5-30 | 0.0017±0.0005 | 0.0013±0.0003 |
| *Schizachyrium scoparium*, midgrass community | Ungrazed | 0-5 | 0.0826±0.0157[a]* | 0.0263±0.0050 |
| | | 5-15 | 0.0180±0.0013[b] | 0.0128±0.0022 |
| | | 5-30 | 0.0073±0.0012 | 0.0066±0.0015 |
| | Grazed | 0-5 | 0.0336±0.0031* | 0.0155±0.0025 |
| | | 5-15 | 0.0095±0.0013 | 0.0059±0.0010 |
| | | 5-30 | 0.0027±0.0004 | 0.0030±0.0008 |
| *Bouteloua gracilis* shortgrass community | Ungrazed | 0-5 | 0.0407±0.0032* | 0.0091±0.0021 |
| | | 5-15 | 0.0049±0.0005 | 0.0059±0.0010 |
| | | 5-30 | 0.0028±0.0004 | 0.0021±0.0005 |
| | Grazed | 0-5 | 0.0379±0.0025* | 0.0080±0.0041 |
| | | 5-15 | 0.0044±0.0006 | 0.0043±0.0008 |
| | | 15-30 | 0.0024±0.0005 | 0.0021±0.0005 |

For *S. scoparium* plants in the tallgrass community, SOC and N in the 0-5 cm soil depth were significantly higher (16% and 10% for SOC and N, respectively) beneath compared to between plants in the ungrazed site (Figures 1a, 2a). SOC and N in the 0-5 cm soil depth beneath plants were significantly lower (23% and 18%, respectively) in the long-term grazed compared to the ungrazed site (Figures 1b, 2b). Pool sizes $tiller^{-1}$ $plant^{-1}$ were significantly ($p<0.10$) higher (36% for both SOC and N) in the long-term grazed compared to the ungrazed site (Table 3).

For *S. scoparium* plants in the midgrass community, results followed the same trend as in the tallgrass community. SOC and N in the 0-5 cm soil depth were significantly higher (45% and 25%, respectively) beneath compared to between plants in the ungrazed site (Figures 1c, 2c). SOC and N in the 0-5 cm soil depth beneath plants were significantly lower (24% and 19%, respectively) in the long-term grazed compared to the ungrazed site (Figures 1d, 2d). SOC and N pool sizes $tiller^{-1}$ $plant^{-1}$ were significantly higher (66% and 100%, respectively) in the long-term grazed compared to the ungrazed site (Table 3).

For *B. gracilis* plants in the shortgrass community, SOC and N in the 0-5 cm soil depth were significantly higher (41% and 30%, respectively) beneath compared to between plants in the ungrazed site (Figures 1e, 2e). In contrast to the two previous communities, SOC and N were significantly higher in the 0-5 cm (43% and 53%, respectively) and 5-15 cm (55% and 75%, respectively) soil depths in long-term grazed compared to the ungrazed site (Figures 1f, 2f). Correspondingly, pool size $tiller^{-1}$ $plant^{-1}$ for SOC was 19% higher in the long-term ungrazed compared to the grazed site. while no difference was observed for N (Table 3).

*Table 3.* Relationship of soil organic carbon and total nitrogen (means ± SE) from cores beneath caespitose grasses (depth = 30 cm) to plant structure within three communities along an environmental gradient in the North American Great Plains. Pool size directly beneath plants was calculated as the product of total pool size (g $m^{-2}$) and individual plant basal area ($cm^2$) divided by 10,000. Expression of pool size below plants on a tiller $plant^{-1}$ basis was determined by dividing tiller $plant^{-1}$ into pools below plants. Asterisks indicate significant (* $p<0.10$, ** $p<0.05$) differences between grazing histories within each community (t-test, $n=10$)

| Species | | Organic carbon | | Total nitrogen | |
|---|---|---|---|---|---|
| | | Ungrazed | Grazed | Ungrazed | Grazed |
| *Schizachyrium scoparium* tallgrass community | basal area ($cm^2$) | 96±13** | 172±23 | 96±13** | 172±23 |
| | pool size below plant | | | | |
| | (g $plant^{-1}$) | 86±11** | 135±20 | 6.9±0.9** | 10.8±1.6 |
| | (g $cm^{-2}$ $plant^{-1}$) | 0.902±0.032** | 0.780±0.018 | 0.073±0.002** | 0.062±.001 |
| | (tiller number $plant^{-1}$) | 77±10** | 49±6 | 77±10** | 49±6 |
| | (g $cm^{-2}$ $tiller^{-1}$ $plant^{-1}$) | 0.0135±0.0017* | 0.0184±0.0022 | 0.0011±0.0001* | 0.0015±0.0002 |
| *Schizachyrium scoparium* midgrass community | basal area ($cm^2$) | 187±17 | 218±13 | 187±17 | 218±13 |
| | pool size below plant | | | | |
| | (g $plant^{-1}$) | 145±13 | 164±15 | 14.2±1.3 | 15.7±1.4 |
| | (g $cm^{-2}$ $plant^{-1}$) | 0.779±0.021 | 0.748±0.036 | 0.076±0.002 | 0.071±0.003 |
| | (tiller number $plant^{-1}$) | 231±14** | 132±9 | 231±14** | 132±9 |
| | (g $cm^{-2}$ $tiller^{-1}$ $plant^{-1}$) | 0.0035±0.0002** | 0.0058±0.0004 | 0.0003±0.0000** | 0.0006±0.0000 |
| *Bouteloua gracilis*, shortgrass community | basal area ($cm^2$) | 257±14 | 240±10 | 257±14 | 240±10 |
| | pool size below plant | | | | |
| | (g $plant^{-1}$) | 66±4** | 80±5 | 5.7±0.3** | 7.7±0.6 |
| | (g $cm^{-2}$ $plant^{-1}$) | 0.258±0.008** | 0.337±0.024 | 0.022±0.001** | 0.032±0.003 |
| | (tiller number $plant^{-1}$) | 142±12** | 223±19 | 142±12** | 223±19 |
| | (g $cm^{-2}$ $tiller^{-1}$ $plant^{-1}$) | 0.0019±0.0002 | 0.0016±0.0002 | 0.0002±0.0000 | 0.0002±0.0000 |

*Table 4.* Mean (± SE) values for soil organic carbon and total nitrogen (g $m^{-2}$) beneath and between *Panicum virgatum* plants in a tallgrass community (Konza Prairie Research Natural Area) and for *Schizachyrium scoparium* plants in a field seeded in 1941 near Ft. Hays State University (Hays, Kansas). Asterisks indicate a significant ($p<0.05$) difference between soil core locations within each soil depth (t-test, $n=10$)

| Species | Depth (cm) | Grazing history | Organic carbon | | Total nitrogen | |
|---|---|---|---|---|---|---|
| | | | Beneath plant | Between plant | Beneath plant | Between plant |
| *Panicum virgatum* | 0-5 | Ungrazed | 2129.4±86.5 | 2106.7±72.8 | 154.7±5.5 | 157.7±5.0 |
| | | Grazed | 1833.7±54.6 | 1783.6±36.4 | 136.5±3.6 | 136.5±3.2 |
| | 5-15 | Ungrazed | 2915.4±101.7 | 3039.7±135.6 | 237.3±6.8 | 248.6±9.0 |
| | | Grazed | 2825.0±90.4 | 2881.5±56.5 | 226.0±7.9 | 226.0±5.7 |
| | 15-30 | Ungrazed | 3239.1±146.4 | 3147.6±91.5 | 292.8±9.2 | 274.5±7.3 |
| | | Grazed | 3037.8±128.1 | 3239.1±73.2 | 256.2±7.3 | 274.5±5.5 |
| *Schizachyrium scoparium* | 0-5 | Seeded | 2051.6±119.6* | 1637.6±73.6 | 156±7.4 | 142.6±6.0 |
| | 5-15 | Seeded | | | 189.0±6.3 | 189.0±6.3 |
| | 15-30 | Seeded | | | 179.9±11.4 | 196.2±9.9 |

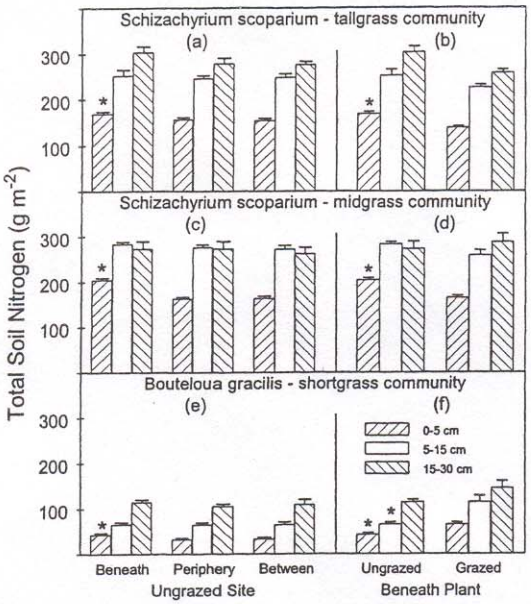


*Figure 2.* Pools (mean ± SE) of total soil nitrogen (g $m^{-2}$) in soils beneath, at the periphery and between dominant caespitose grasses in a long-term (>25 yrs) ungrazed site at each community (**a**, **c** and **e**), and beneath caespitose grasses only in long-term (>25 yrs) grazed and ungrazed communities along an environmental gradient in the North American Great Plains (**b**, **d** and **f**). Asterisks (*) indicate a significant ($p$<0.05) difference within a soil depth.

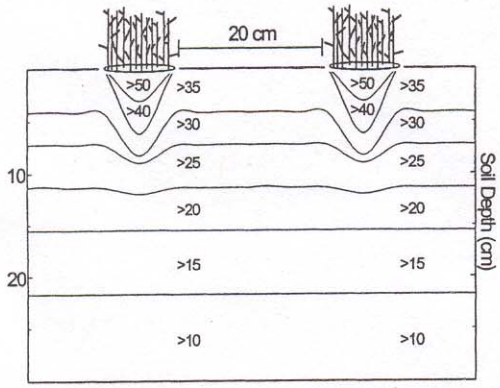


*Figure 3.* Mean pattern ($n$=10) of soil organic carbon concentrations (g $kg^{-1}$) in soils beneath a pair of *Schizachyrium scoparium* plants from a long-term (>25 yrs) ungrazed site in a midgrass community near Hays, Kansas. Soil cores were collected directly beneath plants, between plants, and at the plant peripheries. Soil cores were separated into depth increments of 0-5, 5-15, and 15-30 cm. Logistic regression equations were developed to determine the distribution patterns beneath and between plants.

In the tallgrass community, SOC and N beneath and between rhizomatous *P. virgatum* plants were similar at all soil depths for both the long-term grazed or ungrazed site (Table 4). SOC and N in the 0-5 cm soil depth beneath *S. scoparium* plants were significantly greater (14% and 9%, respectively) than beneath *P. virgatum* plants in the ungrazed site (t-test, $n$=10, $p$<0.05).

In the seeded field, SOC, but not N, in the 0-5 cm soil depth beneath *S. scoparium* plants was significantly higher (25%) than between plants (Table 4). SOC and N in the 0-5 cm soil depth beneath *S. scoparium* plants were significantly lower (19% and 23%, respectively) in the seeded field compared to the ungrazed site (t-test, $n$=10, $p$<0.01), but were not statistically different than the grazed site (t-test, $n$=10, $p$>0.05).

## Discussion

Caespitose grasses accumulated SOC and N in soils directly beneath individual plants and nutrient accumulation differed in response to long-term grazing along the environmental gradient. SOC and N in soils beneath *S. scoparium* plants in the tall- and midgrass communities were lower in long-term grazed sites, but higher beneath *B. gracilis* plants in the long-term grazed site in the shortgrass community. SOC, but not N, was greater in soils beneath compared to between 50-year old *S. scoparium* plants in a seeded feld. The rhizomatous grass, *P. virgatum*, in the tallgrass community, did not significantly accumulate SOC and N beneath compared to between plants in contrast to the caespitose grass, *S. scoparium*. Therefore, hypotheses one and two, pertaining to the gradual diminishment of SOC and N from the center of plants to areas between plants and greater SOC and N accumulation beneath compared to between caespitose grasses in an abandoned field seeded in 1941, respectively, were rejected. Hypothesis three addressing greater SOC and N accumulation beneath caespitose compared to rhizomatous plants was not rejected and hypothesis four which proposed lower SOC and N accumulation beneath caespitose grasses in long-term grazed compared to ungrazed sites was not rejected in two of the three communities.

The zone of maximum SOC and N accumulation was restricted vertically to the upper soil depth (0-5 cm) and horizontally within the basal area occupied by individual plants, which coincides with the location of greatest root mass for caespitose grasses (Hook et al., 1994). Root turnover is an important N input into low productivity soils in addition to the incorporation of aboveground litter (Vasquez de Aldana et al., 1996). Documentation of greater SOC and N accumulation

beneath compared to between caespitose grasses is in agreement with previous investigations conducted in this region (Burke et al., 1995; Hook et al., 1991; Kelly et al., 1996; Vinton, 1994; Vinton and Burke, 1995), but these results further illustrate the fine-scale pattern of soil heterogeneity induced by nutrient accumulation directly beneath individual caespitose grasses (e.g. Schlesinger et al., 1996). The fine-scale pattern of SOC and N accumulation beneath individual caespitose grasses very likely results from both root and shoot organic matter input (Vasquez de Aldana et al., 1996) and deposition of plant litter redistributed from surface soils between plants during the long life-span of these grasses (e.g. Coppinger et al., 1991).

The dynamics of SOC and N accumulation in soils beneath a caespitose grass (*S. scoparium*) in the seeded field of the midgrass community indicate that SOC accumulates more rapidly than total N. It is not unexpected that SOC would accumulate more rapidly than N based on large inputs of carbon-rich litter from root and canopy turnover and deposition of redistributed plant litter. A comparable rate of SOC accumulation was documented beneath *B. gracilis* plants in fields abandoned for a comparable time period (53 yrs) in the shortgrass community (Burke et al., 1995). However, it is difficult to envisage the adaptive value of nutrient accumulation on a decadal time scale given an estimated maximum longevity of 30-80 years for caespitose grasses (Briske and Derner, 1997; Gatsuk et al., 1980).

The caespitose species, *S. scoparium*, induced greater fine-scale soil heterogeneity in the tallgrass community than did the rhizomatous species, *P. virgatum*. This difference corroborates the patterns of soil heterogeneity that have previously been documented for these distinct grass growth forms in the shortgrass (Vinton and Burke, 1995) and tallgrass communities (Vinton, 1994) that we investigated. One potential explanation for less plant-induced soil heterogeneity associated with *P. virgatum* is that this species possesses short, long-lived rhizomes that are known to function as sites of carbon and nitrogen storage (Hartnett, 1989, 1993). Consequently, this species may accumulate resources primarily in rhizomes, rather than soils, to maintain dominance in the tallgrass community. However, direct comparisons of nutrient storage pools within rhizomes and soils beneath caespitose grasses have not been conducted. A second potential explanation for the occurrence of less plant-induced soil heterogeneity associated with the rhizomatous grass growth form is based on the diffuse spatial arrangement of tillers within a large basal area (Briske, 1991). This canopy architecture may not concentrate and capture redistributed organic matter as effectively as the more compact caespitose grass growth form. In addition, greater primary productivity and uniform plant cover in the tallgrass community than in either the mid- or shortgrass community (Sims et al., 1978), may further minimize the development of plant-induced soil heterogeneity.

Smaller pools of SOC and N beneath caespitose grasses in long-term grazed compared to ungrazed sites of the tall- and midgrass communities may be related causally to grazing-induced modifications of population structure of *S. scoparium*. Intensively grazed caespitose grass populations are frequently characterized by higher densities of plants with smaller mean basal areas compared to ungrazed populations (Briske and Richards, 1995; Butler and Briske, 1988; Pfeiffer and Hartnett, 1995). Intensive grazing may decrease organic matter input into soils in the immediate vicinity of grasses and eventually reduce nutrient pools beneath individual plants by limiting availability of photosynthetic and/or meristematic tissue necessary for growth (e.g., Briske and Richards, 1995). This may potentially suppress the ability of caespitose grasses to accumulate nutrients, monopolize resources, and maintain dominance. However, a reduction in SOC and N pools would require several years based on the time required for soil organic matter turnover in temperate regions (Burke et al., 1987; Schimel et al., 1994). Therefore, grazing-induced population degradation of caespitose grasses in tall- and midgrass communities must initially be mediated by the suppression of plant function because population structure can be modifed by intensive grazing within a shorter time frame (Butler and Briske, 1988).

Grazing-induced modifications to population structure may indirectly mediate nutrient accumulation beneath caespitose grasses in tall- and midgrass communities because ungrazed populations with a higher proportion of large plants may produce and incorporate greater amounts of organic matter into soils and more effectively capture redistributed organic matter. In contrast, long-term grazing in the shortgrass community results in larger plant basal areas for *B. gracilis* (Milchunas et al., 1989), which may be partially responsible for greater SOC and N accumulation beneath individual plants in the grazed site of the shortgrass community. Increases in SOC and N have been documented in previous investigations in a shortgrass (Vokhiwa, 1994) and nearby midgrass communi-

ty (Manley et al., 1995). However, other investigators have not found significant differences in SOC and N between grazed and ungrazed sites in the shortgrass community (Burke et al., 1997).

The interpretation of a grazing-induced suppression of plant function, rather than a direct reduction of nutrient accumulation, is supported by a disproportionate decrease in tiller number plant$^{-1}$ compared to SOC and N pools for *S. scoparium* plants in the long-term grazed sites for both the tall- and midgrass communities. Lower tiller number plant$^{-1}$, while SOC and N pool sizes remained relatively constant, suggest that grazing suppressed tiller number plant$^{-1}$ to less than maximum numbers potentially supported by resource availability. Grazing is known to reduce tiller recruitment, tiller number plant$^{-1}$, and basal area in *S. scoparium* (Butler and Briske, 1988; Murphy and Briske, 1992), while *B. gracilis* is much more resistant to grazing (Milchunas et al., 1989). Tiller number plant$^{-1}$ and SOC and N pools were proportionately greater beneath *B. gracilis* plants in long-term grazed compared to ungrazed sites which maintained similar concentrations of SOC and N tiller$^{-1}$ plant$^{-1}$. This correlative relationship between nutrient accumulation beneath plants and tiller number plant$^{-1}$ suggests that the magnitude of nutrient accumulation may partially regulate plant structure. However, nutrient accumulation beneath plants has not been demonstrated to directly increase plant growth or fitness (Aguilera and Lauenroth, 1995). In addition, availability of inorganic N may potentially decrease with increasing amounts of total N because of greater N immobilization (Ihori et al., 1995).

Contrasting plant responses to grazing at various locations along the environmental gradient are substantiated by previous investigations (e.g. Hartnett, 1989; Milchunas et al., 1989) and support the generalized grazing model proposed by Milchunas et al. (1988). This model hypothesizes that grazing will increase plant species diversity in mesic, but not semiarid grasslands with long evolutionary histories of grazing. Greater species diversity may potentially be associated with a grazing-induced reduction of *P. virgatum* and *S. scoparium* dominance in the tallgrass community, and *S. scoparium* dominance in the midgrass community. However, continued dominance of *B. gracilis* in grazed sites of the shortgrass community may potentially constrain increases in species diversity. The selection pressures of grazing and aridity which are central to the generalized grazing model (Milchunas et al., 1988), may have also influenced the ability of caespitose grasses to accumulate nutrients in soils beneath them by mediating grazing resistance, competitive ability and population structure.

## Acknowledgements

Research was supported by a USDA Rangeland Special Grant (92-38300-7459) and the Texas Agricultural Experiment Station. The authors acknowledge the assistance of E Miller, B Hays, and B Hendon with data collection and sample preparation, O Jenkins for providing statistical advice, and I Burke, R Jackson, D Milchunas, M Vinton, and H de Kroon, for constructive evaluations of earlier drafts of the manuscript. We thank D Hartnett (Kansas State University), R Nicholson (Ft Hays State University), and D Milchunas and M Lindquist (Colorado State University) for assistance with identification and access to field sites.

## References

Aguilera M O and Lauenroth W K 1995 Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. J. Ecol. 83, 87–97.

Bark D 1987 Konza Prairie Research Natural Area, Kansas. *In* The Climates of the Long-Term Ecological Research Sites. Ed. D Greenland. pp 45–50. Institute of Arctic and Alpine Research, Occasional Paper Number 44. University of Colorado, Boulder, CO.

Belsky A J, Amundson R G, Duxbury J M, Riha S J, Ali A R and Mwonga S M 1989 The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. J. Appl. Ecol. 26, 1005–1024.

Briske D D 1991 Developmental morphology and physiology of grasses. *In* Grazing Management: an ecological Perspective. Eds. R K Heitschmidt and J W Stuth. pp 11–26. Timber Press, Portland, Oregon.

Briske D D and Derner J D 1997 Clonal biology of caespitose grasses. *In* Population Ecology of Grasses. Ed. G Cheplick. Cambridge University Press, Cambridge (*In press*).

Briske D D and Richards J H 1995 Plant responses to defoliation: A physiological, morphological, and demographic evaluation. *In* Wildland Plants: Physiological Ecology and Developmental Morphology. Eds. D J Bedunah and R E Sosebee. pp 635–710. Society for Range Management, Denver, CO.

Burke I C, Lauenroth W K and Coffin D P 1995 Soil organic matter recovery in semiarid grasslands: Implications for the conservation reserve program. Ecol. Appl. 5, 793–801.

Burke I C, Reiners W A, Sturges D L and Matson P A 1987 Herbicide treatment effects on properties of mountain big sagebrush soils after fourteen years. Soil Sci. Am. J. 51, 1337–1343.

Butler J L and Briske D D 1988 Population structure and tiller demography of the bunchgrass *Schizachyrium scoparium* in response to herbivory. Oikos 51, 306–312.

Coppinger K D, Reiners W A, Burke I C and Olson R K 1991 Net erosion on a sagebrush steppe landscape as determined by cesium-137 distribution. Soil Sci. Am. J. 55, 254–258.

Ganskopp D, Angell R and Rose J 1992 Response of cattle to cured reproductive stems in a caespitose grass. J. Range Manage. 45, 401–404.

Gatsuk L E, Smimova O V, Vorontzova L I, Zaugolnova L B and Zhukova L A 1980 Age states of plants of various growth forms: A review. J. Ecol. 68, 675–696.

Halvorson J J, Bolton H, Smith J L and Rossi R E 1994 Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. Great Basin Nat. 54, 313–328.

Halvorson J J, Smith J L, Bolton H and Rossi R E 1995 Evaluating shrub-associated spatial patterns of soil properties in a shrub-steppe ecosystem using multiple-variable geostatistics. Soil Sci. Am. J. 59, 1476–1487.

Hartnett D C 1989 Density- and growth stage-dependent responses to defoliation in two rhizomatous grasses. Oecologia 80, 414–420.

Hartnett D C 1993 Regulation of clonal growth and dynamics of *Panicum virgatum* (Poaceae) in tallgrass prairie: Effects of neighbor removal and nutrient addition. Am. J. Bot. 80, 1114–1120.

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

Hook P B, Lauenroth W K and Burke I C 1994 Spatial patterns of roots in a semiarid grassland: abundance of canopy openings and regeneration gaps. J. Ecol. 82, 485–494.

Hulett G K and Tomanek G W 1969 Remnant prairies on the shallow limy range site in north central Kansas. J. Range Manage. 22, 19–23.

Ihori T, Burke I C and Hook P B 1995 Nitrogen mineralization in native cultivated and abandoned fields in shortgrass steppe. Plant Soil 171, 203–208.

Jackson R B and Caldwell M M 1989 The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. Oecologia 81, 149–153.

Jackson R B and Caldwell M M 1993a Geostatistical patterns of soil heterogeneity around individual perennial plants. J. Ecol. 81, 683–692.

Jackson R B and Caldwell M M 1993b The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecology 74, 612–614.

Kelly R H, Burke I C and Lauenroth W K 1996 Soil organic matter and nutrient availability responses to reduced plant inputs in shortgrass steppe. Ecology 77, 2516–2527.

Kieft T L 1994 Grazing and plant-canopy effects on semiarid soil microbial biomass and respiration. Biol. Fert. Soils. 18, 155–162.

Lauenroth W K and Sala O E 1992 Long term forage production of North American shortgrass steppe. Ecol. Appl. 2, 397–403.

Manley J T, Schuman G E, Reeder J D and Hart R H 1995 Rangeland soil carbon and nitrogen responses to grazing. J. Soil Water Cons. 50, 294–298.

Milchunas D G and Lauenroth W K 1993 Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol. Monogr. 63, 327–366.

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

Milchunas D G, Lauenroth W K, Chapman P L and Kazempour M K 1989 Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80, 11–23.

Murphy J S and Briske D D 1992 Regulation of tillering by apical dominance: Chronology, interpretive value, and current perspectives. J. Range Manage. 45, 419–429.

Niewenhuize J, Maas Y E M and Middleburg J J 1994 Rapid analysis of organic carbon and nitrogen in particulate materials. Marine Chem. 45, 217–224.

Pfeiffer K E and Hartnett D C 1995 Bison selectivity and grazing response of little bluestem in tallgrass prairie. J. Range Manage. 48, 26–31.

Rice B L, Westoby M, Griffin G F and Friedel M H 1994 Effects of supplementary soil nutrients on hummock grasses. Aust. J. Bot. 42, 687–703.

Riegel D A, Albertson F W, Tomanek G W and Kinsinger F E 1963 Effects of grazing and protection on a twenty-year-old seeding. J. Range Manage. 22, 60–63.

Ruess R W and McNaughton S J 1987 Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. Oikos 49, 101–110.

SAS Institute Inc 1988 SAS/STAT User's Guide, Release 6.03 Edition. SAS, Cary, NC.

Schlesinger W H, Raikes J A, Hartley A E and Cross A F 1996 On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77, 364–374.

Schlesinger W H, Reynolds J F, Cunningham G L, Huenneke L F, Jarrell W M, Virginia R A and Whitford W G 1990 Biological feedbacks in global desertification. Science 247, 1043–1048.

Schimel D S, Braswell B H, Holland E A, McKeown R, Ojima D S, Painter T H, Parton W J and Townsend A R 1994 Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Global Biogeochem. Cycles 8, 279–293.

Sims P L, Singh J S and Lauenroth W K 1978 The structure and function of ten western North American grasslands. I. Abiotic and vegetation characteristics. J. Ecol. 66, 251–281.

Steel R G D and Torrie J H 1980 Principles and procedures of statistics: A biometrical approach. McGraw-Hill Book Company, New York.

Truscott D R and Currie P O 1989 Cattle preferences for a hybrid grass: Chemical and morphological relationships. J. Range Manage. 42, 22–27.

Vasquez de Aldana B R, Geerts R H E M and Berendse F 1996 Nitrogen losses from perennial grass species. Oecologia 106, 137–143.

Vincent K R and Chadwick O A 1994 Synthesizing bulk density for soils with abundant rock fragments. Soil Sci. Soc. Am. J. 53, 455–464.

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, Fort Collins, CO.

Vinton M A and Burke I C 1995 Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology 76, 1116–1133.

Vokhiwa Z M 1994 Carbon and nitrogen dynamics in grazed and protected semiarid shortgrass steppe. Dissertation, Colorado State University, Fort Collins, CO.

Zinke P J 1962 The pattern of influence of individual forest trees on soil properties. Ecology 43, 130–133.

*Section editor: R Merckx*