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Herbivore effects on above- and belowground plant production and soil nitrogen availability in the Trans-Himalayan shrub-steppes

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Abstract Large mammalian herbivores may have positive, neutral, or negative effects on annual net aboveground plant production (NAP) in different ecosystems, depending on their indirect effects on availability of key nutrients such as soil N. In comparison, less is known about the corresponding influence of grazers, and nutrient dynamics, over annual net belowground plant production (NBP). In natural multi-species plant communities, it remains uncertain how grazing influences relative allocation in the above- and belowground compartments in relation to its effects on plant nutrients. We evaluated grazer impacts on NAP, NBP, and relative investment in the above- and belowground compartments, alongside their indirect effects on soil N availability in the multiple-use Trans-Himalayan grazing ecosystem with native grazers and livestock. Data show that a prevailing grazing intensity of 51% increases NAP (+61%), but reduces NBP (−35%). Grazing also reduced C:N ratio in shoots (−16%) and litter (−50%), but not in roots, and these changes coincided with increased plant-available inorganic soil N (+23%). Areas used by livestock

and native grazers showed qualitatively similar responses since NAP was promoted, and NBP was reduced, in both cases. The preferential investment in the aboveground fraction, at the expense of the belowground fraction, was correlated positively with grazing intensity and with improvement in litter quality. These results are consistent with hypothesized herbivore-mediated positive feedbacks between soil nutrients and relative investment in above- and belowground compartments. Since potentially overlapping mechanisms, such as N mineralization rate, plant N uptake, compositional turnover, and soil microbial activity, may contribute towards these feedbacks, further studies may be able to discern their respective contributions.

Introduction

Large mammalian herbivores can exert important regulatory influences over material and energy flow in terrestrial ecosystems (McNaughton 1976, 1985). Since they are a prominent feature of nearly half of the earth's terrestrial realm (Olff et al. 2002), understanding the ecosystem consequences of large mammalian herbivory is of global relevance. Herbivore effects on net annual aboveground plant production (NAP) can range from positive (McNaughton 1985; Frank and McNaughton 1993) to negative (Pastor et al. 1993) in different ecosystems (reviewed in Milchunas and Lauenroth 1993), depending on their indirect effects on the availability of focal plant resources (Wise and Abrahamson 2005). The mechanisms which determine herbivore influence on NAP have been investigated with theoretical models (Dyer et al. 1986; DeAngelis 1992;

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Loreau 1995; de Mazancourt et al. 1998), and empirical studies suggest that a positive feedback may operate between herbivore effects on NAP and nutrient availability (chiefly N) in soil (Ritchie et al. 1998).

In comparison, less is known about the consequences of herbivory for annual net belowground primary production (NBP). Although studies have found that herbivores can have positive (Frank et al. 2002), neutral (McNaughton et al. 1998) or negative effects (Archer and Tieszen 1983) on NBP in different ecosystems, unlike in the case of NAP, the roles of different mechanisms in determining such variation remain inadequately resolved (Bardgett et al. 1998). Since alteration of soil N availability by herbivores can potentially change the relative strengths of above- and belowground competition (Wilson and Tilman 1991; Cahill 1999), patterns of biomass investment in above- and below-ground compartments may also be influenced by herbivory. Studies have often documented the effects of grazing on NAP, NBP and N cycling separately in the same ecosystem, and found that grazing can have positive effects on all three aspects [e.g., North American temperate grasslands (Frank and Groffman 1998; Frank et al. 2002)]. Studies have also investigated the relationships between grazing-related changes in NBP and in soil N dynamics [e.g., North American tallgrass prairie (Johnson and Matchett 2001)]. But, very few studies have approached the inter-related aspects of NAP and NBP vis-à-vis soil N availability simultaneously (Biondini et al. 1998; Schoenecker et al. 2004).

While grazer effects on N cycling may be due to the conversion of plant tissue into dung and urine (Hobbs 1996), additional indirect effects may arise when herbivory alters the N content of plant tissue and litter (Chapman et al. 2003). These indirect effects on N cycling may be due to a combination of physiological and community-level responses. Grazing may alter N uptake by plants with subsequent changes in leaf and litter quality (Briske and Richards 1995), a mechanism which has often been investigated in laboratory monocultures (Ruess 1984; Hamilton et al. 1988). However, in natural communities featuring multiple plant species, in addition to such physiological effects, grazing may also influence N cycling by altering community composition. Thus, when grazing favors species that produce high-quality litter, accelerated N cycling may increase soil N availability; and when it favors species that produce low-quality litter, depressed N cycling may reduce soil N availability (Ritchie et al. 1998; Chapman et al. 2003). Here, we report results from a field experiment in the Trans-Himalayan ecosystem in northern India, on the simultaneous impacts of grazing on NAP and NBP in relation to its effects on the availability of inorganic soil N. Our first objective was to ascertain whether grazing effects on these three aspects, averaged across the study site, were positive, neutral, or negative. Our second objective was

to evaluate how these aspects are inter-related; and we investigated whether variation in grazer effects on NAP and NBP across the landscape was related to the co-variation in soil N availability.

Materials and methods

Study area and experimental design

The Spiti region ($12,000$ km^2) of Northern India is part of the greater Trans-Himalayan grazing ecosystem, which includes the Tibetan highlands and marginal mountains (1.6 million km^2 in India, China and Nepal). Starting in 2005, we set up replicated herbivore exclosures with adjacent paired control plots ($n = 24$, each 100 m^2) in different rangelands (each 4–6 km^2 in area) around the village of Kibber ($32°$N, $78°$E). Plots were established on representative patches of terrain and vegetation cover (e.g., by avoiding cliffs, rocky outcrops and barren screes). The climate is cold and arid with elevation ranging between $4,300$ and $4,500$ m, and temperatures drop below $-30°$C between November and March, allowing a short growth season for plants [May–August (Bagchi et al. 2006)]. Although detailed long-term meteorological records are not available from this remote location, between 1997 and 2007 the nearest weather station (8 km away) recorded 164 cm of annual average snowfall (range 85–210 cm) and 283 mm of annual average rainfall (range 156–313 mm). Soils in our plots were slightly alkaline (pH 7.84 ± 0.07), with sandy-loam texture ($45.87\% \pm 2.15$ sand), and with a total soil N content of $0.14\% \pm 0.01$. Different parts of the study site were grazed by native herbivores (ca. 450 animals including yak, *Bos grunniens*; bharal, *Pseudois nayaur*; and ibex, *Capra sibirica*) and by various introduced livestock (ca. 750 animals including cattle, yak-cattle hybrids, horse, donkey, goat and sheep). High ridges and deep canyons which restrict animal and human movement across this mountainous terrain, also lead to minimal overlap between rangelands used by the livestock and those used by the native herbivores (Bagchi et al. 2004; Mishra et al. 2004; Bagchi and Ritchie 2010). Consequently, our experimental setup consisted of 14 paired plots that were primarily used by native herbivores, and ten that were primarily used by livestock. Vegetation composition varied spatially from being dominated by sedges (*Carex*, *Kobresia*), to being co-dominated by grasses (*Elymus*, *Festuca*, *Poa*) and forbs (*Lindelofia*, *Eurotia*, *Cousinia*) along with small shrubs (*Artemisia*, *Caragana*). Further floristic details are provided elsewhere (Bagchi and Ritchie 2010; Bagchi and Ritchie in press).

Here we report data on annual NAP and NBP, quality of shoot and root tissue and litter material (C:N ratios), and

inorganic soil N availability. These data were collected during the growth seasons of 2006 and 2007 (May–August), coinciding with 2–3 years of herbivore exclusion. In 2006, we measured NAP of ungrazed plots at monthly intervals as the sum of positive increments for each month. At the end of the growth season, in August 2006, we also measured standing biomass in ungrazed plots including discolored leaves since they represent current season's production (Sala and Austin 2000) and could be distinguished from the previous season's litter. However, since rapidly senescing plants were rare, monthly estimates of ungrazed NAP were not different from the end-of-season estimates (paired t-test, $t_{23} = 0.43$, $P = 0.75$). Thus, in 2007 we estimated ungrazed NAP through end-of-season standing biomass alone, and report these data for both 2006 and 2007 (average of two 1-m^2 quadrats at each location in August each year). We measured NAP of the paired and adjacent grazed plots using 1-m^2 movable exclosures following McNaughton et al. (1996), at monthly intervals between May and August (average of two plots at each location, 2006 and 2007). We used positive increments from the monthly measurements. Negative increments were rare, and were considered as zero. Based on these measurements, we calculated grazing intensity as forage consumption relative to production (1–standing biomass$_{grazed}$/NAP$_{grazed}$; as %) following McNaughton (1985).

NBP was estimated in 2007 in the same plots using root-ingrowth cores. Between May and August, we deployed two cores with 1-mm wire-mesh, each 20 cm deep and 5 cm in diameter. Average live belowground biomass from the two sub-samples was used to estimate NBP in each plot (dry weight, g m^{-2}). The depth of root-ingrowth cores was determined through a pilot survey which corroborated results of previous studies from other parts of the Central Asian eco-region (Xu et al. 2004) that 95% of the root biomass is located in the top 15 cm of soil, and bedrock depth was often approached at 20–22 cm depth. Since various methods of estimating NBP have different limitations (reviewed by Milchunas 2009), the estimates from the root-ingrowth method are indicators of NBP that may suitably represent the differences in production among the treatment categories.

We used ion-exchange resin bags (Binkley and Matson 1983) to estimate soil N availability over the growing season. Five resin bags (DOWEX MR-3), each with 5 g resin in non-dyed hose were buried 5–10 cm deep in each fenced and control plot in May and removed in August (for 2006 and 2007). These sub-samples were pooled before analysis. Soil N availability was considered as the sum of [NH$_4^+$] and [NO$_3^-$] extracted by 1 N KCl solution from 5 g resin (mg g^{-1} resin), followed by analysis with a flow-injection autoanalyzer (Robertson et al. 1999). Rates of N cycling are interpreted from estimates of N availability using various

methods that have different limitations (Frank and Groffman 2009). Estimates from the resin-adsorption method indicate the rate at which inorganic N is produced in the soil and becomes available for plant uptake since the resin competes for N with roots and microbes. This method provides an index of N availability rather than rate of N cycling per se (Stark 2000), and may suitably represent the differences between the treatment categories. Observed differences among grazed and ungrazed plots in resin-extractable N can be due to: (1) changes in N mineralization rates, (2) changes in root uptake, and/or (3) indirect grazing effects on microbial abundance. Since grazing can potentially affect all three aspects (Ruess 1984; Briske and Richards 1995; Ritchie et al. 1998; Frank and Groffman 1998; Hamilton and Frank 2001; Sankaran and Augustine 2004), they can contribute simultaneously to the differences in resin-extractable N among the treatments.

We analyzed the C:N ratio of shoots (from June, mid-season) and litter (from August–September, post-senescence) collected from each plot in 2006 and 2007. Root samples were taken in August 2007 (end-season). Samples were analyzed for C and N content using a dry combustion analyzer (Robertson et al. 1999).

Data analysis

Grazer effects on NBP and root C:N ratio were analyzed using ANOVA to compare the fenced (ungrazed) and the paired adjacent control (grazed) plots. Grazer effects on NAP, shoot and litter C:N ratio, and N availability in soil were analyzed using repeated measures ANOVA. Data on C:N ratios required ln transformation to meet statistical assumptions. Herbivore-type (native grazers or livestock) was included as an additional categorical explanatory variable in these analyses. A significant interaction term between herbivore type and herbivore exclusion would indicate that the alternative grazer assemblages have different effects on the response variable. Annual net total plant production (NTP) was calculated as the sum of NAP and NBP for each plot. Relative aboveground fraction was calculated as NAP/NTP. Likewise, the relative belowground fraction can be calculated as NBP/NTP. But, since these two derived variables are inversely auto-correlated, we only used the former in subsequent analysis.

The ratio of grazed and ungrazed values is often used to summarize plant response to defoliation (Strauss and Agrawal 1999), and these ratios often require ln transformation for statistical analyses. We calculated change in aboveground allocation due to grazing as the ln ratio of relative allocation in grazed plots and paired adjacent ungrazed plots, i.e., ln (aboveground fraction$_{grazed}$/aboveground fraction$_{ungrazed}$). For our data, a positive ln ratio would indicate that herbivores increased aboveground allocation whereas a

negative value would indicate that they decreased it. The corresponding effects on belowground fraction can be calculated similarly, but, since these two fractions are inversely auto-correlated, only the former was used in subsequent analysis. Likewise, herbivore effects on shoot, root and litter C:N, and N availability in soil, were calculated as corresponding ln ratios. We used a general linear model (GLM) to evaluate whether, and how, grazer effects on relative aboveground allocation were related to grazer effects on the C:N ratios of shoot, root and litter, soil N availability, and grazing intensity. Grazer effect on aboveground allocation (ln ratio) was used as a response variable, while the corresponding ln ratios for shoot, root and litter C:N, and N availability in soil, along with grazing intensity and herbivore-type (native species or livestock) were incorporated as predictor variables. Since there were many potential predictor variables, we adopted a model selection approach for this GLM (Burnham and Anderson 2002) using Akaike information criteria (AIC). Model parameterization attempted to arrive at a minimal and parsimonious final model consisting of only the most important predictors based on the contribution of each additional variable to model AIC (Burnham and Anderson 2002). All analyses were conducted in SAS version 9.1 (SAS Institute, Cary, N.C.). Data are reported as mean ± 1 SE, and multiple

comparisons of means were conducted using a Tukey–Kramer adjustment of error ($\alpha = 0.05$).

Results

Average annual NAP was 47.8 ± 2.2 g m^{-2}. Grazing had a positive effect on NAP and it was higher in areas used by livestock (Fig. 1a), but there were no interaction effects (Table 1). Average grazing intensity was $50.8 \pm 3.1\%$ and it did not vary systematically either between years ($P = 0.22$), or by herbivore type ($P = 0.26$).

Average annual NBP was 513.3 ± 60.9 g m^{-2}. Grazing had a negative effect on NBP and it was lower in areas used by livestock (Fig. 1b), but there was no interaction effect (Table 2). The average aboveground fraction, calculated as NAP relative to NTP, was 0.14 ± 0.02. Grazing had positive effects on the aboveground fraction and it was higher in areas used by livestock (Fig. 1c) but there was no interaction effect (Table 2).

Average shoot C:N ratio was 23.8 ± 0.7. Grazing decreased shoot C:N and it was lower in areas used by livestock (Fig. 2a), but there were no interaction effects (Table 1). Average root C:N ratio was 24.6 ± 1.7 and did not vary systematically between grazing and herbivore-type

Fig. 1 Comparison of grazed and ungrazed **a** annual net aboveground primary production (*NAP*), **b** annual net belowground primary production (*NBP*), and **c** relative aboveground allocation in the Spiti region of northern India. Data indicate that grazing stimulates NAP (**a**) and reduces NBP (**b**), which is associated with increased aboveground allocation (**c**). Data from plots grazed primarily by livestock (*open circles*) and native herbivores (*filled circles*) are shown separately
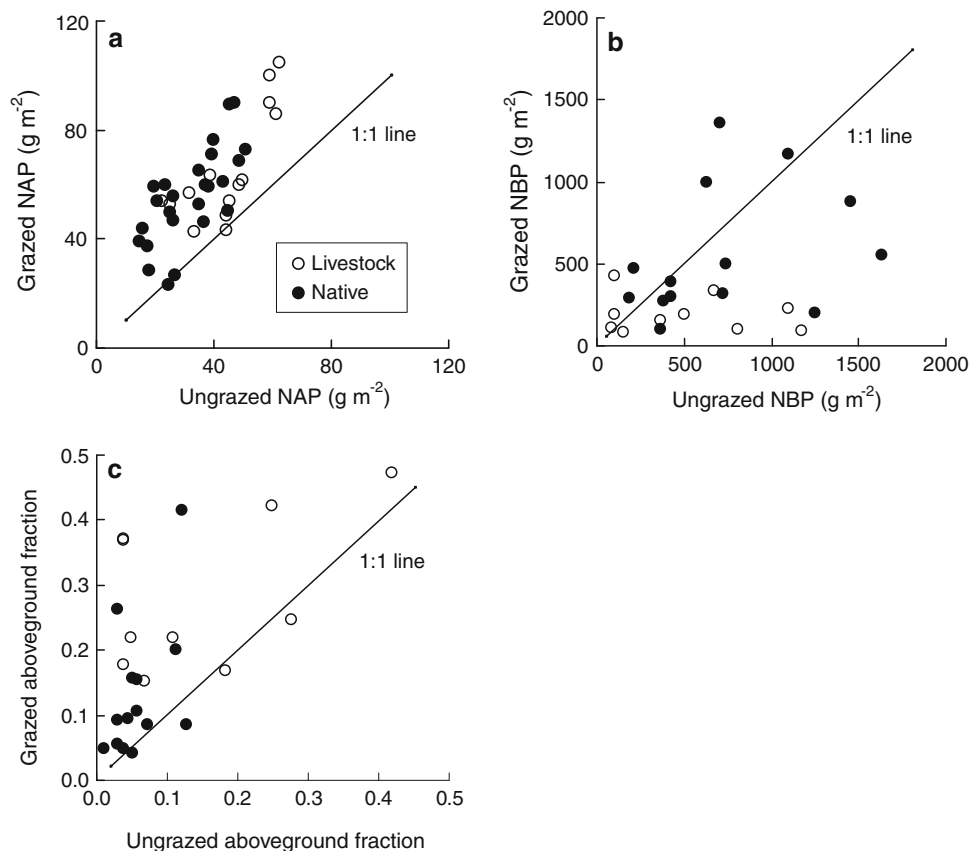
Table 1 Summary of results of repeated measures ANOVA over time to evaluate effects of grazing (grazed vs. ungrazed) and herbivore type (livestock vs. native grazers) on annual net aboveground production (*NAP*), shoot C:N ratio, litter C:N ratio and resin-extractable inorganic N in soil

Effect	NAP		Shoot C:N		Litter C:N		Resin N	
	F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Grazing	$F_{1,44} = 33.31$	<0.001	$F_{1,44} = 10.99$	0.002	$F_{1,44} = 23.58$	<0.001	$F_{1,44} = 27.53$	<0.001
Herbivore type	$F_{1,44} = 10.13$	0.003	$F_{1,44} = 49.13$	<0.001	$F_{1,44} = 8.03$	0.007	$F_{1,44} = 68.90$	<0.001
Grazing × Herbivore type	$F_{1,44} = 0.10$	0.98	$F_{1,44} = 0.16$	0.68	$F_{1,44} = 1.94$	0.17	$F_{1,44} = 20.43$	<0.01
Time	$F_{1,26} = 0.10$	0.82	$F_{1,25} = 0.01$	0.96	$F_{1,25} = 5.11$	0.03	$F_{1,26} = 4.21$	0.06
Time × Grazing	$F_{1,26} = 0.45$	0.51	$F_{1,25} = 0.15$	0.70	$F_{1,25} = 1.48$	0.23	$F_{1,26} = 0.57$	0.45
Time × Herbivore type	$F_{1,26} = 1.39$	0.24	$F_{1,25} = 0.11$	0.73	$F_{1,25} = 1.89$	0.18	$F_{1,26} = 1.33$	0.25
Three-way interaction	$F_{1,26} = 0.68$	0.41	$F_{1,25} = 0.48$	0.49	$F_{1,25} = 2.63$	0.12	$F_{1,26} = 0.39$	0.53

Table 2 Summary of results of two-way ANOVA to evaluate effects of grazing (grazed vs. ungrazed) and herbivore type (livestock vs. native grazers) on annual net belowground production (*NBP*), relative aboveground allocation, and root C:N ratio

Effect	NBP		Aboveground allocation		Root C:N	
	$F_{1,44}$	*P*	$F_{1,44}$	*P*	$F_{1,31}$	*P*
Grazing	4.12	0.04	11.84	0.001	1.25	0.27
Herbivore type	6.09	0.02	16.50	<0.001	3.27	0.07
Two-way Interaction	0.52	0.47	1.17	0.28	0.06	0.79

treatments (Fig. 2b), and there was no interaction effect (Table 2). Average litter C:N ratio was 60.0 ± 5.9. Grazing decreased litter C:N and it was lower in areas used by livestock (Fig. 2c). Grazer effect on litter C:N ratio was stronger during the third year of herbivore exclusion, compared to the second year, and there was a significant effect of time (Table 1).

Average resin-extractable N was 9.9 ± 0.4 mg g^{-1} resin. Grazing had positive effects on resin-extractable N and this effect was greater in areas used by livestock due to a significant interaction (Fig. 2d; Table 1). There was no correlation between grazer effects on NBP and on resin-extractable N ($r^2 = 0.07$, $P = 0.20$).

The ln ratio of change in relative aboveground allocation was positive (0.80 ± 0.17), indicating increased aboveground allocation under grazing. The GLM attempted to explain the variation in changes in aboveground allocation due to grazing with co-variation in shoot, root, and litter quality, soil N availability, herbivore type and grazing intensity. The minimal GLM model contained only two predictor variables (final AIC = 58.5, ΔAIC = −17.7, $F_{2,22} = 16.16$, $P < 0.001$) that accounted for the variation in relative aboveground allocation. Partial coefficients of the two selected predictor variables showed that change in litter quality (0.42 ± 0.21, $P = 0.05$) and grazing intensity (0.28 ± 0.06, $P = 0.001$), were both positively related to change in relative aboveground allocation due to grazing.

Discussion

Our results indicate that grazing, on average across the landscape, has positive effects on NAP but negative effects on NBP, and these lead to a relative increase in aboveground allocation at the expense of that belowground (Fig. 1). These trends were qualitatively consistent between areas used by introduced livestock and the native herbivores. Increased aboveground allocation coincides with increased soil N availability which is consistent with the changes seen in shoot and litter C:N ratios (Fig. 2). Previous work in other parts of the Central Asian highlands has found that grazing can have positive effects on NAP and shoot quality (Klein et al. 2007), and negative effects on NBP (Gao et al. 2008). Consistent with other reports from Central Asian highlands (Ni 2004; Gao et al. 2008; Yang et al. 2010), we also found that the majority of plant production occurs belowground (Fig. 1). In this high-altitude eco-region, aboveground biomass (presumed to be correlated with NAP) ranges between 40 and 194 g m^{-2} and belowground biomass (presumed to be correlated with NBP) ranges between 210 and 1,254 g m^{-2} (Yang et al. 2010). So, our estimates of NAP and NBP, as well as how each fraction is influenced by grazing, appear to be representative of the general pattern seen in this eco-region (Ni 2004; Klein et al. 2007; Gao et al. 2008; Yang et al. 2010). Similar high root:shoot ratios have also been documented in other relatively high-altitude regions [e.g., North American shortgrass ecosystem (Derner et al. 2006)].

A better understanding of how these above- and belowground responses are inter-related can be obtained by viewing them alongside the indirect grazer effects on soil N availability. But, various mechanisms may influence the relationship between responses of plants and soil N to grazing (Ruess 1984; Hamilton et al. 1988; Briske and Richards 1995; Ritchie et al. 1998; Hamilton and Frank 2001; Chapman et al. 2003; Sankaran and Augustine 2004). Plausible non-exclusive explanations for the difference in soil N availability between grazed and ungrazed plots (Fig. 2d)

Fig. 2 Grazers effects on C:N ratio of **a** shoot, **b** root, and **c** litter, and on **d** resin-extractable inorganic N in soil in the Spiti region of Northern India. Data show that grazing reduces C:N ratio of shoot and litter, but has weak effects on root C:N ratio. Data from plots grazed primarily by livestock (*open circles*) and native herbivores (*filled circles*) are shown separately
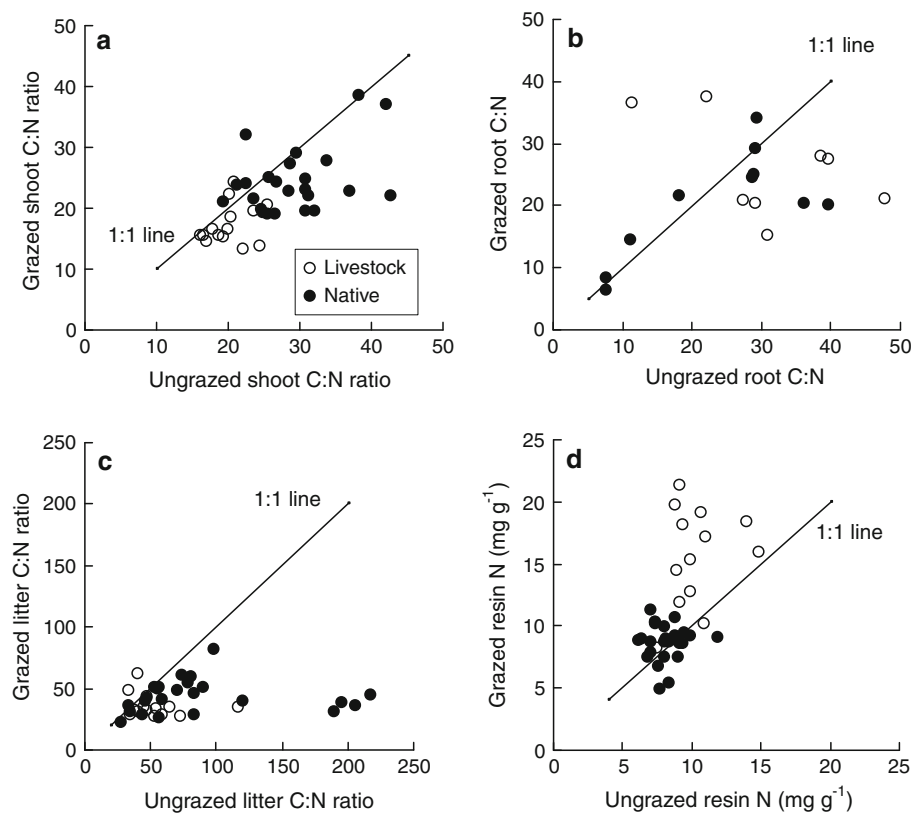
include changes in: (1) N mineralization rate, (2) soil microbial abundance, (3) plant N uptake, and (4) plant community composition.

First, the trend in soil N availability (Fig. 2d) is consistent with the trend in shoot (Fig. 2a) and litter quality (Fig. 2c), but, these may not directly reflect changes in N mineralization rate or plant N uptake. Instead our data might suggest either: (1) the changes in plant-available N were unrelated to changes in potential root uptake, or (2) reduction in NBP due to grazing was incompletely compensated by changes in N uptake. Second, grazer effects on microbial abundance can range from positive to negative (Hamilton and Frank 2001; Sankaran and Augustine 2004) and such variation is likely to be related to grazer effects on soil C input (Gallardo and Schlesinger 1992). Grazing can have negative consequences (Fig. 1) for potential soil C input (Bagchi and Ritchie 2010), and may also alter microbial abundance in our plots. Third, differences in shoot and litter quality may be due to the joint effects of physiological responses (Ruess 1984; Hamilton et al. 1988; Briske and Richards 1995), and changes in species composition (Ritchie et al. 1998). We did observe significant compositional changes after 3 years of herbivore exclusion in these plots (details in Bagchi and Ritchie 2010). So, our results align with the hypothesis that NAP may be stimulated by grazing when it favors species with high tissue quality (Ritchie et al. 1998). But, several overlapping and mutually non-exclusive mechanisms may be contributing in tandem to these patterns, and their relative importance may be discerned through the use of stable isotopes.

The positive partial correlations between grazer effects on relative aboveground allocation with litter quality and with grazing intensity suggest that a greater fraction of total production appears in the aboveground compartment, at the expense of the belowground compartment, when: (1) improvement in litter quality due to grazing is high, and (2) when grazing intensity is high. However, as a large fraction of total plant biomass is belowground, net N input to soil from root turnover is likely to exceed that from litter. We found that although grazing is associated with declines in NBP (Fig. 1b), it does not influence root C:N ratio (Fig. 2b; Table 2). In comparison, grazing influences NAP (Fig. 1a) as well as shoot (Fig. 2a) and litter quality (Fig. 2c). So, while root turnover may provide overall large N inputs to soil, the differences in N availability between grazed and ungrazed plots (Fig. 2d) may be influenced, at least partially, by changes in NAP and the quality of shoots and litter.

Since the above- and belowground aspects have seldom been studied alongside soil nutrients (Biondini et al. 1998; Schoenecker et al. 2004), particularly in multi-species natural communities, our results provide a simultaneous assessment of herbivore control over material and energy flow through grazing ecosystems. The hypothesized effects of

herbivores on NAP and nutrient dynamics (de Mazancourt et al. 1998) are well supported by field experiments (e.g., Ritchie et al. 1998; Biondini et al. 1998; Chapman et al. 2003). Declines in belowground production and increased aboveground investment under grazing (Fig. 1) have also been recognized (Klein et al. 2007; Gao et al. 2008). And, as has been previously documented in other ecosystems [e.g., North American savannas (Ritchie et al. 1998); and mixed grass prairies (Biondini et al. 1998)], we also found significant improvements in shoot and litter quality which might explain the increase in plant-available soil N (Fig. 2). These patterns of co-variation between grazer effects on NAP, shoot and litter quality, and soil N availability, suggest a potential positive feedback mechanism between grazer effects on nutrients and plant production (Ritchie et al. 1998; Chapman et al. 2003).

These data also highlight potential differences between grazing by native herbivores and introduced livestock. There has been much inconclusive debate over whether and how results from natural grazing ecosystems can be applied to managed rangelands, and vice versa (Levin 1993). Specifically, it has remained uncertain whether a common set of mechanisms determines grazer effects in natural and managed ecosystems, and how insights gained in one ecosystem can be applied to the other. Our results show that the impacts of livestock and native grazers were qualitatively similar—both increased NAP and decreased NBP. However, areas used by livestock had comparatively lower belowground investment and higher aboveground investment, a pattern which is related to grazing-mediated variation in plant community composition (Bagchi and Ritchie 2010). These results show that, despite qualitative similarities, it may be difficult to readily extrapolate insights from natural ecosystems to livestock production systems and vice versa, because quantitative effects of grazers may vary between different plant communities (e.g., North American prairies, Schoenecker et al. 2004; East African savannas, Augustine and McNaughton 2006).

In summary, these data show that: (1) grazing can stimulate NAP when there is a concomitant increase in soil N availability, (2) increased soil N availability may be associated with preferential aboveground allocation at the expense of belowground allocation, and (3) several overlapping and mutually non-exclusive pathways may contribute to increased soil N availability and the subsequent feedbacks with production. Use of alternative techniques, such as stable-isotope labeling, may help determine the relative contributions from each pathway. These insights help to integrate and clarify the proposed positive feedbacks between grazer effects on nutrient cycling and plant production (McNaughton 1985; de Mazancourt et al. 1998; Ritchie et al. 1998), and indirect effects of nutrient cycling

on relative biomass investment (Wilson and Tilman 1991; Cahill 1999).

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