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Below-ground carbon and nitrogen accumulation in perennial grasses: A comparison of caespitose and rhizomatous growth forms

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Abstract

An experiment was conducted to compare below-ground soil organic carbon and total nitrogen accumulation between caespitose and rhizomatous perennial grasses in long-term (<25 yrs) grazed and ungrazed sites in semi-arid and mesic communities in the North American Great Plains. Development of greater nutrient pools beneath than between clones occurred at minimal clone basal areas (<60 cm^2) for both caespitose species. Caespitose grasses accumulated substantially greater pools of carbon (20–200 fold) and nitrogen (50–500 fold) in soils to a depth of 10 cm beneath clones than rhizomatous grasses accumulated in rhizomes in both communities. Carbon and nitrogen pools in soils beneath caespitose clones exceeded combined (soil + rhizome) pools for rhizomatous grasses for a majority of the clone basal areas (>90 cm^2) in the mesic community. In contrast, both pool sizes were smaller beneath the caespitose grass at all clone basal areas than the combined pools for the rhizomatous grass in the semi-arid community. The occurrence of larger soil nutrient pools beneath the rhizomatous species in the semi-arid community was largely a consequence of niche separation for microsites characterized by soils with higher nutrient concentrations, rather than plant-induced increases in nutrient concentrations. Although nutrient islands do not occur beneath rhizomatous grasses, their distribution in the semi-arid community was restricted to microsites characterized by soils with higher SOC and N concentrations. A greater efficiency of nutrient accumulation per unit rhizome mass and the maintenance of rhizome nutrient pools of similar magnitude to those of the rhizomatous grass in the mesic community may also contribute to the distribution of rhizomatous grasses in semi-arid communities. The existence of nutrient islands beneath a wide range of clone sizes in both mesic and semi-arid communities provides circumstantial evidence to suggest that nutrient islands beneath caespitose grasses may contribute to clone fitness in this growth form.

Introduction

Caespitose (i.e. tussock or bunch) and rhizomatous perennial grasses represent distinct grass growth forms that variously dominate grassland and savanna systems. Morphological distinctions in below-ground shoots mass (rhizomes), clone size and size and density of ramets (tillers) characterize these two growth forms. In addition, caespitose grasses tend to concentrate nutrients in shallow soils directly beneath clones in both mesic and semi-arid grasslands (Burke et al., 1998, 1999; Derner et al., 1997; Hook et al., 1991; Jackson and Caldwell, 1993; Vinton and Burke, 1995), but rhizomatous grasses do not concentrate nutrients even when grown in the same environments as caespitose grasses (Derner et al., 1997; Vinton and Burke, 1995). However, the absence of substantial nutrient concentrations in soils beneath rhizomatous grasses may be offset by the presence of rhizomes that function as important below-ground storage organs for both carbon and nitrogen in this growth form (Cheplick and Gutierrez, 2000; Heckathorn and DeLucia, 1994; Suzuki and Stuefer 1999).

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We hypothesize that the occurrence of unique patterns of below-ground nutrient accumulation between these two growth forms may represent distinct functional strategies based on the general observation that caespitose and rhizomatous grasses dominate semi-arid and mesic grasslands, respectively (e.g. Sims et al., 1978). Different patterns of nutrient accumulation between these two important grass growth forms in contrasting environments raise several intriguing questions. What is the relative magnitude of nutrient pools in caespitose and rhizomatous species? Are nutrient pools in rhizomes and soils of comparable magnitude beneath rhizomatous species? Does the relative magnitude of nutrient pools vary between growth forms in mesic and semi-arid environments? Below-ground nutrient pools of caespitose and rhizomatous grasses have not previously been compared, and direct comparisons are hindered by procedural difficulties associated with delineation of rhizomatous clones, variation in form and availability of nutrients in rhizomes compared to soils, and distinct topo-edaphic sites frequently occupied by these two growth forms.

Herbivory is a pervasive process in grasslands that can mediate below-ground nutrient accumulation by influencing productivity and tissue turnover (Burke et al., 1998). However, herbivory is anticipated to have a more immediate effect on below-ground nutrient accumulation of rhizomatous than caespitose grasses because soil organic carbon (SOC) and total soil nitrogen (N) respond much more slowly than do labile carbon and nitrogen in rhizomes (Burke et al., 1995; Derner et al., 1997). For example, intensive herbivory reduced both rhizome mass and nutrient concentrations compared to ungrazed *Panicum virgatum* clones within a 1–2 year period (Hartnett, 1989). However, significantly greater SOC and N pools beneath compared to between clones of the caespitose grass *Bouteloua gracilis* disappeared within 3 years following plant death, indicating that these nutrient pools are relatively responsive to short-term plant inputs (Kelly et al., 1996; Kelly and Burke, 1997). Nevertheless, the effect of long-term herbivory on nutrient accumulation in soils beneath caespitose grasses remains unclear. The effects of long-term herbivory on SOC and N pools beneath caespitose grasses have been shown to vary between mesic and semi-arid communities (Derner et al., 1997; Schuman et al., 1999) as well as within semi-arid systems (Burke et al., 1997, 1999; Derner et al., 1997).

We designed an investigation to compare below-ground SOC and N pools between caespitose and rhizomatous grasses in contrasting environments and grazing histories. A dominant caespitose and rhizomatous grass were identified in long-term (>25 yrs) grazed and ungrazed sites in a mesic, tall-grass and a semi-arid, short-grass community in the North American Great Plains. Specific hypotheses were: (1) the combined pools (soils + rhizomes) of carbon and nitrogen accumulation in the rhizomatous growth form would be similar to that of carbon and nitrogen accumulation in soils beneath the caespitose growth form when expressed on an unit area basis, and (2) long-term herbivory would modify below-ground carbon and nitrogen pools within caespitose and rhizomatous grasses in a similar manner. We anticipated that a comparative evaluation of below-ground nutrient pools in caespitose and rhizomatous grasses would contribute to a greater understanding of the relative distribution of these two growth forms along a productivity gradient, and provide additional insight into the functional significance of nutrient accumulation in soils beneath caespitose grasses.

Materials and methods

Site descriptions

This study was conducted at two locations (short-grass and tall-grass prairies) along an east-west precipitation/productivity gradient in the North American Great Plains. These locations are characterized by substantial differences in mean annual precipitation (2.7-fold), total organic carbon (2.9-fold) and nitrogen (2.3-fold) in the surface soil (0–10 cm) (Zak et al., 1994), and aboveground net primary productivity (ANPP) (5.5-fold) and leaf area index (12-fold) (Lane et al., 2000). At both locations, long-term ungrazed and moderately (removal of 40–60% of net primary productivity) grazed sites were selected.

The semi-arid, short-grass community was located at the Central Plains Experimental Range (CPER) in north-central Colorado, approximately 60 km north-east 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) with *Pascopyrum smithii* the major rhizomatous grass, and mean ANPP is 1000 kg ha^{-1}. Grazed and ungrazed sites were adjacent on an Ustollic Haplargid soil (fine-loamy, mixed,

mesic) on a footslope topographic position. Neither the grazed nor ungrazed sites have been burned since the research station was established. The ungrazed site was established in 1939, and was moderately grazed before then.

The mesic, tall-grass community was located at the Konza Prairie Research Natural Area (KPRNA) in eastern Kansas near Manhattan (39° 05′ N, 96° 35′ W). Mean annual precipitation is 835 mm and mean annual temperature is 12.8 °C (Bark, 1987). Vegetation is dominated by *Andropogon gerardii, Sorghastrum nutans* and *Schizachyrium scoparium* with a mean ANPP of 4000 kg ha^{-1}. Grazed and ungrazed sites were adjacent on an Aquic Argiudoll soil (fine, montmorillonitic, mesic) on a midslope topographic position. Both grazed and ungrazed sites are burned annually. The ungrazed site was established in 1969, and was grazed moderately prior to that time.

Schizachyrium scoparium, (caespitose) and *A. gerardii* (rhizomatous), and *B. gracilis* (caespitose) and *P. smithii* (rhizomatous) clones were sampled in the mesic and semi-arid community, respectively. These species were selected as they represent the most prevalent caespitose and rhizomatous grasses in each community (Milchunas et al., 1989; Sims et al., 1978).

Sampling method – Caespitose grasses

Ten soil samples (2 cm diameter × 10 cm deep) were collected from beneath and between caespitose clones for determination of fine-earth bulk density at each site. These soils were passed through a 2-mm sieve and dried at 105 °C for 5 days. Soil samples (2 cm diameter × 10 cm deep) for nutrient analyses were taken from the center of 30 caespitose clones, with various sized basal areas (tall-grass: 25–522 cm^2, short-grass: 25–869 cm^2), at each site in July 1997. An additional six soil samples were taken from locations between clones at each site for comparisons with soils beneath versus between clones. These soils were dried at 60 °C for 5 days before being ground with a ring pulverizer (Model TE250, Angstrom, Inc., Belleville, Michigan, USA). Soil volume was based on the volume of the soil core. Soil samples were analyzed for soil organic carbon (SOC) (Niewenhuize et al., 1994) and total soil nitrogen (N) using a Carlo-Erba NA-1500 (Fisons Instruments, Danvers, Massachusetts, USA) elemental analyzer. Average precision (standard deviation for duplicate samples) was 0.64 g kg^{-1} and 0.06 g kg^{-1} for SOC and N, respectively.

Pool sizes of SOC and N were calculated in a cylinder directly beneath the basal area of individual caespitose clones using elemental concentrations, bulk density, depth (10 cm) and individual clone basal area. A cylindrical volume directly beneath the basal area of individual clones was selected because it provided the least arbitrary approach for defining a resource volume accessible to clones and it has been experimentally verified as a reasonable approximation of the resource volume accessible to a caespitose grass (Derner and Briske, 1999).

Sampling methods – Rhizomatous grasses

Twenty-eight 30×15×10 cm blocks of soil were removed from patches dominated (>50% cover) by rhizomatous species to determine rhizome carbon and nitrogen pools in both grazed and ungrazed sites in each community using randomly located points. One-half (14) of the blocks were removed in mid-May (vegetative) and the remaining half in mid-July (reproductive) to assess seasonal variation in rhizome nutrient pools. Soils from each block were passed through a 2-mm sieve and a subsample retained for SOC and N analysis. Rhizomes were placed in ziploc bags and stored on ice until they were washed and placed in an oven within 2 h of collection. Rhizomes were dried at 60 °C for 5 days, weighed and ground with a Wiley mill to pass a 40-mesh screen. Subsets of two each of soil and rhizome samples were then pooled to produce seven larger samples for each grazing history-harvest date combination to facilitate sample processing, minimize sample variability and reduce analyses costs. Analyses for soil and rhizome carbon and nitrogen concentrations and calculation of nutrient pools were conducted as previously described. Average precision (standard deviation for duplicate samples) for rhizome concentration analyses was 2.36 g kg^{-1} for carbon and 0.15 g kg^{-1} for nitrogen. We used bulk density values from soils between caespitose clones to calculate soil pool sizes because they are similar to the values of soils occupied by the rhizomatous species (J.D. Reeder, *unpublished data*). Rhizomes were also analyzed for total non-structural carbohydrates (TNC) by the Range Science Nutritional Analysis Laboratory (Colorado State University) with an average precision (standard deviation for duplicate samples) of 0.48%. Combined carbon and nitrogen pools for rhizomatous clones were determined by adding soil and rhizome nutrient pools for the July sampling period. The July

Table 1. Values from linear regression equations for clone basal area and soil organic carbon (SOC) or total nitrogen (N) pools in soils within a cylindrical volume (depth = 10 cm) directly beneath individual caespitose clones in two plant communities. Asterisks indicate significant ($P < 0.05$) differences in slopes of regression lines between grazing histories within a species. See Figure 1 for regression lines

Community	Species	Variable	Grazing	C.V.	R^2	Intercept	Slope
Tallgrass	*Schizachyrium scoparium*	SOC	Ungrazed	22.2	0.93	−9.5	0.445*
			Grazed	15.5	0.97	−3.7	0.399
		N	Ungrazed	14.6	0.97	−0.4	0.029
			Grazed	11.3	0.98	−0.3	0.029
Shortgrass	*Bouteloua gracilis*	SOC	Ungrazed	41.7	0.77	−1.2	0.197*
			Grazed	24.6	0.92	2.9	0.261
		N	Ungrazed	37.9	0.80	0.0	0.015*
			Grazed	26.5	0.91	0.4	0.019

sampling period closely coincides with the accumulation of peak standing biomass in these grasslands.

Statistical analyses

The influence of grazing history on the size of carbon and nitrogen pools beneath caespitose clones at each community was assessed by comparing slopes of linear regression equations developed using clone basal area as the independent variable (pg 258, Steel & Torrie, 1980) (Table 1). These slopes were then compared with slopes generated from regression equations using elemental concentrations of soils between clones to estimate pool sizes for the same range of clone basal areas. These comparisons enabled us to determine if the presence of a caespitose clone influenced small-scale soil heterogeneity. In order to effectively compare below-ground carbon and nitrogen pool sizes between the two distinct grass growth forms, the combined (soil + rhizome) carbon and nitrogen pools beneath the rhizomatous clones needed to be expressed on a similar basal area basis as the caespitose clones. To accomplish this, we generated linear regressions of combined pools beneath rhizomatous clones using elemental concentrations of soils beneath rhizomatous clones as the dependent variable and caespitose clone basal area as the independent variable. Slopes from these equations were then compared against those previously developed for nutrient pools beneath caespitose clones in each community.

A two-factor ANOVA analyses was used to determine relationships between grazing history (ungrazed and grazed) and harvest date (May and July) for rhizome variables in each community. Means were separated by Duncan's multiple range test at the 0.05 level of probability.

Results

Soil bulk density

Fine-earth bulk density of soils was significantly lower beneath than between *S. scoparium* clones in both the ungrazed (0.76 ± 0.03 vs. 0.84 ± 0.02 g cm^{-3}, mean ± 1 SE, beneath vs. between) and grazed (0.81 ± 0.01 vs. 0.88 ± 0.02 g cm^{-3}) sites in the tall-grass community. Values were also significantly lower in soils beneath than between *B. gracilis* clones in both the ungrazed (0.75 ± 0.04 vs. 0.99 ± 0.02 g cm^{-3}) and grazed (1.08 ± 0.02 vs. 1.13 ± 0.01 g cm^{-3}) sites in the short-grass community. Soil bulk density beneath *S. scoparium* clones was similar between grazing histories, but it was significantly greater beneath *B. gracilis* clones in the grazed than in the ungrazed site.

Caespitose grasses

Concentrations of SOC and N directly beneath clones in both grazed and ungrazed sites increased with increasing clone basal area for *S. scoparium* clones in the mesic community, but not for *B. gracilis* clones in the semi-arid community (data not shown). Therefore, the increase in nutrient pool size with increasing clone basal area is a function of both greater nutrient concentrations and basal area in the mesic community, but

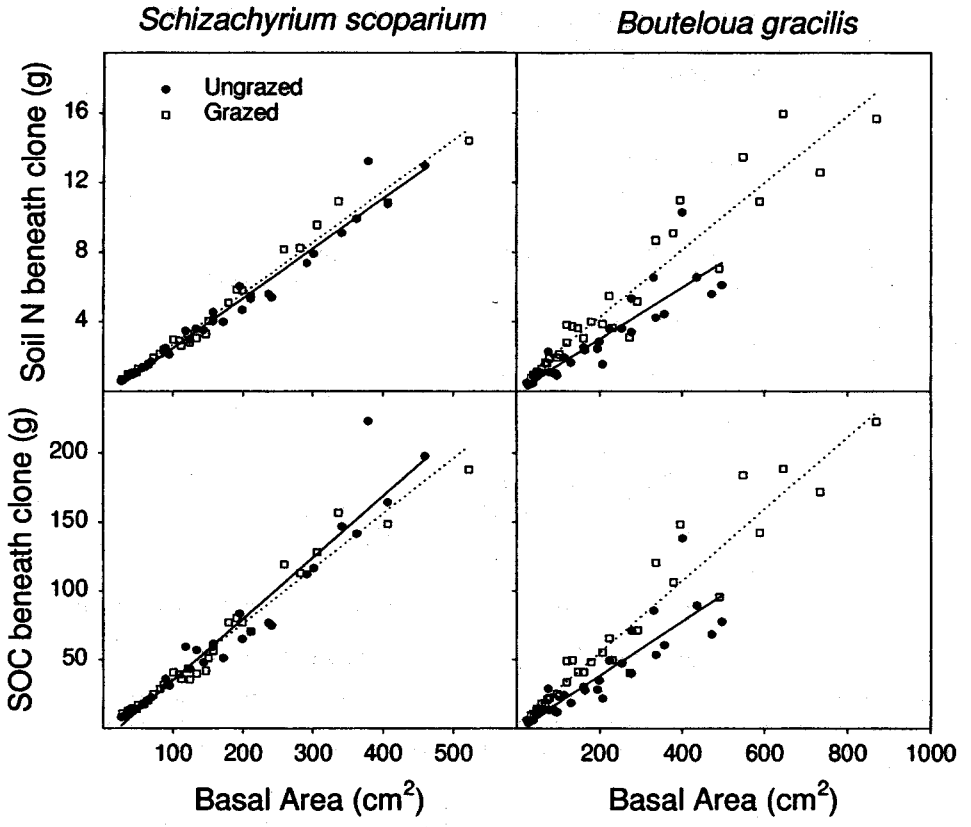

Figure 1. Soil nitrogen (N) and organic carbon (SOC) pools beneath a range of clone basal areas for the perennial caespitose grasses *Schizachyrium scoparium* and *Bouteloua gracilis* in a tall-grass and a short-grass community, respectively. Significant ($P<0.05$) differences between slopes of the linear regression lines are presented in Table 1.

only a function of greater basal area in the semi-arid community (Figure 1).

N pools beneath *S. scoparium* clones in the mesic community were not affected by grazing history (Figure 1) because nitrogen concentrations (3.4 ± 0.1 vs. 3.3 ± 0.1 g kg^{-1} ungrazed vs. grazed, P=0.5502, n=30) and soil bulk density were similar in both sites. However, SOC pools were significantly larger in the ungrazed site because SOC concentrations were significantly greater (48.4 ± 1.6 vs. 44.6 ± 1.1 g kg^{-1}), ungrazed vs. grazed, P=0.0310, n=30), even though soil bulk density was similar between sites. In contrast, both SOC and N pools were significantly larger beneath *B. gracilis* clones in the grazed site because of higher soil bulk density as concentrations did not differ statistically (SOC: 25.3 ± 1.5 vs. 25.7 ± 0.9 g kg^{-1}, ungrazed vs. grazed, P=0.5996, n=30; N: 2.0±0.1 vs. 2.0± 0.1g kg^{-1}, ungrazed vs. grazed, P=0.8481, n=30).

SOC and N pools beneath clones were significantly larger than between clones on both the grazed and ungrazed sites for both *S. scoparium* and *B. gracilis* (Figure 2). Pools of SOC and N beneath *S. scoparium* clones were larger than between clones when basal area exceeded 60 cm^2 on the ungrazed site. Similarly on the grazed site, pools were larger when basal area exceeded 35 and 50 cm^2 for SOC and N, respectively. Nutrient pools beneath *B. gracilis* clones were larger than between clones when basal area exceeded 40 cm^2 for SOC and at all basal areas for N on the ungrazed site. Nutrient pools beneath *B. gracilis* clones were larger than those between clones at all basal areas sampled on the grazed site.

Rhizomatous grasses

Rhizome mass of *A. gerardii* was similar between grazing histories in May, but 36% greater in the grazed than the ungrazed site in July (Figure 3a). Nitrogen concentrations of 2–4% were similar to those reported

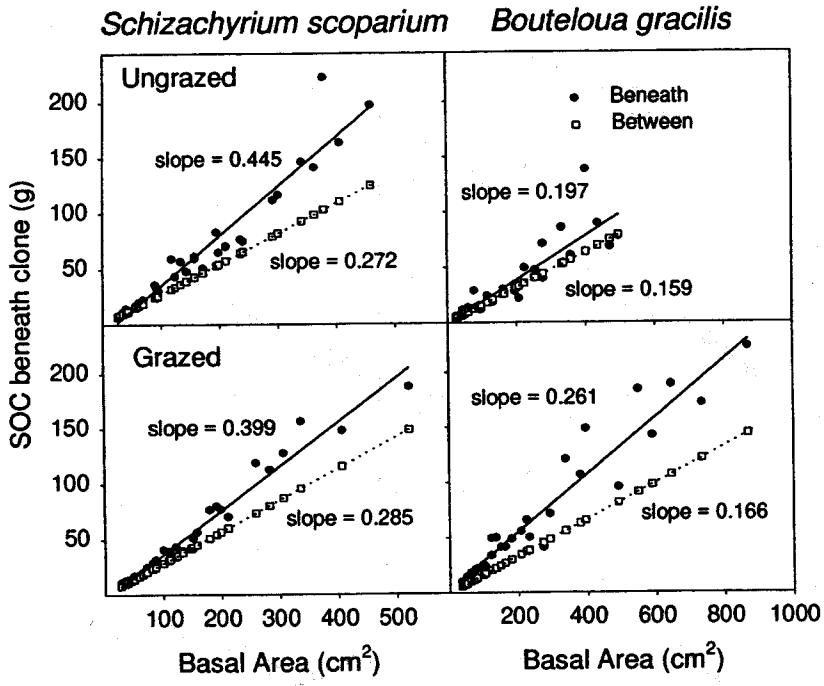

Figure 2. Soil organic carbon (SOC) pools beneath and between the perennial caespitose grasses *Schizachyrium scoparium* and *Bouteloua gracilis* in a tall-grass and a short-grass community, respectively. SOC pools between clones were estimated for both long-term ungrazed and grazed sites at each community. Differences between slopes within a grazing history and species are significant ($P<0.05$).

by Heckathorn and DeLucia (1994). These concentrations were 14% and 66% higher for May and July, respectively, in the grazed site (Figure 3b). Nitrogen pools were similar between grazing histories in May, but pools in the grazed site were 50% larger than the ungrazed site in July (Figure 3c). Higher nitrogen concentrations and greater rhizome mass in the grazed site both occurred in July. Nitrogen pools in rhizomes comprised 0.6% of the combined (soil+rhizome) nitrogen pool beneath *A. gerardii* clones in both grazing histories. In contrast to observed responses with nitrogen, carbon concentrations were 5% and 3% lower in May and July, respectively, on the grazed compared to the ungrazed site (Figure 3d) Carbon pools displayed a similar pattern as did nitrogen (Figure 3e), but the 31% greater pool size in the grazed site in July was a result of greater rhizome mass only. Pools of carbon in rhizomes represent 4.6% of the combined belowground carbon pool beneath *A. gerardii* in both grazing histories. TNC concentrations were similar between grazing histories in May, but 21% lower in the grazed site in July (Figure 3f). Pools of TNC were similar between grazing histories at both harvest dates, but 29% larger in July than May (Figure 3g). These pools represent approximately 10 and 15% of the total carbon pool in rhizomes for May and July, respectively. Grazing history did not significantly affect SOC and N concentrations or pools in soils beneath *A. gerardii* (data not shown).

Rhizome mass of *P. smithii* was reduced with grazing by 47% and 64% in May and July, respectively (Figure 3a). Nitrogen concentrations were reduced by 21% and 25% in May and July, respectively, in the grazed site (Figure 3b). In contrast, carbon concentrations were unaffected by grazing history (Figure 3d). Nitrogen pools were substantially lower in the grazed than ungrazed site in both May (59%) and July (73%) because of lower nitrogen concentrations and less rhizome mass. In the grazed site, the nitrogen pool in rhizomes comprised 0.2% of the combined belowground nitrogen pool beneath *P. smithii* clones, while this percentage increased to 0.6% in the ungrazed site. Carbon pools were reduced with grazing, 47% and 64% in May and July, respectively, because of less rhizome mass only (Figure 3c, e). These pools represent 0.5% of the combined belowground carbon pool in the grazed site beneath *P. smithii* clones, and 1.5% in the ungrazed site. TNC concentrations were 45% higher in the grazed site in May, but 10% lower in July (Figure 3f). Pools of TNC were 68% lower

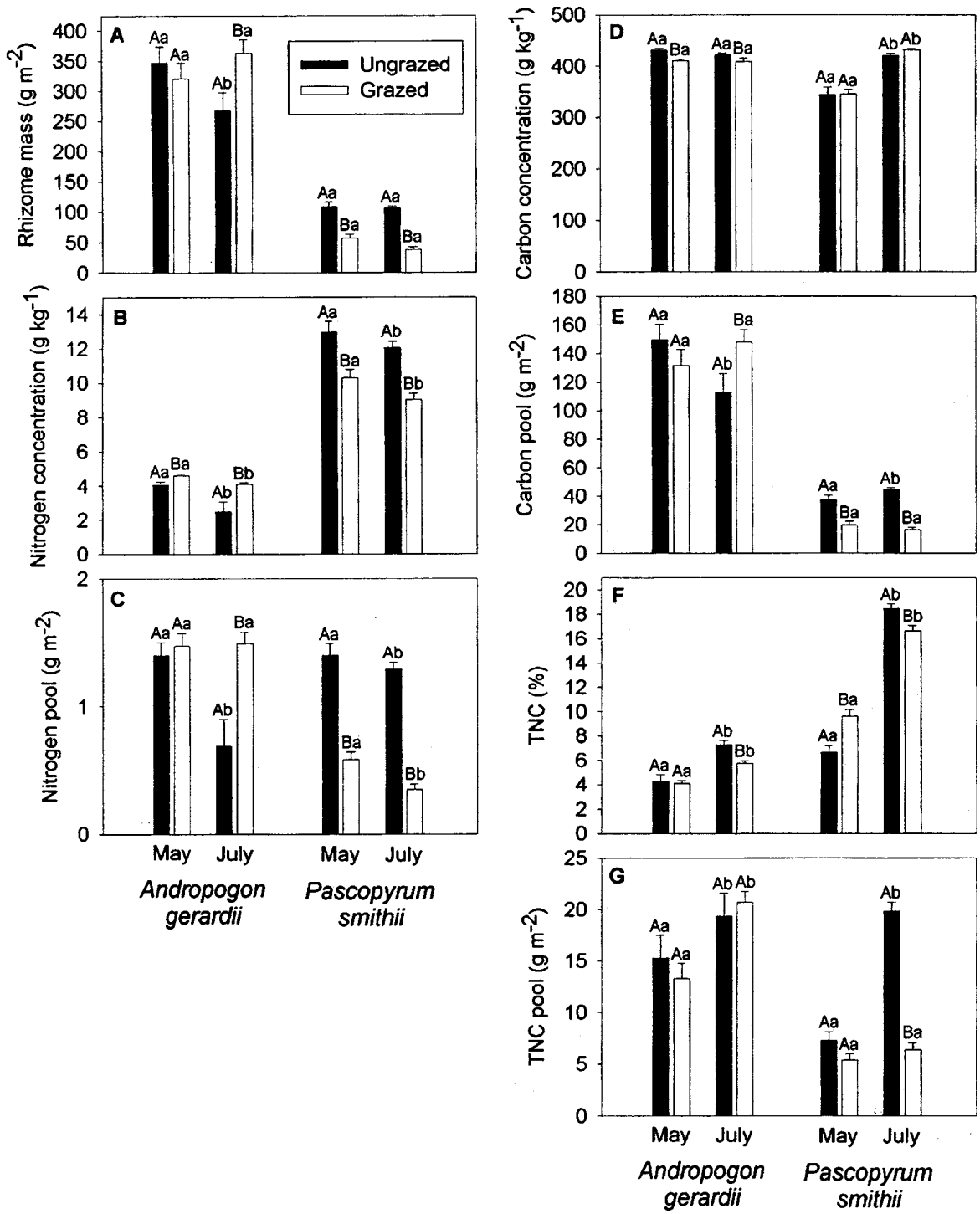

Figure 3. Mean (+ SE n=7) mass (A), nitrogen concentrations and pools (B and C), carbon concentrations and pools (D and E) and total non-structural carbohydrate (TNC) concentration and pools (F and G) for rhizomes of perennial grasses *Andropogon gerardii* and *Pascopyrum smithii* in a tall-grass and a short-grass community, respectively. Values from clones in long-term (>25 yrs) ungrazed and grazed sites are represented by solid and open bars, respectively. Values within a species and harvest date with the same uppercase letter are not significantly (P<0.05) different for grazing history. Values within a species and grazing history with the same lower case letter are not significantly (P<0.05) different for harvest date.

in the grazed compared to the ungrazed site in July after being similar in May (Figure 3g). Pools of TNC in the ungrazed site represent approximately 19 and 44% of the total carbon pool in rhizomes in May and July, respectively, and 27 and 39% in May and July, respectively, for the grazed site. Although SOC and N concentrations in soils beneath *P. smithii* were similar between grazing histories, SOC and N pools were 26 and 23% greater in the grazed site, respectively, because of increased soil bulk density (data not shown).

Comparisons between growth forms

SOC and N pools directly beneath *S. scoparium* clones exceeded combined (soil + rhizome) pools for *A. gerardii* in the ungrazed site when basal area of the caespitose clones exceeded 90 and 70 cm^2, respectively (Figure 4). A similar relationship existed for the grazed site when basal areas of caespitose clones surpassed 50 and 60 cm^2 for carbon and nitrogen, respectively.

Pool size comparisons between the rhizomatous and caespitose species responded differently in the short-grass than in the tall-grass community. SOC and N pools directly beneath *B. gracilis* clones did not exceed combined pools for *P. smithii* in either the ungrazed or grazed sites at any basal area (Figure 4).

Caespitose grasses accumulated substantially greater pools of carbon and nitrogen in soils to a depth of 10 cm beneath clones (Figure 1) than rhizomatous grasses accumulated in rhizomes (Figure 3) in both communities. For example, pools of carbon and nitrogen in soils beneath *S. scoparium* were 20–40 times and 150–250 times greater, respectively, than pools found in rhizomes of *A. gerardii* in the mesic community. Likewise in the short-grass community, pools of carbon and nitrogen in soils beneath *B. gracilis* were 75–200 times and 50–500 times greater, respectively, than pools in rhizomes of *P. smithii*.

Discussion

These data corroborate a growing body of evidence indicating that caespitose grasses promote the development of fine-grained soil heterogeneity (Derner et al., 1997; Hook et al., 1991; Schlesinger et al., 1996; Vinton and Burke, 1995). We further demonstrate that caespitose grasses accumulate substantially greater pools of carbon and nitrogen in soils directly beneath clones than rhizomatous grasses accumulate in belowground shoots in both mesic and semi-arid environments. In addition, nutrient accumulation in soils beneath the caespitose grass was also greater than combined (soil + rhizome) nutrient pools beneath the rhizomatous grass in the mesic community, but the reverse occurred in the semi-arid community (Hypothesis one). Nutrient pools beneath the two growth forms were not consistently modified by grazing within the two communities. SOC, but not N, pools beneath the caespitose grass decreased with grazing in the mesic community, while pools of both carbon and nitrogen in rhizomes increased with grazing in July only. In contrast, both SOC and N pools beneath caespitose clones increased with grazing in the semi-arid community, while nutrient pools in rhizomes decreased with grazing in both May and July (Hypothesis two). Consequently, both hypotheses were rejected.

Caespitose grass growth form

The occurrence of enhanced nutrient accumulation in soils beneath clones with minimal clone basal areas, 35–60 cm^2 and <40 cm^2 for *S. scoparium* and *B. gracilis*, respectively, suggests that nutrient islands are present throughout much of the life history of caespitose clones. This interpretation increases the probability that nutrient islands may contribute to clone fitness, even though accurate clone basal area – age relationships have not been established for caespitose clones (Gatsuk et al., 1980). Nutrient pools increased in response to horizontal expansion of clone diameters, but SOC and N concentrations also increased over the range of clone basal area in the mesic, but not the semi-arid, community. However, horizontal clonal expansion accounted for approximately 60–75% of the increase in pools size compared to increased elemental concentrations in the mesic community.

The establishment of nutrient islands beneath clones of small basal areas is difficult to reconcile with previous reports indicating that several decades are required for their formation (Burke et al., 1995; Derner et al., 1997). This discrepancy may be partially associated with the comparison of cultivated and noncultivated soils to obtain these temporal estimates. Previously cultivated sites have substantially lower SOC and N concentrations relative to native soils (Burke et al., 1997; Derner et al., 1997; Knops and Tilman, 2000), which may delay the rate of nutrient accumulation in soils beneath clones. An alternative

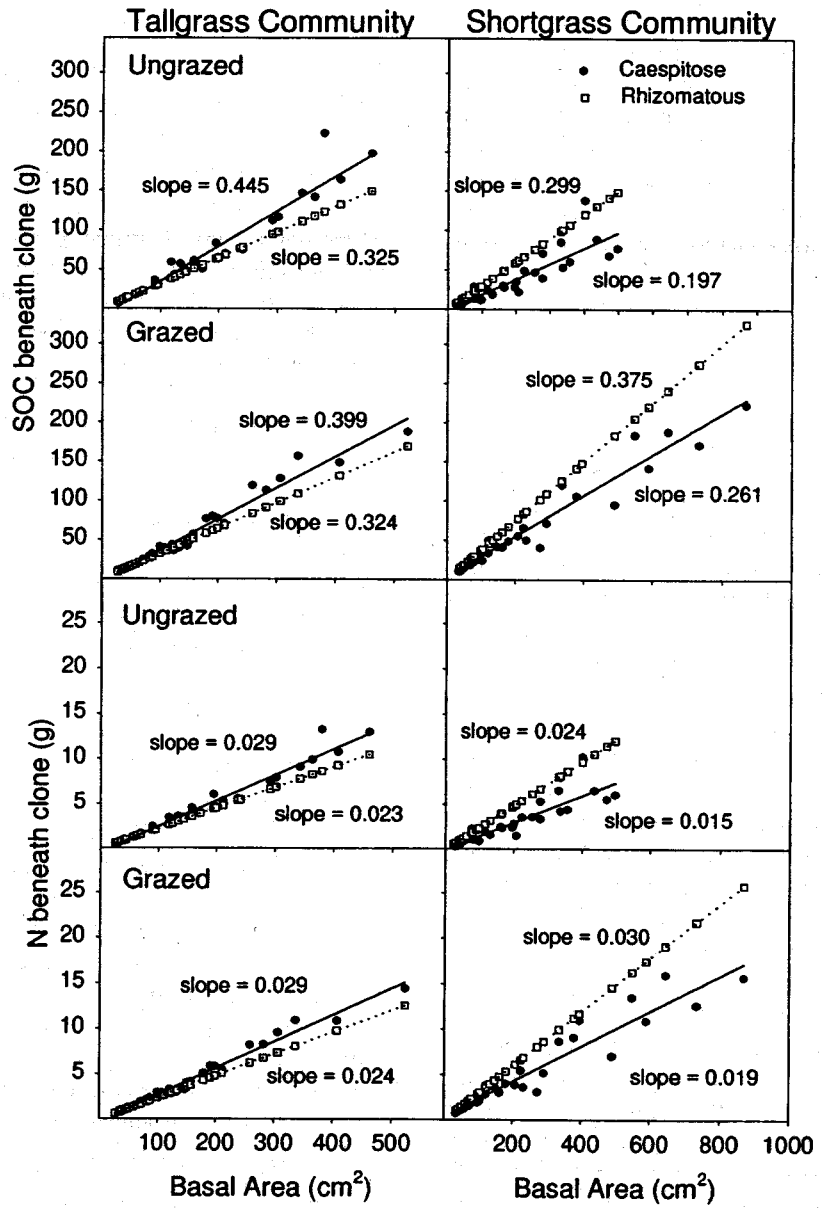

Figure 4. Soil nitrogen (N) and organic carbon (SOC) pools beneath the perennial caespitose grass *Schizachyrium scoparium* and perennial rhizomatous grass *Andropogon gerardii* in a tall-grass community, and beneath the perennial caespitose grass *Bouteloua gracilis* and perennial rhizomatous grass *Pascopyrum smithii* in a short-grass community. Nutrient pools beneath rhizomatous grasses were estimated for both long-term ungrazed and grazed sites at each community. Differences between slopes of prediction lines are significant for each comparison ($P<0.05$).

explanation may be that a portion of the small clones sampled were clone fragments that existed on nutrient islands previously formed by larger clones. However, it is unlikely that the remaining small clones could incorporate sufficient carbon and nitrogen into soils to maintain these large nutrient islands (Kelly et al., 1996; Kelly and Burke, 1997).

The contrasting responses of nutrient accumulation to grazing displayed by these two caespitose species are likely driven by population-level responses to grazing (Derner et al., 1997). Long-term grazing of *S. scoparium* frequently results in populations characterized by a high density of clones with smaller basal areas compared to ungrazed populations (Butler and

Briske, 1988; Pfeiffer and Hartnett, 1995), which would result in the reduction of nutrient pools sizes beneath individual clones. In contrast, *B. gracilis* populations subjected to long-term grazing are frequently characterized by similar densities of clones with larger basal areas in grazed compared to ungrazed sites (Milchunas et al., 1989), resulting in greater nutrient pools beneath individual clones.

Rhizomatous grass growth form

Rhizome pools were a very small (0.2–4.6%) component of the combined (soil + rhizome) nutrient pool for both rhizomatous species. However, a much greater proportion of nitrogen (ca. 8–12%) within rhizomes is available and can be rapidly incorporated into plant growth (Heckathorn and DeLucia, 1994), than is available for plant uptake from the soil N pool (ca. 2%, Derner and Briske, 1999; Wedin and Pastor, 1993). A comparison of available nitrogen in soils beneath rhizomatous grasses and in rhizomes, using the 2% estimate for soils and 10% for rhizomes, reveals that available nitrogen in rhizomes constitutes only 1–3% of that found in the soil to a depth of 10 cm in both the semi-arid and mesic communities. However, the ecological significance of nitrogen storage in rhizomes may be greater in the semi-arid compared to the mesic community because of lower total nitrogen availability in soils (Zak et al., 1994).

Distinct differences in nutrient concentrations per gram of rhizome mass between these two rhizomatous grasses suggest that the efficiency of nutrient storage in rhizomes is greater in the semi-arid than in the mesic community. Rhizome nitrogen pools were similar in the two rhizomatous species because a 75% reduction in rhizome mass from the mesic to the semi-arid community was compensated by 2.2–4.9-fold increase in rhizome nitrogen concentrations. Greater resource storage per gram of rhizome mass suggests that *P. smithii* possesses a more efficient strategy of nutrient storage than *A. gerardii* assuming that construction and maintenance costs per gram of rhizome mass were similar between these two species. More efficient nutrient storage has previously been suggested to occur in environments characterized by low above-ground productivity (Chapin et al., 1990) and large seasonal fluctuations in growth conditions (Suzuki and Stueffer, 1999), which are both found in the semi-arid, short-grass community.

Comparisons between growth forms

Nutrient accumulation in soils beneath the caespitose growth form was more directly influenced by prevailing abiotic variables than was nutrient accumulation in soils beneath rhizomatous species. Nutrient pools beneath caespitose clones were 40 – 50% lower in the semi-arid compared to the mesic community, which generally parallels the large (75%) decrease in above-ground productivity along this east-west gradient (Lane et al., 2000). This suggests that nutrient accumulation beneath caespitose clones is strongly influenced by above-ground productivity and resulting organic matter input into soils (Burke et al., 1998; Kelly et al., 1996; Vasquez de Aldana et al., 1996). In contrast, both the soil and rhizome nutrient pools beneath the rhizomatous species remained relatively constant in the mesic and semi-arid communities. However, the occurrence of large soil nutrient pools beneath the rhizomatous species in the semi-arid community is largely a consequence of niche separation for microsites characterized by deeper, fine textured soils that contain greater amounts of water and nutrients (Monson et al., 1986), rather than to plant-induced increases in nutrient concentrations i.e. nutrient islands are not formed beneath rhizomatous grasses (Derner et al., 1997; Vinton and Burke, 1995).

The existence of nutrient islands beneath a wide range of clone basal areas in both mesic and semi-arid communities provides additional circumstantial evidence to suggest that nutrient islands beneath caespitose grasses may contribute to clone fitness in this growth form. We have previously demonstrated that the caespitose grass *S. scoparium* has the capacity to rapidly and precisely increase clonal growth in response to an increase in below-ground resource availability beneath individual clones (Derner and Briske, 1999). The distribution of rhizomatous species in the semi-arid community appears to be strongly associated with nutrient availability because their distribution is restricted to microsites characterized by soils with higher SOC and N concentrations. A greater efficiency of nutrient accumulation per unit rhizome mass and the maintenance of rhizome nutrient pools of similar magnitude to those of the rhizomatous grass in the mesic community may also contribute to the distribution of rhizomatous grasses in semi-arid environments.

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