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Effects of Grazing on the Roots and Rhizosphere of Grasses

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Introduction

Fertilizer inputs are currently being reduced in many areas (Commission, European Communities, 1992) and the resultant drop in pasture fertility will reduce the stock carrying capacity. As a consequence, individual plants will be defoliated less frequently (Curll and Wilkins, 1982) and less nitrogen will be deposited as urine (Thomas *et al.*, 1988), thus influencing plant competition and composition. Research to date has concentrated on the effects of grazing on above-ground aspects, and it has recently been stated that 'the effects of herbivory on the timing, mass and quality of below-ground inputs remains one of the greatest unresolved issues of the dynamics of nutrient cycling' (Ruess and Seagle, 1994). The soil microbiota in grasslands consists of populations of microorganisms, including bacteria, fungi, protozoa, nematodes, and micro- and macroarthropod groups (Ingham and Detling, 1986). These all rely for their growth, at least in part, on carbon or nitrogen substrates via litter, root production, sloughage and exudation. Figure 4.1 illustrates the main links in the detrital trophic food web and shows the primary role of plant roots, the connectivity and some of the many trophic interactions. Although nearly all soil organisms belong to the detrital food web, significant numbers of root herbivores exist in grassland soil (Curry, 1994), also relying on plant roots for their survival. Any alteration in plant-derived carbon, such as through defoliation, will have consequences at many levels in the food web (Fig. 4.1). Since microbial activity, supported in part by root-derived carbon, drives soil nutrient cycling, the production and use of carbon from root systems is also a key issue in the functioning of soil ecosystems (van Veen *et al.*, 1989).

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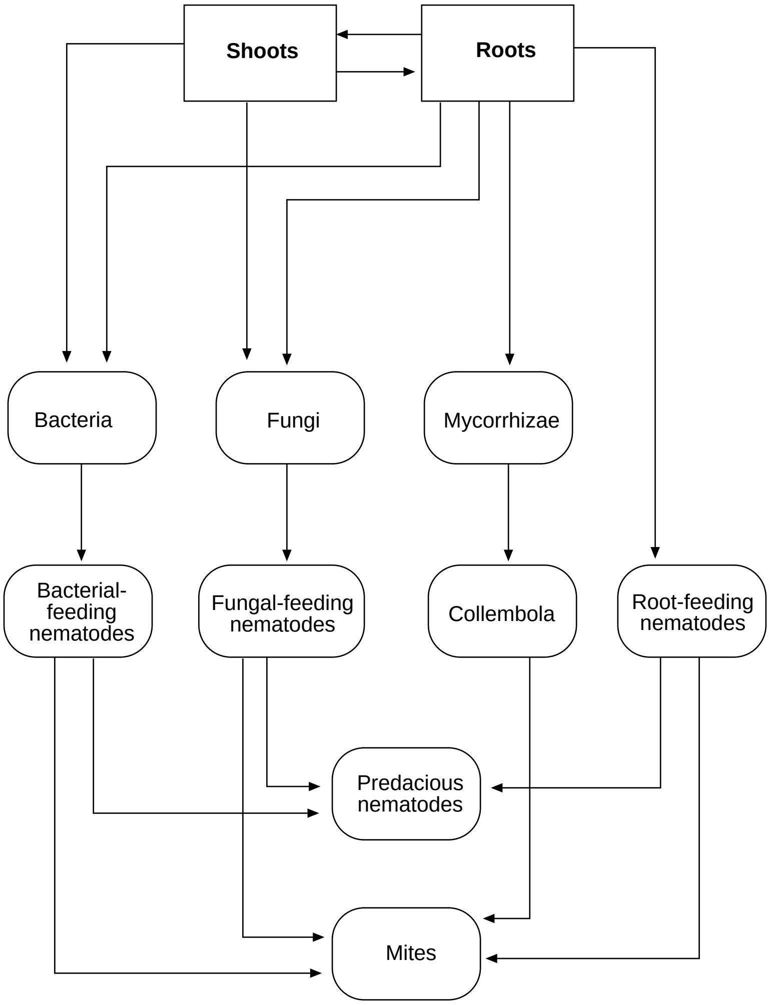


Fig. 4.1. Conceptual diagram of detrital food web for short-grass prairie (modified from Ingham *et al.*, 1986 and Hunt *et al.*, 1987), showing flows and connectivity between trophic levels. Omitted are flows from every organism through death and defaecation.

The coupling of rhizodeposition processes to microbial activity and nutrient cycling is affected both by the quantity and quality of plant inputs and by soil nutrient availability. Rhizodeposition, in particular the exudate components, stimulates the growth of distinct microbial communities. Shifts in quantity and quality of rhizodeposition, as occur following defoliation, affect microbial community structure and, therefore, also microbially driven processes in soil. Soil nutrient availability is a strong determinant of both the quality and quantity of rhizodeposition. Low availability of nutrients generally results in an increase in rhizodeposition. This can be related to release of specific compounds that increase the availability of phosphorus, zinc, iron and aluminium (Pellet *et al.*, 1995; Rengel, 1997). In the case of N limitation, increased rhizodeposition may non-specifically increase N cycling processes, ultimately increasing availability to the plant. However, it is unclear to what degree effects of N supply on plant partitioning and root architecture are contributory to these shifts in rhizodeposition, which highlights the need for an integrated approach to developing an understanding of productivity in grazed systems.

As a consequence of the many complex interactions between the plant and the soil, results obtained from field observations examining the effects of alteration in grazing habit on species composition are hard to extrapolate. In general, it has been predicted that, as pastures become more extensive and nutrient limitations increase, species that can maximize assimilation of nutrients through a high biomass allocation to structures that enhance nutrient absorption (Tilman, 1988) or minimize loss of nutrients (Chapin, 1980) will increase. However, competition for nutrients could be modified by species differences in resistance or tolerance to grazing. Under grazing, it has been suggested that minimizing loss of nutrients could be of greater importance than a high biomass allocation to roots (Berendse *et al.*, 1992). It was shown that nitrogen losses through cutting were greater in species from nutrient-rich habitats (e.g. *Arrhenatherum elatius*) than in species from nutrient-poor habitats (e.g. *Festuca rubra*) (Berendse *et al.*, 1992). According to Elberse and Berendse (1993), plant morphology and architecture seemed more relevant adaptations to habitats with contrasting nutrient supplies than plant allocation. As a consequence, it is important to understand the physiological response of the whole plant to grazing at the individual species level. Grazing effects will also be separated into the two main factors, defoliation and urine deposition, to understand the individual processes involved.

This review identifies the main effects of shoot herbivory on individual species and long-term effects on the plant root system, such as root biomass distribution, morphology and architecture, which have direct implications for competition between individual plants in a grazed grassland. This chapter also investigates the short-term changes in root exudation and effects on the soil microbiota. The effects of grazing on below-ground plant properties and soil microbiota are important in understanding how sustainable a system is or how likely it is to change with altered grazing pressure.

Plant Root System Responses to Defoliation

Root biomass as affected by defoliation

It has long been recognized that regular defoliation can alter root biomass and distribution. In general, root mass has been shown to reduce with defoliation (Ennik and Hofman, 1983; Holland and Detling, 1990; Matthew *et al.*, 1991). A reduction in root biomass with increasing defoliation intensity has been found in grasses from several environments, from temperate grasslands (Mawdsley and Bardgett, 1997) to semi-arid environments (McNaughton *et al.*, 1983; Ruess, 1988; Seagle *et al.*, 1992). As well as root biomass being affected by defoliation, root length and elongation rate have been shown to be reduced by defoliation (Evans, 1971; Brouwer, 1983; Ennik and Hofman, 1983; Richards, 1984; Jarvis and Macduff, 1989; Matthew *et al.*, 1991).

Root mass reduction can be related to the intensity and frequency of defoliation (Ennik and Hofman, 1983; Danckwerts and Gordon, 1987; Karl and Doescher, 1991; Wilsey, 1996). In prairie grassland, Holland and Detling (1990) studied a grazing chronosequence and found root biomass decreased in relation to increased grazing impact; they attributed this to a reduced allocation of carbon to the root system, although they did not assess the role of rhizodeposition or root turnover. However, contrasting responses have been found. For example, Milchunas and Lauenroth (1993), from data analysed and modelled in their study of the effects of grazing, found that, while differences in above-ground net primary productivity with grazing were related to differences in species composition, differences in root mass between grazed and ungrazed sites were not related to differences in above-ground net primary productivity. Negative impacts of grazing on above-ground net primary productivity were accompanied by both increases and decreases in root mass. McNaughton *et al.* (1998) found no evidence that grazing inhibited root biomass or productivity in Serengeti grasslands, where water is the major limitation for growth. In the field, the response of plants to grazing can be affected by other factors, such as light, nutrients, temperatures and water (McNaughton, 1979). As a consequence of these many interrelated factors operating in the field, studies on the physiology of individual grass species under controlled conditions need to be conducted to allow an understanding of these interacting responses.

Species, herbivore and fertility interactions

Within a grazed sward, there can be many individual species, heterogeneously distributed, which differ in size, age, growth rate and reproductive capacity (Bullock, 1996). They also present contrasting preferences to the grazing animal, as shown by Fraser and Gordon (1997).

Different species and varieties (Jones, 1983) and genotypes (Harris, 1973) can show contrasting above-ground morphological adaptations to variations in cutting height and frequency. Plants grazed frequently can develop a short, prostrate canopy, which can be more resistant to grazing if less biomass is available to herbivores, and a greater amount of photosynthetic and meristematic tissue remains available for regrowth following defoliation. Under increasing grazing pressure, pasture mass decreases and the grass structure changes to a high density of smaller tillers per unit area of pasture (Grant *et al.*, 1983). As well as this grazing avoidance behaviour, plants can also exhibit grazing tolerance, e.g. storage of reserves, compensatory photosynthesis and increased nutrient uptake (Rosenthal and Kotanen, 1994). It has been suggested that grasslands with a long history of grazing tend to be dominated by grazing-tolerant species (Milchunas *et al.*, 1988). In grazing-intolerant plants with relatively weak shoot meristematic activity after defoliation, it has been suggested that the proportion of carbon resources allocated to roots is higher than in tolerant species (Richards, 1993). Root growth reductions might be a mechanism to reduce below-ground carbon demand in defoliated plants, allowing greater allocation of carbon to the shoot (Richards, 1984). Also related to this is an increased nutrient absorption capacity in defoliated plants (Rosenthal and Kotanen, 1994). However, this may not be sufficient to compensate for losses when soil nutrient availability is low (Chapin and McNaughton, 1989).

Individual species responses

Root biomass

In order to try to understand the contrasting responses to grazing found in mixed pastures, an experiment was conducted in a greenhouse on monocultures of five grass species found on pastures ranging in intensity of management from unimproved to improved by the addition of lime and fertilizer. The species *Festuca ovina, F. rubra, Agrostis capillaris*, *Poa trivialis* and *Lolium perenne* were subjected to three clipping treatments for a total of 1 year; unclipped (UC), clipped every week to 4 cm from the stem base (WC) and clipped every 8 weeks to 4 cm from the stem base (IC). For all species, clipping each week removed a significant amount of leaf material, thereby having a direct impact on the plant (Fig. 4.2). In general, clipping reduced root biomass, particularly for the slower-growing species *F. ovina, F. rubra* and *A. capillaris* (Fig. 4.2). In contrast, however, defoliation had no significant effect on the root biomass of *P. trivialis*, a species found in productive pastures. For *L. perenne*, a species found on improved pastures, weekly clipping (WC) significantly reduced root biomass relative to the less intensive defoliation (IC), but not relative to the uncut treatment (UC). Deinum (1985) found that the root biomass of *L. perenne* was greater where only parts of the foliage were removed periodically, in contrast to where defoliation was frequent and complete. These results illustrate the importance of considering intensity and frequency of defoliation when investigating physiological responses to defoliation. Another aspect is the cutting treatment used to simulate herbivory in the field. It is very difficult to make comparisons between studies where plants have been defoliated in different ways. For example, a constant grazing height was used in this study of British pasture grasses, but the contrasting vertical distribution of plant parts and the species grazing preference that has been observed (Bakker *et al.*, 1998) throw some doubt on a constant sward height being the most appropriate simulation of defoliation under field conditions. This again illustrates the need for an integrated approach in the understanding of grazing effects.

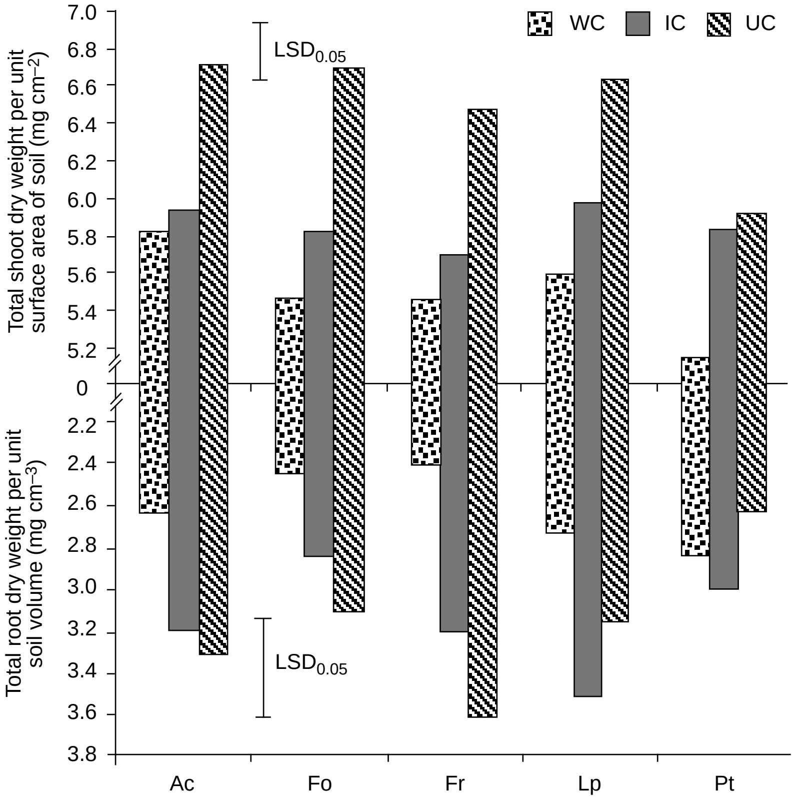


Fig. 4.2. Shoot biomass per surface area of ground (mg cm^{-2}) and root biomass per volume of soil (mg cm^{-3}) of five grass species, Ac (*Agrostis capillaris*), Fo (*Festuca ovina*), Fr (*Festuca rubra*), Lp (*Lolium perenne*) and Pt (*Poa trivialis*). Plants had been grown for 1 year from seed and given one of three defoliation treatments: unclipped (UC), weekly clipped (WC) and clipped every 8 weeks (IC), both to 4 cm from the stem base. LSD, least significant difference.

Genotypic responses

Responses to defoliation can also vary within a species. For example, Fig. 4.3 shows some results for two genotypes from a range of genotypes as an illustration of the contrasting responses to defoliation. Vegetative tillers of genotypes AC1 and AK5 of *A. capillaris* both showed a similar reduction in shoot biomass after five twice-weekly clippings to 4 cm above the stem base (Fig. 4.3a). Only genotype AK5 showed a significant reduction in root biomass with clipping (Fig. 4.3b), and only AC1 showed an increase in root-tip number and root length with clipping (Fig. 4.3c and d). Having established that significant differences exist in root responses between genotypes to defoliation, future studies will examine the importance and consequences of these responses for competition in a mixed population.

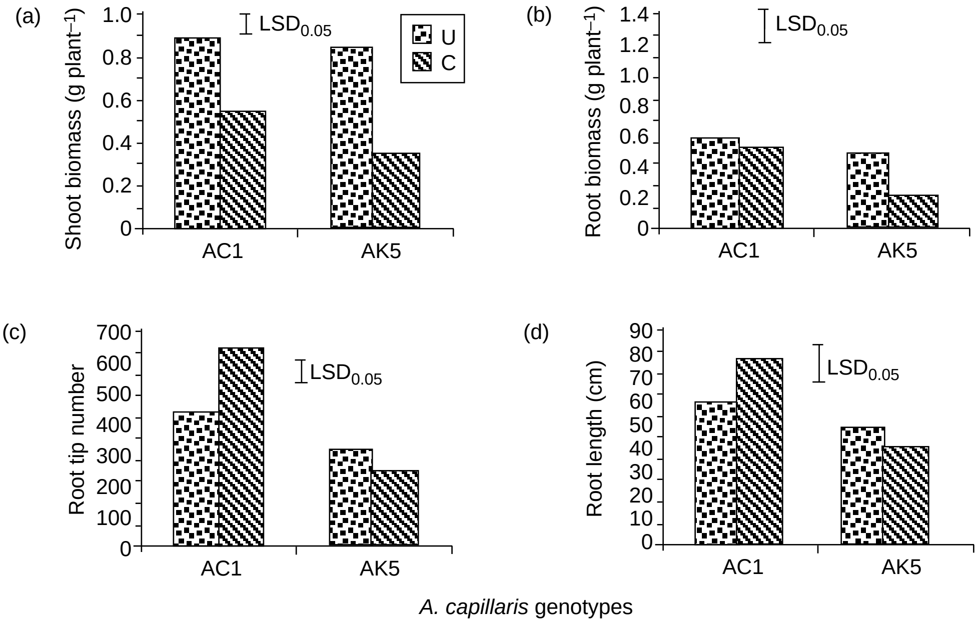


Fig. 4.3. Genotypic differences for shoot biomass (a), root biomass (b), root tip number (c) and root length (d) for uncut (U) and twice weekly cut (C) genotypes of *Agrostis capillaris,* ACI and AK5. LSD, least significant difference.

The number of root tips and branching characteristics could increase the ability, in the short term, to compete for nutrients, but, in the longer term, an ability to reallocate growth to the shoots would be a more beneficial characteristic. Richards (1984) found that, after clipping, root length extension was reduced by half in grazing-tolerant genotypes but not in grazing-intolerant species, as had been observed in the field.

Root distribution

The majority of grass roots can be found in the top 15 cm of soil in the field (Macklon *et al.*, 1994). In a study of three perennial grasses, *Cenchrus ciliaris*, *Digitaria cummutata* and *Stipa lagascae*, Chaieb *et al.* (1996) found that repeated clipping resulted in a reduced biomass and a more superficially distributed root system. This even greater than normal surface location of roots could expose the plant to water stress during summer drought. The same authors found that, with continual overgrazing (repeated cutting of all shoots to ground level), more than 65% of the roots of all three species were found in the top 15 cm of soil. However, when medium grazing was simulated (two to three cuttings), the root system was increasingly superficial for only one species.

Table 4.1. Percentage of total root biomass in the 0–6 cm soil zone. Mean values from five replicate pots and SE in parentheses. Five pasture species grown in miniswards for a period of 1 year. Defoliation treatments were weekly clipped (WC), clipped every 8 weeks (IC) and undefoliated (UC). LSD, least significant difference = 4.

	Grass species				
Clipping treatment	*Agrostis capillaris*	*Festuca ovina*	*Festuca rubra*	*Lolium perenne*	*Poa trivialis*
WC	40 (7)	36 (2)	48 (4)	55 (8)	77 (5)
IC	60 (7)	47 (6)	65 (4)	64 (5)	68 (6)
UC	53 (6)	52 (5)	66 (4)	52 (5)	67 (3)
Maximum depth of rooting (cm)	38	36	36	37	29

In our study of British pasture species (see Fig. 4.2), only one species, *P. trivialis*, showed an increase in the percentage of root biomass found in the surface soil with regular clipping (Table 4.1). *Poa trivialis* can be drought-sensitive (Grime *et al.*, 1988) and has a low persistence under close cutting, probably due to this increased surface root distribution. For the three slower-growing species, *F. rubra*, *F. ovina* and *A. capillaris*, the percentage of roots in the surface zone decreased with regular clipping.

Root diameter

In general, root diameter has been shown to be reduced by repeated defoliation (Table 4.2; Evans, 1971; Chapin and Slack, 1979; Chapin, 1980), but Arredondo and Johnson (1998) found that, with defoliation, diameter decreased in one grass species but increased in another. This response also depends upon N supply (Table 4.2).

Root architecture

In a study using a slant-board system, the effects of repeated defoliation on the root length, morphology and architecture of *L. perenne* and *F. ovina* were examined. In *L. perenne*, defoliation had no significant effect on the total root axis length, but the length of the primary axis increased significantly with defoliation under low N supply (Table 4.2a). In contrast, for *F. ovina*, the slower-growing species, root length was inhibited by defoliation (Table 4.2b), mainly manifested by a reduction in the length of first-order laterals at both N levels. The proportion of total root length as first-order laterals and the total number of links were significantly reduced by defoliation. The low-N undefoliated *F. ovina* root system, where the carbon-to-nitrogen ratio was highest, represents a lower topological index, which would increase total resource transport efficiency (Fitter, 1985,

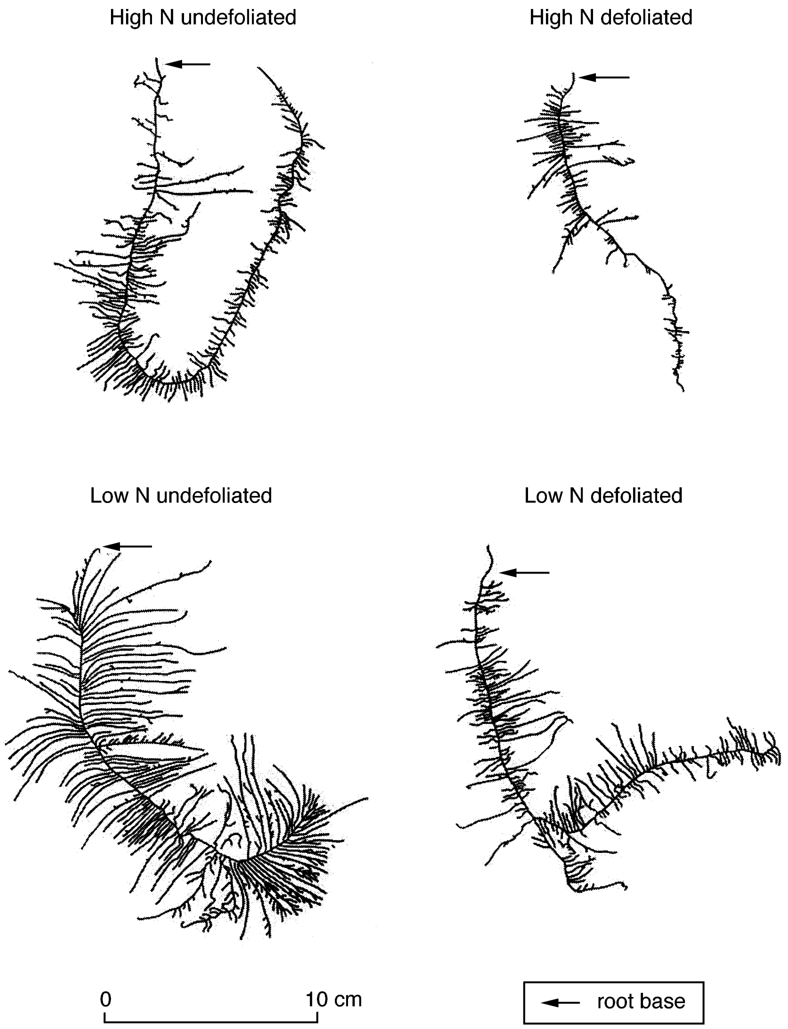
Table 4.2. Topological analysis of root axes of *Lolium perenne* (a) at day 14 and *Festuca ovina* (b) at day 28, either defoliated twice weekly (D) or undefoliated (U) and either grown under high-N (HN) (2.0 mM NH_4NO_3) or low-N (LN) 0.02 mM NH_4NO_3) nutrition. Least significant difference (LSD); $P < 0.05$.

	Treatments (mean)					
	UHN	DHN	ULN	DLN	LSD_1	LSD_2
(a) *Lolium perenne*						
Total root length (mm)	2720	1736	2053	3067	2163	2761
Primary root axis length (mm)	266	372	343	512	118	133
First-order lateral length (mm)	2241	1325	1661	2421	1930	2462
Root fresh weight (mg)	137	76	111	119	62	51
Log altitude/log magnitude	0.95	0.99	0.99	0.98	0.05	0.06
Root diameter (mm)	306	225	259	217	41	37
(b) *Festuca ovina*						
Total root length (mm)	2677	903	3816	1529	1549	1760
Primary root axis length (mm)	303	203	252	232	78	67
First-order lateral length (mm)	2235	670	3091	1178	1308	1473
Root fresh weight (mg)	101	33	89	48	39	44
Log altitude/log magnitude	0.97	0.98	0.92	0.98	0.05	0.06
Root diameter (mm)	217	151	127	144	34	24

LSD_1 when comparing effect of N at same level of defoliation.
LSD_2 when comparing effect of defoliation at same level of N.

1986, 1987). This increased branching has also been observed in relation to elevated CO_2 (Berntson and Woodward, 1992). Under low-N conditions with defoliation, the root system of *F. rubra* was less branched, reflecting the reduced propensity to branch when carbon was limited due to shoot defoliation (Fig. 4.4). In a study of the effects of clipping on seedlings of grasses, Arredondo and Johnson (1998), found that the root branching of 'Hycrest', a cultivar of hybrid crested couch grass (*Agropyron desertorum* (Fisch. ex Link) Schult. × *Agropyron cristatum* (L.) Gaert.), which is grazing-tolerant, was unaffected. In contrast, defoliation significantly increased the number of second-order laterals in 'Whitmar', a cultivar of bluebunch couch grass (*Pseudoroegneria spicata* (Pursh) A. Löve), which is grazing-sensitive. In a later study, they found that the largest plasticity in root architecture was observed for 'Whitmar' for defoliated and undefoliated plants, and suggested this plasticity as the main mechanism allowing it to forage in heterogeneous soil conditions (Arredondo and Johnson, 1999).

Specific architectural responses to defoliation have also been found among species for arid-zone perennials (Hodgkinson and Baas Becking, 1977). For *Danthonia caespitosa*, root branching was reduced with defoliation, and this caused it to be susceptible to drought. The root system of *Medicago sativa*, on the other hand, was little affected by defoliation, which the authors attribute to the reserve


High N undefoliated

High N defoliated

Low N undefoliated

Low N defoliated

Fig. 4.4. The effect of repeated defoliation for 28 days under contrasting levels of nitrogen supply (High N – 2.0 mM NH_4NO_3, and low N – 0.02 mM NH_4NO_3) on the branching characteristics of root axes of *Festuca ovina.*

organic compounds in the tap root (Hodgkinson, 1969) and early resumption of current photosynthate supply to the lateral roots, thus allowing *Medicago* to tolerate drought conditions. When assessing contrasting species responses to defoliation, the contribution of the tap root and other structural compartments needs also to be considered.

Some workers have reported that there is, following grazing, a short-term storage of carbon in roots, allowing a rapid mobilization of carbon (Dyer *et al.*, 1991; Holland *et al*., 1996), and of other nutrients (Polly and Detling, 1989) for plant regrowth. However, other workers, e.g. Oesterheld and McNaughton (1988), have suggested that root reserves do not contribute significantly to plant regrowth, although this reliance is very much species-dependent. For a more detailed appraisal of this, see Thornton *et al.* (Chapter 5, this volume). The arguments that, in grazing-tolerant species, reduction in root growth represents an adaptation for rapid regrowth of shoots (Richards, 1984) may not always be valid. As can be seen, a rapid reduction in root growth is not always advantageous, and all aspects of root morphology, distribution and architecture need to be considered. These results highlight the difficulty in making generalizations at the mixed-sward level about the effects of defoliation on root characteristics. Species and genotype composition in a sward and its interaction with defoliation intensity and frequency and soil fertility need to be considered more fully.

Mycorrhizae

Grass roots form arbuscular mycorrhizae in most natural and agricultural ecosystems (Newman and Reddell, 1987), and consequently the effect of defoliation on the mycorrhizal symbiosis is of concern. Much of the research has been in the field with moderate defoliation treatments and has tended to show no effect (Wallace, 1987; Allen *et al*., 1989). Other studies have shown a decrease in arbuscular mycorrhizal colonization under heavy grazing (Bethlenfalvay and Dakessian, 1984). In a study of three perennial grasses, of similar morphology, Allsopp (1998) found that in *Digitaria eriantha* and *L. perenne* mycorrhizal infection was reduced by defoliation, but hyphal densities were not. In contrast, in *Themeda triandra*, which is a species intolerant of heavy grazing, defoliation severely affected plant regrowth, P accumulation, arbuscular colonization and external hyphal production. Allsopp (1998) suggested that in some grass species, such as *Digitaria* and *Lolium*, an external hyphal network may help compensate for the loss of root mass due to defoliation.

Root dynamics

The effects of grazing on fine root growth and dynamics have been identified as a crucial link in understanding herbivore interactions within carbon and nutrient cycling processes (Holland and Detling, 1990; Pregitzer *et al*., 1993; Ruess *et al*., 1998). Immediately after defoliation, rapid and extensive root death can occur (Evans, 1971; Hodgkinson and Baas Becking, 1977; Allsopp, 1998). However, as it is difficult to extract and distinguish roots that are actively growing from those that are inactive or dead, many studies have ignored this distinction. Also, root biomass can be a poor reflection of below-ground growth, as root production and root mortality occur simultaneously. To complete the picture on the effects of grazing on roots, the dynamics of root growth also has to be considered. In a sward box study by the authors on *A. capillaris*, regular defoliation reduced root biomass density and also increased the percentage of necromass (Table 4.3), agreeing with

Table 4.3. Effect of regular defoliation twice weekly (RC) and uncut (UC) for 3 months on root weight density and percentage necromass in a sward box experiment of *Agrostis capillaris*. Analysis of variance on untransformed data, with $n = 3$.

	Treatment mean		
	RC	UC	$LSD_{0.05}$
Dry weight density ($mg\ cm^{-3}$) in 0–15 cm zone	0.37	1.47	0.58
% necromass in 0–5 cm zone	17.6	8.3	5.1

LSD, least significant difference.

results in the field, where heavy grazing increased the dead root mass on mixed-grass steppes (van der Maarel and Titlyanova, 1989). This increase in proportion of dead root material could act as a resource for decomposer organisms, potentially change microorganism community structure and act as a subsequent source of nutrients for plant growth.

Carbon Flow in the Rhizosphere

Roots release a broad range of organic compounds to the soil, which are utilized as substrates by rhizosphere microorganisms. These organic inputs to soil comprise exudates (primarily sugars, amino acids and organic acids), secretions (including enzymes and metallophores), lysates and sloughed-off cells, collectively termed rhizodeposition. The amount and relative proportions of rhizodeposition components vary dependent on a host of factors, including plant species, developmental stage, climatic conditions and availability of nutrients and water in the soil matrix (Kraffczyk *et al.*, 1984; Meharg and Killham, 1988; Grayston *et al.*, 1996; Paterson *et al.*, 1997). In particular, factors affecting the balance of plant partitioning of resources, such as defoliation and soil mineral nutrient availability, strongly affect the process of rhizodeposition. Therefore defoliation is a factor which affects C input to soil and, consequently, the coupling of plant productivity to microbial activity and soil nutrient cycling. To understand the effects of grazing on microbial communities and consequently on nutrient cycling, it is necessary to determine the quantitative and qualitative impacts of grazing on rhizodeposition.

Partial shoot defoliation has been found to result in increased release of organic compounds from roots, in particular, the low-molecular-weight soluble exudates (Hamlen *et al.*, 1972; Bokhari and Singh, 1974; Dyer and Bokhari, 1976; Holland *et al.*, 1996). Increased rhizodeposition of sugars and amino acids would be expected to stimulate microbial activity in the rhizosphere, and this mecha-

Table 4.4. Effect of defoliation (weekly to 4 cm) and N supply (2 mM (High N) or 0.01 mM (Low N) NH_4NO_3) on root growth and rhizodeposition of *Lolium perenne* and *Festuca rubra* grown for 36 days in percolated axenic sand culture systems. Results are means of six replicates ± standard errors.

		Total root length (m)	Specific root length ($m\ g^{-1}$)	Cumulative rhizodeposition (% plant net C assimilate)*
High N	*L. perenne* non-defoliated	17.7 ± 3.6	69.3 ± 4.9	0.81 ± 0.15
	L. perenne defoliated	13.7 ± 1.8	77.1 ± 11.4	1.83 ± 0.60
	F. rubra non-defoliated	12.7 ±1.8	108.1 ± 10.8	1.7 ± 0.18
	F. rubra defoliated	9.7 ± 1.3	123.6 ± 8.2	4.1 ± 0.52
Low N	*L. perenne* non-defoliated	11.0 ± 1.2	229.8 ± 11.5	40.1 ± 1.4
	L. perenne defoliated	11.3 ± 1.2	222.4 ± 15.0	44.1 ± 2.5
	F. rubra non-defoliated	8.1 ± 0.7	198.2 ± 22.1	12.2 ± 0.91
	F. rubra defoliated	6.2 ± 0.3	247.5 ± 27.3	18.3 ± 1.27

*Net plant assimilate was calculated as the amount of C in the plant biomass at harvest plus the amount of C collected as rhizodeposition throughout the growth period.

nism has been invoked to explain increased microbial activity in grazed systems (Bardgett *et al.*, 1998). Increased rhizodeposition following defoliation has been suggested to be a consequence of increased partitioning of assimilate below ground, as a means of grazing tolerance (Bardgett *et al.*, 1998). The correlation of increased assimilate allocation to roots with increased rhizodeposition following defoliation has been demonstrated for several species (Holland *et al.*, 1996; Hamlen *et al.*, 1972). However, as stated earlier, it is more common for grasses to have a net export of carbon to support shoot regrowth (Miller and Rose, 1992; Thornton *et al.*, Chapter 5, this volume). Despite this, rhizodeposition from grasses has also been found to increase following defoliation (Bokhari and Singh, 1974). Paterson and Sim (1999) found transient (1–2-day) increases in release of organic compounds from roots of *L. perenne* and *F. rubra* following defoliations at weekly intervals, at both high and low N supply (Table 4.4).

The physiological bases for increased rhizodeposition from grasses following defoliation have yet to be elucidated. Several possible mechanisms merit further investigation: (i) degradation of C and N storage compounds in roots during remobilization may transiently increase the concentrations of sugars and amino acids, promoting diffusive release of these exudates; (ii) defoliation reduces the energy status of roots (Ofosubudu *et al.*, 1995), and this may perturb the reuptake of root-released organic compounds (Mühling *et al.*, 1993), increasing net exudation; and (iii) the physical damage caused by defoliation may initiate an electrical action or slow wave potential propagated through the plant, which is capable of depolarizing root transmembrane potentials (Stahlberg and Cosgrove, 1996; Stankovic *et al.*, 1998). Such depolarization would remove chemipotential gradients (primarily of H^+) required to energize reuptake of rhizodeposits (Mühling *et al.*, 1993).

As discussed in previous sections, mineral nitrogen supply strongly affects assimilate allocation in grasses and also the quantity of rhizodeposition, with release of organic compounds generally increasing with reduced N supply (Bowen, 1969; Hodge *et al.*, 1996). For *L. perenne* and *F. rubra*, low N supply significantly increased the proportion of plant-assimilated C released through rhizodeposition (Table 4.4). The effect of N supply on rhizodeposition was greater for *L. perenne*, with cumulative release of 5.8 ± 0.6 and 16.6 ± 1.2 mg C during the first 36 days of growth of non-defoliated plants at high and low N, respectively. As biomass accumulation was greatly reduced at low N, rhizodeposition as a proportion of the plant C budget increased from 0.81% at high N to 40.1% at low N, for non-defoliated plants (Table 4.4). Low N supply also increased the proportion of plant C released by roots of *F. rubra*, from 1.7 to 12.2% of plant-assimilated C, for high and low N, respectively. However, this effect was less than for *L. perenne*, and for *F. rubra* absolute amounts released from the smaller plants at low N were not significantly greater than those from plants grown at high N. For both species, an increased release of plant C as rhizodeposition at low N supply was concurrent with an increased specific root length, associated with optimization of biomass investment for nutrient capture. Increased root length relative to root mass has been found previously to increase the proportion of plant C that is released through rhizodeposition (Xu and Juma, 1994). Increased rhizodeposition from the finer roots produced under nutrient limitation may provide a means by which N cycling and returns to the plant are increased via the microbial loop (Clarholm, 1985).

Grazing Effects on Soil Microorganisms

As grazing systems become more extensive, plant growth and competition become more dependent on the use of available soil resources. Interactions between roots and associated microorganisms, mediated by rhizodeposition, will be central to our understanding of fluxes to and from plant-available carbon pools. As carbon is the main driving force for microbial activity in the soil, variations in the quantity and quality of root and shoot material and plant root exudates may result in the selection of microorganisms specific to the rhizosphere of individual plant species (Grayston *et al.*, 1996). Impacts on microbial community size, activity and diversity would affect nutrient availability and thus plant species competition.

In upland grassland, the size of the soil microbial community is commonly found to be greater under low-fertility than under high-fertility conditions (Bardgett *et al.*, 1993, 1996, 1997; Grayston *et al.*, 2000), closely related to trends in root biomass observed in the field. Using the National Vegetation Classification (NVC), gradients of grassland types were chosen in ten different biogeographical areas of the UK. These ranged from improved, intensively managed *Lolium–Cynosurus* grassland (NVC – MG6), through semi-improved *Festuca–Agrostis–Galium* grasslands, *Holcus–Trifolium* subcommunity (NVC – U4b), to unimproved, extensive *Festuca–Agrostis–Galium* grassland (NVC – U4a)

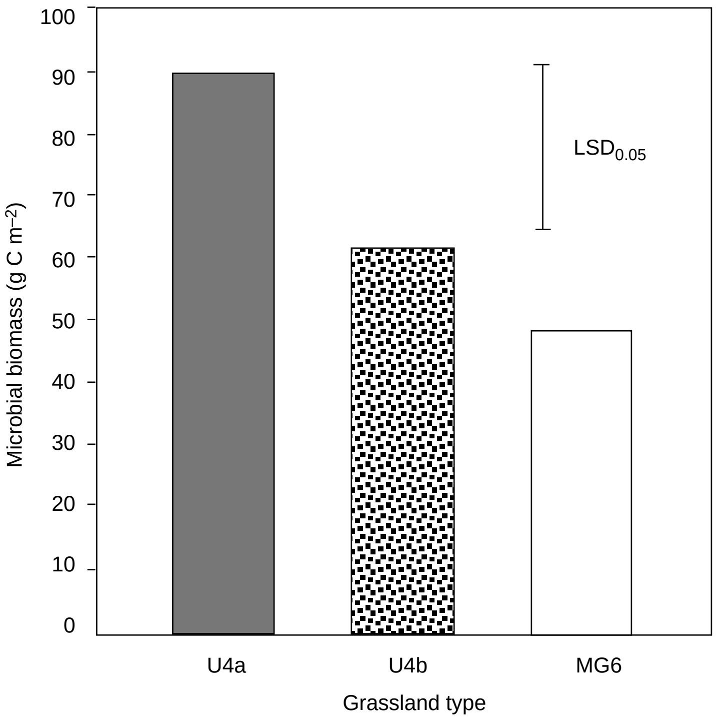


Fig. 4.5. Microbial biomass measured using fumigation technique in unimproved (U4a), semi-improved (U4b) and improved (MG6) grasslands, across ten sites in the UK. LSD, least significant difference.

(Grayston *et al.*, 2000). Soil microbial biomass increased as the soil fertility decreased, moving from improved to unimproved grasslands (Fig. 4.5). This was accompanied by a shift in microbial community structure, with an increase in the proportion of fungi to bacteria in the unimproved grasslands (Grayston *et al.*, 2000). These changes in microbial community structure under varying fertility levels have been recorded in other grassland studies (Bardgett *et al.*, 1993, 1996, 1998). Quantitative and qualitative differences in rhizodeposition, due to variation in the plant species, growth rate, root biomass, root architecture and variation in litter and root turnover, are all likely to have had an impact on the microbial communities in these grasslands (Grayston *et al.*, 1998a). For example, clover, which is found in improved grasslands, has a greater exudation rate than grasses (Martin, 1971). The carbon released as exudates in improved grasslands may be readily decomposable substrates, part of the 'fast pool' of carbon, resulting in preferential stimulation of bacterial growth. In contrast, unimproved grasslands contain more recalcitrant compounds, which are the preferred substrates of fungi (Grayston *et al.*, 2000). The use of community-level physiological profiles (CLPP) to characterize microbial communities based on their metabolic profiles (Grayston

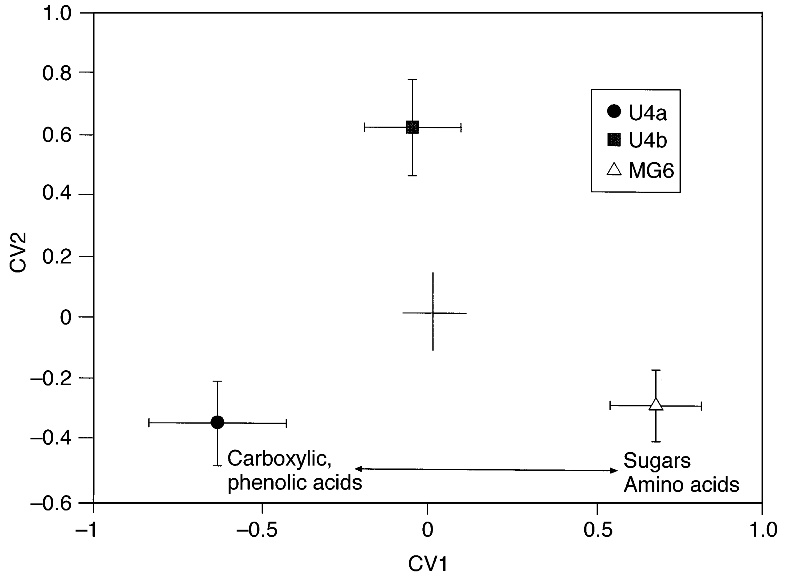


Fig. 4.6. Canonical variate analysis of metabolic profiles of microbial communities from unimproved (U4a), semi-improved (U4b) and improved (MG6) grasslands (bars are SE).

and Campbell, 1996; Grayston *et al.*, 1998a) and as a possible indicator of carbon source availability in the rhizosphere (Grayston *et al.*, 1998b) supports the above hypotheses. Microbial communities from improved grasslands have greater utilization of sugars and amino acids, whereas those from unimproved grasslands have greater utilization of phenolic and carboxylic acids (Fig. 4.6). This may reflect the greater exudation and growth rate of plant species in improved grasslands and the higher organic matter (phenolic acid) content of unimproved grassland (Grayston *et al.*, 2000).

The root turnover rates of contrasting species found in pastures of different fertility and productivity could also help us to understand carbon and nutrient cycling in grassland ecosystems (Caldwell, 1979). In a study by Schläpfer and Ryser (1996), the root turnover of the faster-growing species (*A. elatius*) was faster than that of the slow-growing species characteristic of nutrient-poor grasslands (*Bromus erectus*). Associated with a faster turnover rate would be a greater input of decomposing roots into the soil, thus providing more substrate for bacterial populations to flourish in. This has been suggested as being part of an efficient nutrient conservation strategy in slow-growing species, which helps to explain the long-term success of slow-growing species at low nutrient supply (Grime, 1977; Berendse and Aerts, 1984). It has also been suggested that fast-growing species in general contain less lignin and hemicellulose and more organic N compounds than slow-growing species (Poorter and Bergkotte, 1992; van Arendonk and Poorter, 1994), thereby providing a faster litter decomposition rate in the faster-

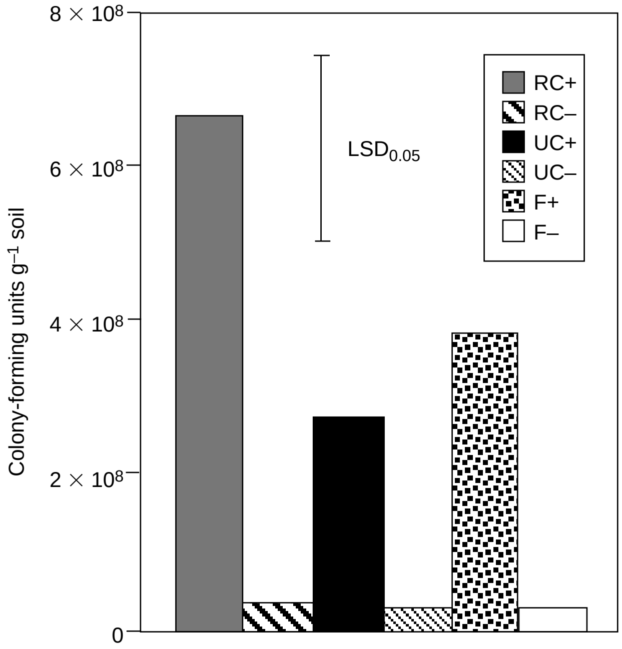


Fig. 4.7. Populations of bacteria (colony-forming units) in the rhizosphere of *Agrostis capillaris* subject to twice-weekly defoliation (RC), or left uncut (UC) and in fallow (F) soil, and in the presence (+) or absence (−) of simulated urine addition, 7 days after urine application. LSD, least significant difference.

growing species (Pastor *et al.*, 1987; Enriquez *et al.*, 1993). The quality of the plant litter, including leaf material, and its relation to the soil microbiota are another important consideration when trying to understand the many interactions observed in the field, as has been discussed in Bardgett *et al.* (1998).

Changes in microbial community structure can also be related to input directly from the grazing animal, which may also account for the differences in communities between grassland types. As improved grasslands typically support more grazing animals than unimproved grasslands, grazing will increase soil nutrient availability, due to increased direct inputs from animal excreta, which will favour bacterial growth. The equivalent of 510 kg N ha^{-1} can be deposited within a single urine patch by sheep (Thomas *et al.*, 1988). This can increase soil heterogeneity and create patches with higher levels of soil and plant N than surrounding areas (Ledgard *et al.*, 1982), increase rates of nutrient cycling (Floate, 1981) and change species composition (Marriott *et al.*, 1987). Scorching is common in urine patches (Floate, 1981) and has been attributed to root death from exposure to NH_3 (Richards and Wolton, 1975). In the experiment described in Table 4.3, a single application of artificial urine accelerated root death in the undefoliated treatment, with 50% of roots disappearing within 8 days of urine deposition, compared with 13 days without ($P < 0.05$). In the 0–15 cm zone of the soil, 15.5% of the roots were dead where

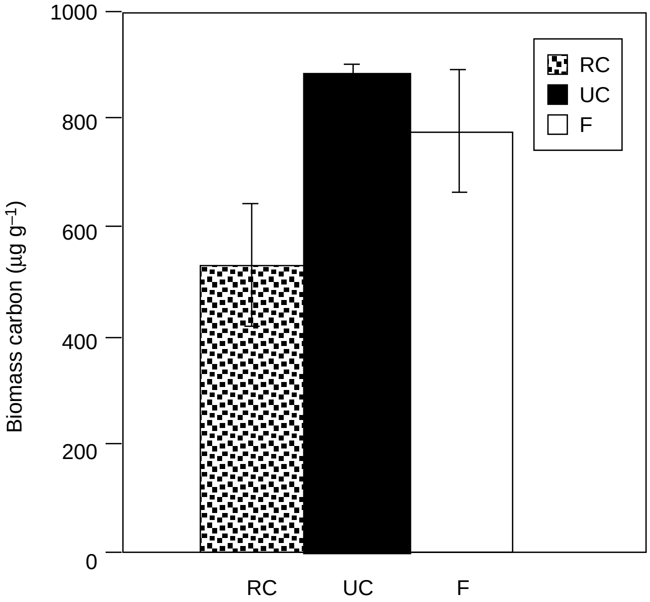


Fig. 4.8. Microbial biomass measured using fumigation technique in the rhizosphere of *Agrostis capillaris* subject to either regular defoliation twice weekly (RC), or left undefoliated (UC) and in fallow (F) soil 2 months after the start of defoliation (bars are SE).

urine had been applied, in contrast to 6.8% in the no-urine treatment ($P < 0.05$). The application of urine stimulated growth of culturable soil bacterial communities (Fig. 4.7), which could be related to this accelerated root death or to a rapid rise in soil pH after urine application, which favours bacterial growth (B.L. Williams, 1999, unpublished results). The application of artificial urine significantly decreased total fungal communities ($P < 0.05$) but stimulated soil bacterial communities. In this same study, regular defoliation decreased the total soil microbial biomass (Fig. 4.8), which was positively correlated with root biomass (see Table 4.3), while defoliation significantly increased the bacterial population only in the presence of urine (see Fig. 4.7). These results illustrate both the direct and the indirect effects of urine and defoliation as individual factors in shifting the community structure of the microbiota. The size of the microbial biomass appears to be related to resource availability, i.e. root biomass, whereas the microbial structure appears to be related to the quality of the resource, i.e. exudate quality and inputs from the grazing animal.

Conclusions

Pasture systems have diverse and dynamic plant communities, consisting of many species, which can respond in contrasting ways to defoliation and urine deposition. To be able to understand and predict change in these communities through time, species selectivity by the grazing animal and species-specific responses, both above and below ground, need to be considered together in multidisciplinary projects. Grazing animals not only shape the above-ground biomass that they feed on but also both directly and indirectly affect the roots and soil microbial communities below ground through factors such as defoliation and urine deposition. Information on the many interactions between plants and their associated microbiota will be essential to our understanding of the grazed ecosystem and how it will respond to change in management inputs. This chapter stresses the importance of considering responses at the whole-plant level in terms of the nutrient and carbon dynamics of the root system, of rhizodeposition and of their relationships with the associated soil microbiota. It also highlights the need for a multidisciplinary approach to the understanding of such a multifaceted system. It will be only through such an approach that a true understanding of the effects of manipulating animal densities on the hills and uplands can be made.

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