LARGE HERBIVORES SUPPRESS DECOMPOSER ABUNDANCE IN A SEMIARID GRAZING ECOSYSTEM

Mahesh Sankaran[1,3] and David J. Augustine[2]

[1]*Natural Environment Research Council (NERC) Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berks SL5 7PY UK*
[2]*Department of Biology, Syracuse University, Syracuse, New York 13244 USA*

Abstract. Ecosystem-level studies of producer–decomposer interactions have focused primarily on plant production and soil texture as regulators of decomposer abundance but have rarely considered the role of grazers in mediating such interactions. Here, we conducted replicated exclosure experiments at both high and low levels of soil fertility to investigate the effects of large, mammalian grazers on decomposer biomass and activity patterns in a semiarid grazing ecosystem in Kenya. Within only two years of grazer exclusion, microbial biomass was greater in soil of fenced grassland across all levels of soil fertility. This consistent negative effect of grazers on microbial biomass occurred despite the fact that grazers stimulated aboveground plant production in nutrient-rich sites and depressed it in nutrient-poor sites. A consideration of all the potential pathways by which grazers influence decomposer populations suggests that observed grazing-induced reductions in microbial biomass were predominantly associated with a depression in the amount of plant carbon inputs to soils. Finally, across all study sites, microbial biomass was highly correlated with soil carbon content, suggesting that landscape-scale constraints on soil organic matter content and plant production overarch grazer effects on microbial abundance. Our results support previous ecosystem-level studies showing that microbial biomass and growth are constrained by plant production and soil C availability. In addition, our findings demonstrate that decomposer abundance can be influenced by an ecosystem's trophic structure, with significant reductions in microbial biomass occurring as a result of herbivores diverting plant carbon away from soils.

Key words: aboveground primary production; grazing; microbial activity; microbial biomass; savanna; soil organic carbon.

INTRODUCTION

Soil microbes comprise a mere fraction of total soil organic matter but are largely responsible for the cycling of nutrients in terrestrial ecosystems (Zak et al. 1994). Since microbes depend on plant-derived carbon sources to meet their energy requirements, plant production frequently limits microbial biomass by regulating the quantity of substrate available for heterotrophic metabolism (Schimel 1986, Myrold et al. 1989, Zak et al. 1994, Tracy and Frank 1998). Factors such as plant species identity and leaf tissue chemistry also impose additional regulatory influences on microbial dynamics through their effects on substrate quality (Bardgett et al. 1998, Bardgett and Wardle 2003). Such linkages between producers and decomposers, generated through the nature and amount of plant inputs to soil, in turn feedback to strongly influence ecosystem C and N cycles (Wedin and Tilman 1990, van der Krift and Berendse 2001).

It has been estimated that annual C inputs to soils from plant litter just suffice to meet maintenance requirements of microbes, allowing for little annual growth of soil microbial populations (Smith and Paul 1990). In systems where the bulk of plant production is channelled into the decomposer food web, microbial biomass should, therefore, be well correlated with ecosystem productivity, and should increase with soil fertility. This relationship holds true across a range of late-successional ecosystems from deserts to hardwood forests (Myrold et al. 1989, Zak et al. 1994). Greater litter inputs to soils in more productive systems results in greater substrate availability for microbial metabolism, and consequently, greater microbial biomass content in soils. However, in ecosystems dominated by large mammalian grazers, decomposer populations may not be as tightly coupled to plant production because increasing productivity can also translate to increased consumption by herbivores (McNaughton et al. 1989, Frank et al. 1998). Consumption and the subsequent channelling of plant energy into secondary productivity and respiration redirects carbon away from soil food webs and can hence serve to limit microbial biomass.

Previous studies of grazer–plant–soil interactions in grassland systems have reported variable effects of grazers on microbial populations. Grazers reduce mi-

crobial biomass in some cases (Garcia and Rice 1994, Holt 1997, Stark and Grellmann 2002), increase it in some (Singh et al. 1991, Bardgett et al. 1997, 2001, Stark et al. 2002), and have no, or idiosyncratic, effects on it in others (Kieft 1994, Tracy and Frank 1998, Wardle et al. 2001). At present, the reasons underlying such varied responses remain unclear. Ultimately, grazer effects on soil microbial populations are contingent on the outcome of two different, and potentially competing, processes that influence patterns of energy availability for decomposers. First, grazers consume plant energy and either respire it, divert it toward secondary production, or translocate it to other areas via dung, thereby reducing its availability to microbes. Second, grazers alter patterns of energy capture by plants, potentially increasing it in some systems (Cargill and Jeffries 1984, McNaughton 1985, Frank and McNaughton 1992) and decreasing it in others (McInnes et al. 1992). Changes in plant energy capture rates are typically accompanied by corresponding changes in plant and litter tissue quality that result from either physiological responses at the individual plant level or from grazer-induced shifts in plant species composition (McNaughton 1979, Pastor et al. 1993, Augustine and McNaughton 1998, Bardgett et al. 1998). Because grazer stimulation of plant production is contingent on the nutrient status of soils (Augustine and McNaughton 1998, Hamilton et al. 1998, Ritchie et al. 1998), grazer–decomposer interactions can potentially vary across soil fertility gradients. However, few studies have used replicated experiments across fertility gradients to address these questions.

We hypothesized that, in nutrient-poor ecosystems, consumption and respiration of plant tissue by grazers, coupled with grazer-induced reductions in plant production and litter quality can result in a relationship between grazers and decomposers that is antagonistic. In nutrient-rich ecosystems, however, grazer enhancement of plant production and litter quality could potentially offset negative effects of herbivore consumption leading to grazer–decomposer relations that are neutral or even positive. To examine these relationships, we quantified microbial biomass and activity patterns across a natural soil fertility gradient in a semiarid grazing ecosystem in central Kenya. First, we expected productive, nutrient-rich sites to support greater microbial populations than nutrient-deficient ones. Second, we used replicated exclosure experiments conducted at both high and low levels of soil fertility to test whether soil nutrient status alters the nature of grazer–decomposer interactions.

STUDY AREA

The study was conducted at the Mpala Research Centre and associated Mpala ranch (MRC) which encompasses some 200 km^2 of semiarid savanna within the Laikipia district of central Kenya (0°17' N, 37°53' E). Study sites were underlain by a single soil type clas-

sified as a well drained, moderate to very deep, friable sandy loam developed from metamorphic basement rocks (Ahn and Geiger 1987). Mean annual rainfall is 500 mm. Vegetation in the study area is a two-phase mosaic consisting of small grassland glades embedded in an *Acacia*-dominated bushland community (Young et al. 1995). Glades are characterized by a short-statured lawn dominated by *Cynodon plectostachyus*, while the herbaceous layer of the bushland community is dominated by stoloniferous grasses such as *Cynodon dactylon* and *Digitaria milijiana*. Glades were created through the abandonment of overnight cattle enclosures (bomas) that concentrated large quantities of cattle manure into 0.5–1.0 ha areas. These bomas are eventually abandoned and develop over time into nutrient-rich grassland. All glade sites included in this study were abandoned >40 years ago based on analyses of aerial photographs. Although glade and bushland soils are similar in texture, glade soils contain 1.6 times more C, 1.7 times more N, and 8.8 times more P than surrounding bushland soils (Augustine 2003*a*). MRC is currently managed for cattle production using traditional Maasai herding methods. Over the past decade, ~2000–3000 cattle were maintained at MRC. Stocking rates were relatively constant at 14–16 cattle/km^2 during January 1999–May 2000 (43–50 kg/ha). Cattle density declined from 15 cattle/km^2 in May 2000 to a low of 7.2 cattle/km^2 in April 2001 as a result of emigration and mortality during a severe drought. Stocking rates increased to 10.8 cattle/km^2 in May 2001 as cattle were returned to MRC and reached 13.5 cattle/km^2 in August 2001 (K. Wreford-Smith, *personal communication*). The most common native grazers and mixed feeders are impala (*Aepyceros melampus*), zebra (*Equus burchellii*), waterbuck (*Kobus ellipsiprymus*), buffalo (*Sycerus caffer*), and eland (*Taurotragus oryx*). Impala occur at densities of ~20 impala/km^2, while all other native grazers occur at low (<1 individual/km^2) densities (Augustine 2002).

METHODS

The effects of grazers and soil fertility on decomposers were determined by comparing soil microbial biomass and activity inside and outside grazing exclosures in glade (high-nutrient) and bushland (low-nutrient) communities at three different study sites distributed across the central and southern regions of MRC. In 1999, we established electrified fences that excluded all large herbivores ranging in size from hares to elephants from a 0.5 ha (70 × 70 m) area, and also established adjacent paired 70 × 70 m control plots in both bushland and glade communities at each of three study sites. Fences followed the design of Thouless and Sakwa (1995), with additional mesh and electrified wires from 0–0.5 m in height that effectively excluded dik-dik and hares. Soil cores (0–15 cm depth, 5 cm diameter; 12 per glade and 20 per bushland plot) were collected at the time of fence construction and a sub-

sample from each were analysed for soil C and N content by Dumas combustion with a Carlo Erba CN analyzer (Fisons Instruments, Milan, Italy). All glades were dominated by *Cynodon plectostachyus*. At bushland sites, we only studied grass communities occurring between shrub canopies to avoid the confounding influence of shrub litter inputs. Bushland swards were dominated by perennial stoloniferous grasses (*Cynodon dactylon* at sites 1 and 2; *Digitaria milanjiana* at site 3). Although dominant grass species differed among bushland sites, species composition was similar inside and outside exclosures at each site throughout the study.

Here, we report on microbial biomass C and N from soils sampled at each of the sites during July and August 2001, corresponding to late wet-season conditions. Sampling occurred two years and four complete growing seasons after exclosure construction. Microbial biomass C and N and microbial respiration rates were determined for soils from six replicate cores (0–15 cm depth) collected from inside and outside grazing exclosures at each of the six study sites. Soils were refrigerated immediately upon collection and maintained at 4°C before being shipped to the Imperial College at Silwood Park, UK, for microbial analyses. Microbial biomass C was measured using the chloroform fumigation-incubation method (Jenkinson and Powlson 1976). Soil samples, re-moistened to 60% field capacity, were fumigated with ethanol-free chloroform for 24 h. Samples were then inoculated with 0.2 g of unfumigated soil, and sealed in a glass jar along with a 20 mL scintillation vial containing 2 mL of 1 mol/L NaOH. Soils were incubated for 10 d in the dark. A similar set of incubations was also concurrently carried out on nonfumigated soils from the sites. The amount of CO_2-C evolved during the incubation was determined by titrating the NaOH with 0.1 mol/L HCl. Microbial biomass carbon (MBC) was estimated following Howarth et al. (1996) as

$$MBC = 1.73C_F - 0.56C_C$$

where C_F and C_C represent the amounts of CO_2-C evolved from the fumigated and unfumigated samples, respectively.

At the end of the 10-d incubation, fumigated and unfumigated samples were extracted with 1 mol/L KCl to determine soil ammonium and nitrate-N levels. Twenty mL of KCl was added to the soils, vigorously shaken, allowed to sit for 24 h, and then filtered. An additional set of extractions was also carried out at the start of the experiment on untreated 5 g soil samples to determine initial amounts of inorganic N present in soils. Filtrates were analyzed for ammonium and nitrate N using a Lachat Quikchem Autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Microbial biomass nitrogen (MBN) was estimated following Harris et al. (1998) as follows:

$$MBN = MBC \times (\{0.56 \times [(N_F - pN_C)/(C_F - qC_C)]\} + 0.095)$$

where, N_F and N_C represent the amounts of N mineralized during the 10-d period from fumigated and unfumigated samples, respectively, and $p = q = [0.29 \times (C_F/C_C)] + 0.23$, representing the fraction of C and N mineralized from sources other than chloroform-killed biomass. The soil metabolic quotient qCO_2, a measure of the specific activity of soil microorganisms (Anderson and Domsch 1985) was calculated as follows:

$$qCO_2 = \frac{CO_2 \text{ respired } (\mu g \ CO_2\text{-C} \cdot g^{-1} \cdot [10 \ d]^{-1})}{MBC \ (\mu g \ C/g \ soil)}$$

In addition to microbial parameters, aboveground plant production (ANPP) was also measured in each of the study sites during the wet season preceding soil sampling (March–August 2001). Aboveground plant production was measured using moveable grazing cages to account for ungulate consumption outside exclosures (McNaughton et al. 1996). Production at each glade and bushland site was monitored using six 1-m^2 plots inside the permanent exclosure and six moveable cages in grazed areas. At bushland sites, we did not sample locations beneath shrub canopies, i.e., all plots were located between shrub canopies. Biomass in moveable cages and permanent exclosures was measured every 24–28 d early in the growing season, every 28–30 d late in the growing season, and every 30–45 d during dry seasons, and cages were moved to new, randomly located positions following biomass measurements. Biomass was measured by canopy interception with 49 pins per 0.5 m^2 passed through the canopy at a 45° angle. The canopy interception method was calibrated with clipped plots for each of four groups: stoloniferous grasses, bunchgrasses, thin-leaved grasses, and forbs (see Augustine 2003*b* for regression equations). Aboveground production inside and outside exclosures was determined by summing the positive increments in biomass measurements between consecutive samples within permanent exclosures and temporary cages, respectively (McNaughton 1985).

Data were analysed as a split-plot ANOVA in a randomized block design with repeated measures. Sites represented the blocks, community type (bushland vs. glade) the whole-plot effect, and grazing treatments the subplot effect. For all microbial measurements, analyses were based on geometric means calculated using the six subsample soil cores collected at each site for different treatment combinations. Since the degrees of freedom for the analyses were limited, an $\alpha = 0.1$ was employed for determination of statistical significance.

RESULTS

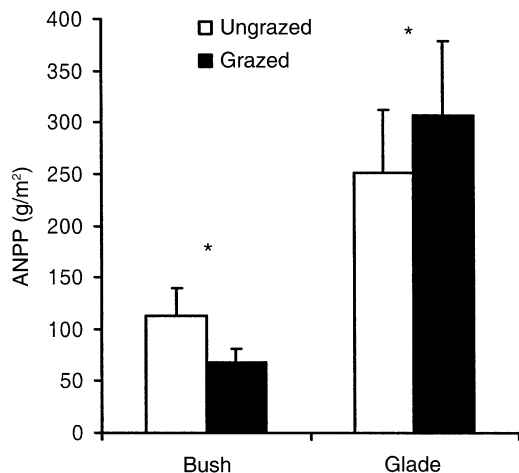Grazer effects on plant production were contingent on the nutrient status of sites (Fig. 1). Grazers stimu-

FIG. 1. Effects of grazing by large herbivores on herbaceous aboveground plant production (ANPP, summed over a five-month period preceding soil sampling) for bushland and glade communities. Error bars show +1 SE based on among-block variation. Asterisks indicates significant differences at the $\alpha = 0.05$ level.

biomass N with soil percentage N (Fig. 2). Microbial biomass C and N likewise increased significantly with aboveground plant production (ANPP) across sites (Fig. 3). However, this relationship was much weaker in the case of ungrazed sites when compared to grazed treatments. In grazed sites, microbial C and N were also significantly positively related with aboveground plant biomass (microbial C, $F_{1,4} = 14.22$, $r^2 = 0.78$, $P = 0.019$; microbial N, $F_{1,4} = 8.07$, $r^2 = 0.67$, $P = 0.047$). However, there was no significant relationship between aboveground plant biomass and microbial parameters in ungrazed sites (microbial C, $F_{1,4} = 2.6$, $P = 0.18$; microbial N, $F_{1,4} = 2.27$, $P = 0.21$).

Neither microbial respiration nor the fraction of soil C respired (percentage C/ 10 d) was influenced by community type or grazing (Table 1). Respired C ranged from ~0.3 to 1.3% of the total soil C pool across sites over the 10-d incubation. The metabolic quotient, i.e., amount of C respired per unit microbial biomass, was also not influenced by community type or grazing (Table 1).

DISCUSSION

Our findings demonstrate a clear negative relationship between grazers and decomposers in this semiarid ecosystem. Within only two years of grazer exclusion, microbial biomass C was higher by 25–47% and microbial N by 20–37% in fenced grasslands, suggesting that grazers regulate decomposer populations in this system by reducing plant carbon inputs to soils. We had originally hypothesized that grazer effects were likely to be negative in nutrient-poor sites, but not so in nutrient-rich sites, since both production and the ability of plants to compensate for tissue removal by herbivores typically increase with soil fertility (Augustine and McNaughton 1998, de Mazancourt et al. 1998, Hamilton et al. 1998). However, despite the fact that grazers stimulated aboveground production in nutrient-rich glades and depressed it in nutrient-poor bushland sites (Fig. 1), grazer effects on microbial biomass were consistently negative across all study sites.

lated aboveground plant production by 22% in nutrient-rich glade sites ($t_6 = 3.47$, $P = 0.013$) and reduced it by 68% in nutrient-poor bushland sites ($t_6 = 2.89$, $P = 0.028$).

No effect of sampling time was detected on microbial biomass C and N estimates ($P > 0.1$ for main effect of time and all time-related interaction terms), so biomass data from July and August were pooled for analyses. Both grazing and community type significantly influenced microbial biomass C and N, although treatment effects were more pronounced for biomass N than for biomass C (Table 1). Nutrient-rich glade soils supported a significantly larger microbial biomass than soils of nutrient-poor bushlands, both inside and outside exclosures (Table 1). In both glades and bushland sites, grazing by large herbivores significantly reduced microbial biomass C and N (Table 1).

Across sites and treatments, microbial biomass C was positively correlated with soil percentage C, as was

TABLE 1. Soil microbial properties and results of statistical analyses from split-plot ANOVAs for respective microbial parameters.

Response	Glade		Bush		Community		Grazing	
	Grazed	Ungrazed	Grazed	Ungrazed	$F_{1,2}$	P	$F_{1,4}$	P
Microbial C (µg/g soil)	344.3 ± 61.4	430.2 ± 63.5	168.6 ± 42.2	248.6 ± 41.9	23.98	0.039	5.56	0.077
Microbial N (µg/g soil)	71.5 ± 8.7	85.8 ± 8.6	30.4 ± 5.8	41.6 ± 5.9	151.32	0.0065	9.79	0.035
Microbial respiration (µg· [g soil]$^{-1}$· [10 d]$^{-1}$)	93.3 ± 8.5	80.3 ± 19.4	84.5 ± 14.3	64.3 ± 3.1	0.46	0.568	2.85	0.167
qCO$_2$ (µg CO$_2$-C· [µg C$_{mic}$]$^{-1}$· [10 d]$^{-1}$)	0.32 ± 0.04	0.22 ± 0.05	0.81 ± 0.31	0.33 ± 0.06	3.86	0.19	2.12	0.22

Note: Values are means ± 1 SE.

grazers can influence plant C allocation strategies in ways that can either increase or depress plant productivity (Whitham et al. 1991), and these effects on net primary production (NPP) influence the magnitude of plant C inputs to the soil (Bardgett et al. 1998, Bardgett and Wardle 2003). Third, regardless of how grazers influence above- and belowground plant production, more than 50% of C consumed by grazers is assimilated and respired rather than returned to the soil (Foose 1982). As a result, the intensity of grazing (percentage of aboveground production consumed) can also be an

FIG. 2. Relationships (A) between microbial biomass carbon and soil organic carbon and (B) between microbial biomass nitrogen and soil total nitrogen in plots. Closed circles represent grazed areas, and open circles represent ungrazed sites. Equations for regression lines: $\text{MBC}_{\text{grazed}} = 245.7(\text{soil C}) - 77.2$ ($r^2 = 0.89$, $P = 0.004$); $\text{MBC}_{\text{ungrazed}} = 290.4(\text{soil C}) - 85.1$ ($r^2 = 0.96$, $P < 0.001$); $\text{MBN}_{\text{grazed}} = 455.4(\text{soil N}) - 12.7$ ($r^2 = 0.97$, $P < 0.001$); $\text{MBN}_{\text{ungrazed}} = 529.1(\text{soil N}) - 13.5$ ($r^2 = 0.95$, $P = 0.001$).

Thus, at least in the short term, soil fertility does not appear to be a simple predictor of grazer impacts on decomposer biomass in soils.

We believe that grazer effects on soil microbial populations can ultimately be interpreted in the context of five general pathways by which grazers influence the quantity and quality of plant carbon inputs to soils (Fig. 4). First, in the short term, grazers can enhance the amount of labile C entering soils by stimulating root exudation in plants (Holland et al. 1996, Guitian and Bardgett 2000, Hamilton and Frank 2001). Second,
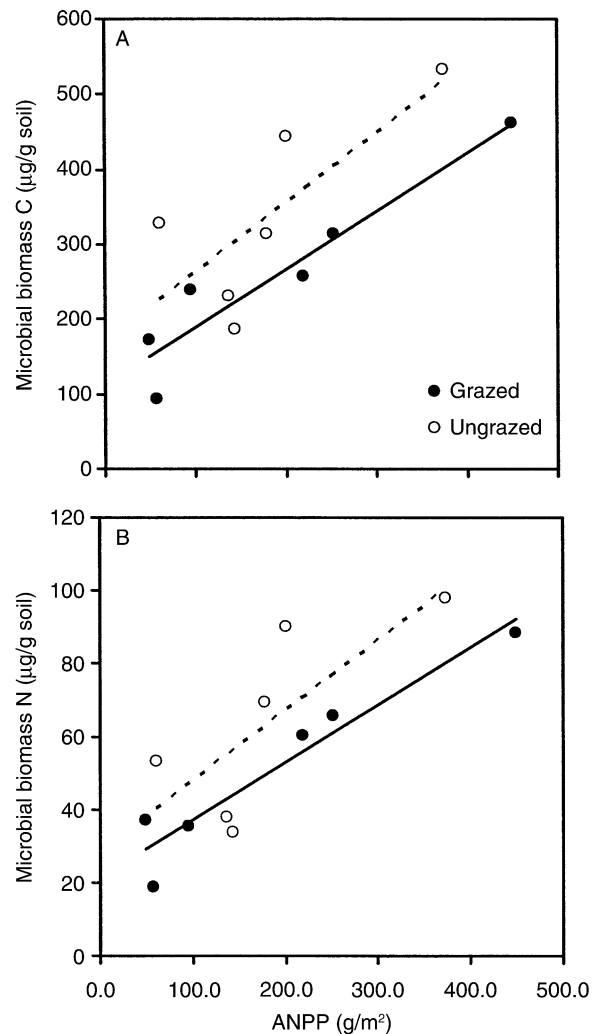

FIG. 3. Relationships between aboveground net primary productivity and (A) microbial biomass carbon and (B) nitrogen in plots. Closed circles represent grazed areas, and open circles represent ungrazed sites. Solid and dotted lines represent best fits for grazed areas and ungrazed sites, respectively. Equations for regression lines: $\text{MBC}_{\text{grazed}} = 0.78(\text{ANPP}) + 111.7$ ($F_{1,4} = 34.8$, $r^2 = 0.89$, $P = 0.004$); $\text{MBN}_{\text{grazed}} = 0.16(\text{ANPP}) + 21.7$ ($F_{1,4} = 43.58$, $r^2 = 0.92$, $P = 0.003$); $\text{MBC}_{\text{ungrazed}} = 0.92(\text{ANPP}) + 171.14$ ($F_{1,4} = 5.15$, $r^2 = 0.45$, $P = 0.086$); $\text{MBN}_{\text{ungrazed}} = 0.19(\text{ANPP}) + 28.72$ ($F_{1,4} = 5.32$, $r^2 = 0.46$, $P = 0.083$).
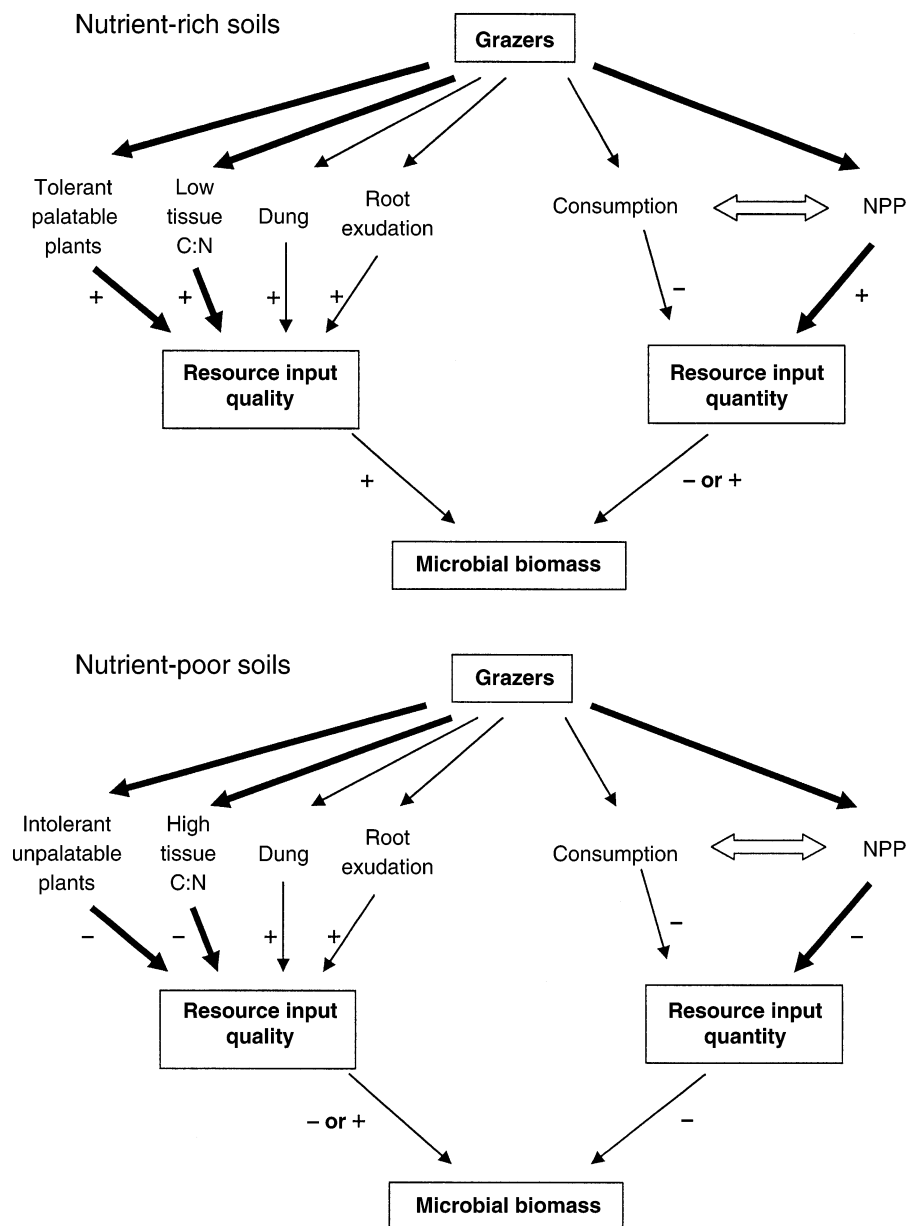
Nutrient-rich soils

Nutrient-poor soils

FIG. 4. Potential pathways by which grazers can influence the quantity and quality of carbon inputs to soils in nutrient-rich and nutrient-poor sites. Arrows in bold represent processes that operate over intermediate to long time scales, and lightface arrows represent processes operating over shorter time scales. In both nutrient-rich and nutrient-poor sites, grazers enhance the quality of carbon inputs to soils over short time scales by stimulating root exudation and through dung deposition. In nutrient-poor soils, the long-term consequences of grazing is depression of both the quantity and quality of carbon inputs to soils. In nutrient-rich soils, grazers enhance resource input quality over long time scales and may either enhance or depress resource input quality depending on the balance between stimulation of NPP (net primary production) and consumptive losses. Note that grazer effect on NPP is itself a function of consumption.

important factor determining how grazers influence soil microbes. Fourth, over the short term, grazers can alter the quality of C inputs to soils either directly, through return in dung, or indirectly by altering the concentration of nutrients and secondary metabolites in grazed vegetation (e.g., by increasing the leaf:stem ratio of grazed vegetation). Finally, over longer time scales,

grazers can influence the quality of aboveground inputs to soils by altering the species composition of plant communities. Increased dominance of unpalatable plant species results in the production of more recalcitrant plant litter (Bryant et al. 1991), which in turn can suppress microbial abundance (Pastor et al. 1993, Bardgett et al. 1998, Stark and Grellman 2002).

With regard to the first pathway, we did not address grazer effects on root exudation and rhizospheric microbial populations in our study. While stimulatory effects of grazers on microbes might indeed have occurred within the rhizosphere of grazed plants at MRC, the uniform suppression of microbial biomass that we observed suggests that rhizopheric effects were insufficient to increase net C availability in bulk soils either in nutrient-rich or nutrient-poor grassland.

In terms of grazer effects on NPP and microbial abundance, we found that grazers stimulated aboveground production in nutrient-rich sites and depressed it in nutrient-poor sites (Fig. 1). However, grazer effects on microbial biomass were consistently negative (Table 1). Clearly, microbial biomass is contingent on both above- and belowground plant inputs to soils. Previous studies have shown that grazers can both reduce (Bokhari and Singh 1974, Holland and Detling 1990, Guitian and Bardgett 2000) and increase (Frank et al. 2002) root production in grasslands and these effects are not a simple function of grazing intensity or soil fertility (McNaughton et al. 1998). Although the degree to which changes in root production influenced microbial biomass at MRC is unclear, a potential explanation for our results may be that grazing, despite stimulating aboveground production in nutrient-rich grassland, depressed belowground and overall productivity.

The intensity of grazing at MRC could also be an important factor mediating grazer effects on microbes. During the 2001 study season, grazers consumed $73 \pm 4\%$ (mean $\pm$ 1 SE) of aboveground production at nutrient-rich grassland sites, and a significantly lower proportion ($43 \pm 7\%$) at nutrient-poor sites (Augustine et al. 2003). Even if half of the forage consumed was returned to the soil as dung (i.e., organic matter digestibility was 50%, a conservative estimate for the palatable forage growing in nutrient-rich grassland; Foose 1982), grazers would have diverted 36% of aboveground production into respiration or ungulate biomass growth. In contrast, grazers only stimulated aboveground plant production (ANPP) in nutrient-rich grasslands by 22%. This difference suggests that stimulation of aboveground production was probably insufficient to balance grazer offtake and is a second potential explanation for why grazers suppressed microbial abundance even though they increased ANPP in nutrient-rich grassland.

Finally, grazers did not cause any changes in species composition of the grassland communities we studied at MRC (Augustine 2002). Therefore, long-term changes in the quality of plant litter inputs to the soil arising from functional shifts in plant species composition are not likely to explain the uniformly negative grazer effect on microbial abundance observed at MRC. Furthermore, short-term changes in the quality of C inputs to soils due to grazing, such as recycling in dung or alteration of litter quality due to physiological changes at the individual plant level, also do not fully explain

our results. For one, greater inputs of labile C in dung should have served to stimulate microbial biomass and activity, with the levels of stimulation more pronounced in nutrient-rich sites where dung inputs were significantly greater compared to nutrient-poor grassland (Augustine et al. 2003). Also, tissue quality as indexed by aboveground plant C:N ratios was, in fact, consistently higher (i.e., C:N ratios were lower) in grazed areas compared to fenced sites (13.1 vs. 20.5, respectively; D. J. Augustine, *unpublished data*). Taken together, this suggests that the negative consequences for microbial populations of a reduced C supply due to herbivore consumption far outweighed any beneficial effects that might have been derived from short-term grazer enhancement of the quality of C inputs to soils.

Consideration of these different pathways by which grazers influence plant carbon inputs to soils also provides insights to the differences between our results and those observed in other grazer-dominated ecosystems. First, in grasslands of Yellowstone National Park (USA) grazed by elk and bison, Tracy and Frank (1998) showed that grazer exclusion for 35–40 years had no discernable impact on microbial biomass. In Yellowstone, grazers have been shown to stimulate both aboveground production (Frank and McNaughton 1992) and belowground production (Frank et al. 2002), and to increase short-term inputs of root exudates to the soil (Hamilton and Frank 2001). All of these factors are expected to have a positive influence on microbial abundance. The lack of significant grazer effects on microbial biomass suggests they may have been offset by grazers consuming an average of 45% of aboveground production annually (Frank and McNaughton 1992).

In high-latitude ecosystems, grazing by reindeer has variable effects on decomposer populations across fertility gradients. In arctic tundra of both high and low fertility, grazing consistently depressed microbial biomass (Stark and Grellman 2002), similar to our findings for MRC. The negative herbivore effect on microbial biomass in the arctic tundra was similarly attributed to consumption by reindeer and rodents diverting C away from microbes (Stark and Grellman 2002). In this arctic tundra, grazers also reduced the abundance of gramminoids with easily decomposable plant tissue (Grellman 2002), but herbivore grazing intensity and the effect on plant productivity were not reported. Other studies found that reindeer grazing stimulated microbial biomass in nutrient-rich, oceanic tundra heaths, while suppressing microbial activity in nutrient-poor, continental tundra heaths (Stark et al. 2002). These differential effects were largely attributed to the fact that grazers increased the abundance of palatable, easily decomposing gramminoids in the nutrient-rich, oceanic tundra, but grazers favored dwarf shrubs with slowly decomposing plant litter in nutrient-poor, continental tundra (Stark et al. 2002). In the nutrient-rich,

oceanic tundra heath, grazers also stimulated above-ground plant productivity (Olofsson et al. 2001). Thus, a positive effect of grazing on microbial abundance occurred where grazers both stimulated productivity and shifted species composition towards more palatable and easily decomposable plants.

Ultimately, grazer effects on soil microbial populations are contingent on how they alter the quantity and quality of resource inputs to soils (Fig. 4). In nutrient-poor sites, grazers are likely to have a negative effect on both in the long term, and consequently depress microbial biomass, since grazing tends to decrease plant production (Augustine and McNaughton 1998, Ritchie et al. 1998) and simultaneously favor unpalatable, slow-growing species with well-defended or nutrient-poor tissues in these systems (Bryant et al. 1991, Ritchie et al. 1998). In nutrient-rich sites, grazer effects on resource input quality tend to be positive over the long term (Augustine and McNaughton 1998, Ritchie et al. 1998), but their net effects on the amounts of C inputs to soils depends on the balance between herbivore consumption and stimulation of plant production, which in turn, varies with grazing intensity (Fig. 4). Grazer stimulation of production is typically highest at intermediate grazing intensities (McNaughton 1979, 1985), and it is at these grazing levels that stimulation of production is likely to offset consumptive losses and result in a net increase in C inputs to soils. Consequently, even in nutrient-rich sites, grazer effects on microbial biomass are likely to be positive only at intermediate grazing intensities and neutral or even negative at low or high grazing intensities. This is consistent with results from previous studies that report maximal microbial biomass at intermediate grazing intensities (Bardgett et al. 2001).

Our study also found that microbial biomass increased with soil fertility, which is consistent with expectations based on energetic constraints (Zak et al. 1994). Nutrient-rich glade soils contained ~1.7 times more soil C and N than nutrient-poor bushland soils (Augustine 2003a) and supported a microbial biomass twice as large as that of bushland sites, both in grazed and ungrazed areas (Table 1). It is important to note that nutrient-rich glades are derived from fertilization of these sites by cattle manure >40 years ago, but soil texture in glades is identical to that of surrounding nutrient-poor bushland soils (Augustine 2003a). Thus, differences in microbial biomass reflect the influence of soil fertility and organic matter content, and are not confounded by effects of soil physical characteristics. The size of the microbial biomass in sites strongly mirrored soil organic C pool sizes across this fertility gradient, in both grazed and ungrazed areas (Fig. 2). Overall, soil fertility effects (glade vs. bushland) explained 65% and 83% of the observed variation in microbial biomass C and N, respectively. In contrast, grazer effects explained only 14% and 7% of the variation observed in microbial biomass C and N, respectively,

across treatment plots. These results suggest that although grazers do limit microbial abundance by consuming aboveground plant tissue, constraints imposed by factors such as soil fertility have a greater influence on microbial abundance at the landscape scale.

Interestingly, despite significant treatment effects on microbial biomass C and N pool sizes, microbial respiration rates remained unchanged across treatments (Table 1). Increases in microbial biomass in response to treatment effects were, therefore, accompanied by compensatory reductions in per capita respiration rates or soil metabolic quotients. On average, soil metabolic quotients tended to be higher under grazing than inside exclosures, and in bushland sites compared to glades. It is commonly assumed that the soil metabolic quotient is elevated when microbes are diverting a greater proportion of carbon to maintenance requirements than to biosynthesis (Anderson and Domsch 1985, Guitian and Bardgett 2000). Microbial populations in low-nutrient bushland sites, therefore, appear to be less efficient at using C for biosynthesis than those in nutrient-rich glade sites. The fact that microbial biomass, but not microbial respiration rates, decreased in response to grazing in this study suggests that grazer-induced changes in C inputs to soils may have been accompanied by corresponding shifts in microbial community composition toward species that allocated more carbon to maintenance requirements than to biosynthesis (Bardgett et al. 1998, 2001). Further studies on shifts in microbial community structure are needed to test this idea.

Research on the role of herbivores in ecosystems has traditionally focused on their direct effects as consumers as modified by plant productivity and predation (e.g., Hairston et al. 1960, Oksanen et al. 1981, McLaren and Peterson 1994) but this body of research has rarely considered potential interactions between herbivores and decomposers. In contrast, ecosystem-level studies of controls over decomposer abundance have focused primarily on the importance of plant productivity and soil texture (Zak et al. 1994). The relationships we found between microbial biomass, soil organic matter, and ANPP are consistent with previous ecosystem-level studies showing that microbial biomass and growth is constrained by plant production and hence soil C availability (Zak et al. 1994). However, our findings also demonstrate that decomposer abundance can be influenced by an ecosystem's trophic structure, with a significant reduction in microbial biomass across all levels of soil fertility caused by the diversion of plant production away from litter and into herbivores. These findings support the contention that the role of herbivores in ecosystem structure and function depends on both their direct effects as consumers and their indirect feedback effects on decomposers.

Literature Cited

Ahn, P. M., and L. C. Geiger. 1987. Kenya soil survey: soils of Laikipia District. Ministry of Agriculture, National Agricultural Laboratories, Kabete, Kenya.

Anderson, J. P. E., and K. H. Domsch. 1985. Determination of ecophysiological maintenance carbon requirements of microorganisms in a dormant state. Biology and Fertility of Soils **1**:81–89.

Augustine, D. J. 2002. Large herbivores and process dynamics in a managed savanna ecosystem. Dissertation. Syracuse University, Syracuse, New York, USA.

Augustine, D. J. 2003a. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. Journal of Applied Ecology **40**:137–149.

Augustine, D. J. 2003b. Spatial heterogeneity in the herbaceous layer of a semi-arid savanna ecosystem. Plant Ecology **167**:319–332.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management **62**:1165–1183.

Augustine, D. J., S. J. McNaughton, and D. A. Frank. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. Ecological Applications **13**: 1325–1337.

Bardgett, R. D., A. C. Jones, D. L. Jones, S. J. Kemmitt, R. Cook, and P. J. Hobbs. 2001. Soil microbial community patterns related to the history and intensity of grazing in sub-montane ecosystems. Soil Biology and Biochemistry **33**:1653–1664.

Bardgett, R. D., D. K. Leemans, R. Cook, and P. J. Hobbs. 1997. Seasonality of the soil biota of grazed and ungrazed hill grasslands. Soil Biology and Biochemistry **29**:1285–1294.

Bardgett, R. D., and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology **84**:2258–2268.

Bardgett, R. D., D. A. Wardle, and G. W. Yeates. 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biology and Biochemistry **30**:1867–1878.

Bokhari, U. G., and J. S. Singh. 1974. Effects of temperature and clipping on growth, carbohydrate reserves and root exudation of western wheatgrass in hydroponic culture. Crop Science **14**:790–794.

Bryant, J. P., F. D. Provenza, J. Pastor, P. B. Reichardt, T. P. Clausen, and J. T. Dutoit. 1991. Interactions between woody-plants and browsing mammals mediated by secondary metabolites. Annual Review of Ecology and Systematics **22**:431–446.

Cargill, S. M., and R. L. Jeffries. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. Journal of Applied Ecology **21**:669–686.

de Mazancourt, C., M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production? Ecology **79**:2242–2252.

Foose, T. 1982. Trophic strategies of ruminant versus non-ruminant ungulates. Dissertation. Department of Biology, University of Chicago, Chicago, Illinois, USA.

Frank, D. A., M. M. Kuns, and D. R. Guido. 2002. Consumer control of grassland plant production. Ecology **83**:602–606.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology **73**:2043–2058.

Frank, D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the Earth's grazing ecosystems. BioScience **48**: 513–521.

Garcia, F. O., and C. W. Rice. 1994. Microbial biomass dynamics in tallgrass prairie. Soil Science Society of America Journal **58**:816–823.

Grellmann, D. 2002. Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. Oikos **98**:190–204.

Guitian, R., and R. D. Bardgett. 2000. Plant and soil microbial responses to defoliation in temperate semi-natural grassland. Plant and Soil **220**:271–277.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–425.

Hamilton, E. W., and D. A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology **82**:2397–2402.

Hamilton, E. W., M. S. Giovannini, S. A. Moses, J. S. Coleman, and S. J. McNaughton. 1998. Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: compensation requires a critical [N]. Oecologia **116**:407–418.

Harris, D., R. P. Voroney, and E. A. Paul. 1998. Measurement of microbial biomass C:N ratio by chloroform fumigation incubation. Canadian Journal of Soil Science **77**:507–514.

Holland, E. A., and J. K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. Ecology **71**: 1040–1049.

Holland, J. N., W. Cheng, and D. A. Crossley, Jr. 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. Oecologia **107**:87–94.

Holt, D. A. 1997. Grazing pressure and soil carbon, microbial biomass and enzyme activities in semi-arid northeastern Australia. Applied Soil Ecology **5**:143–149.

Howarth, W. R., E. A. Paul, D. Harris, J. Norton, L. Jagger, and K. A. Horton. 1996. Defining a realistic control for the chloroform-fumigation incubation method using microscopic counting and 14C-substrates. Canadian Journal of Soil Science **76**:459–467.

Jenkinson, D. S., and D. S. Powlson. 1976. The effects of biocide treatments on metabolism in soil. I. Fumigation with chloroform. Soil Biology and Biochemistry **8**:167–177.

Kieft, T. L. 1994. Grazing and plant-canopy effects on semi-arid soil microbial biomass and respiration. Biology and Fertility of Soils **18**:155–162.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology **73**: 2059–2075.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree-rings on Isle Royale. Science **266**:1555–1558.

McNaughton, S. J. 1979. Grazing as an optimization process: grass ungulate relationships in the Serengeti. American Naturalist **113**:691–703.

McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs **55**:259–294.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. Ecology **79**:587–592.

McNaughton, S. J., D. G. Milchunas, and D. A. Frank. 1996. How can net primary productivity be measured in grazing ecosystems? Ecology **77**:974–977.

McNaughton, S. J., M. Oesterheld, and D. A. Frank. 1989. Ecosystem level patterns of primary productivity and herbivory in terrestrial habitats. Nature **341**:142–144.

Myrold, D. D., P. A. Matson, and D. L. Peterson. 1989. Relationships between soil microbial properties and aboveground stand characterisitics of conifer forests in Oregon. Biogeochemistry **8**:265–281.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240–261.

Olofsson, J., H. Kitti, P. Rautiainen, S. Stark, and L. Oksanen. 2001. Effects of summer grazing by reindeer on composition, vegetation, productivity and nutrient cycling. Ecography **24**:13–24.

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

Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology **79**:165–177.

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

Singh, R. S., S. C. Srivastava, A. S. Raghubanshi, J. S. Singh, and S. P. Singh. 1991. Microbial C, N and P in dry tropical savanna: effects of burning and grazing. Journal of Applied Ecology **28**:869–878.

Smith, J. L., and E. A. Paul. 1990. The significance of soil microbial biomass estimations. Pages 357–393 *in* J. Bollag and G. Stotsky, editors. Soil biochemistry. Dekker, New York, New York, USA.

Stark, S., and D. Grellmann. 2002. Soil microbial responses to herbivory in an arctic tundra heath at two levels of nutrient availability. Ecology **83**:2736–2744.

Stark, S., R. Strommer, and J. Tuomi. 2002. Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. Oikos **97**:96–78.

Thouless, C. R., and J. Sakwa. 1995. Shocking elephants: fences and crop raiders in Laikipia District, Kenya. Biological Conservation **72**:99–107.

Tracy, B. F., and D. A. Frank. 1998. Herbivore inlfuence on soil microbial biomass and nitrogen mineralization in a northern grassland ecosystem: Yellowstone National Park. Oecologia **114**:556–562.

van der Krift, T. A. J., and F. Berendse. 2001. The effect of plant species on soil nitrogen mineralization. Journal of Ecologzy **89**:555–561.

Wardle, D. A., G. M. Barker, G. W. Yeates, K. I. Bonner, and A. Ghani. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs **71**:587–614.

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

Whitham, T. G., J. Maschinski, K. C. Larson, and K. N. Paige. 1991. Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms. Pages 227–256 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. Plant–animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons, New York, New York, USA.

Young, T. P., N. Patridge, and A. Macrae. 1995. Long-term glades in Acacia Bushland and their edge effects in Laikipia, Kenya. Ecological Applications **5**:97–108.

Zak, D. R., D. Tilman, R. R. Parmenter, C. W. Rice, F. M. Fisher, J. Vose, D. Milchunas, and C. W. Martin. 1994. Plant production and soil microorganisms in late-successional ecosystems: a continental-scale study. Ecology **75**:2333–2347.