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Integrating below-ground ecology into sustainable grassland management

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Key points

1. Grasslands produce soils that sustain an abundant and diverse soil food web, providing tremendous opportunity for below-ground interactions to influence nutrient cycling processes and plant production.
2. Fast developing areas of ecological science offer scope to harness positive outcomes of below-ground ecology for enhancing efficient cycling of nutrients in sustainable grassland systems.

Keywords: nitrogen cycling, soil biota, organic nitrogen, mycorrhizal fungi, soil microbes, grazing animals, root exudation

Introduction

Grasslands, including steppes, savannas, and prairies, are important terrestrial ecosystems covering about a quarter of Earth's land surface. The development of agriculture has been very closely linked to these grasslands, and they now form the backbone of the global ruminant livestock industry, completely dominating the landscape of many parts of the world. In recent years, the nature of grassland agriculture in many parts of the world has started to change. Until recently, the drive was to maximise production through the use of large amounts of fertiliser and nitrogen (N) responsive grasses. Now, the need to develop sustainable management strategies that encourage efficient nutrient cycling, thereby minimising the use of fertilisers, has come to the fore. This has largely been driven by agricultural policy aimed at cutting fertiliser use to reduce nutrient losses to air and water, and also to help restore botanical diversity to species-poor agriculturally improved grassland. There is also an increasing drive towards organic production systems, which rely entirely on biological processes of nutrient cycling to meet crop demand. Collectively, these demands highlight the urgent need to develop management strategies for grassland that are directed at encouraging a greater reliance on natural ecological processes, rather than on the input of artificial inputs such as fertilisers.

Grassland lends itself well to management for natural processes of nutrient cycling. This is because they build soil systems that are very different from those of other vegetation types; their high turnover of shoot and root biomass creates a large pool of labile organic matter at the soil surface, and heavy herbivore loads result in large amounts of organic matter being returned to soil as animal waste, which is nutrient replete. These features combine to produce a soil environment that sustains an abundant and diverse soil food web, the main agent of efficient nutrient cycling; hence, there is a tremendous opportunity for soil organisms and their interactions with plants, and their consumers, to influence nutrient cycling processes and plant production. This is what this paper is concerned with: illustrating, using selected examples, how an understanding of ecological interactions between plants and soil biota can be harnessed to promote efficient nutrient cycling and sustainable management in agricultural grassland. I will use three examples from rapidly developing areas of research to demonstrate this. First, I will consider recent developments in the area of plant nutrition that reveal the potential for grassland plants to use organic N forms, as opposed to a complete reliance on

mineral N. Second, I will discuss recent studies that show intimate links between grazers, plants, and soil microbes, which have important consequences for plant production in grazed grassland. Finally, I will consider research that reveals how management of grassland can be altered to maximise soil biodiversity, especially the fungal component of soils, with associated benefits for plant communities. The examples that I use have not yet been integrated into grassland management; the aim here is to illustrate how knowledge of these ecological interactions might be harnessed in sustainable management.

Case 1: A role for organic nitrogen in grassland systems

Historically, a central assumption of terrestrial nutrient cycles was that for soil N to be available for plant uptake it needs to be in an inorganic form. A growing body of evidence now challenges this view, pointing to the importance of dissolved organic nitrogen (DON) in the form of amino acids for plant nutrition. This is especially the case in strongly N limited ecosystems, such as alpine and arctic tundra, where studies reveal that plants can take up amino acids directly, by-passing the need for microbial mineralisation to produce simpler inorganic N forms (Chapin *et al.*, 1993; Kielland, 1994; Schimel & Chapin, 1996; Lipson & Monson, 1998; Raab *et al.*, 1999; Henry & Jefferies, 2003a, b). This is especially significant since DON often represents the dominant form of soluble N in these ecosystems (Kielland, 1994; Jones & Kielland, 2002), thereby providing a previously unrecognised source of N for plant growth.

Whilst most research in this area has focussed on natural ecosystems, recent work reveals that DON may also be of significance for plant nutrition in agricultural settings. There are two lines of evidence to support this. First, studies of temperate grassland reveal that amino acids can reach significant concentrations in soil, sometimes reaching equal abundance to mineral N (Bardgett *et al.*, 2003). Second, studies done under both laboratory and field conditions show that grassland plants have the potential to take-up amino acids from soil directly, as in natural settings (Näsholm *et al.*, 2000; Streeter *et al.*, 2000; Bardgett *et al.*, 2003; Weigelt *et al.*, 2005). This is not a straightforward issue, however. For example, it has also been argued that due to fast microbial turnover of organic N in agricultural soils, the main route for plant uptake of N is as mineral N after microbial mineralisation (Hodge *et al.*, 1998, 1999; Owen & Jones, 2001). That organic N uptake is of limited importance in agricultural situations is also evidenced by *in situ* measurements of N uptake by plants in temperate grasslands, which show that whilst glycine can be taken up directly by plants, microbial turnover and release of this N into the plant-soil system is the major pathway for N acquisition (Bardgett *et al.*, 2003). Despite this, field studies do reveal that amino acids could be of some significance for plant nutrition in low productivity, unfertilised grasslands where amino acids are relatively abundant in soil (Bardgett *et al.*, 2003). This implies, therefore, that there is potential for organic N use in certain situations; hence, the challenge is to identify these situations and management strategies that best optimise organic N availability in soil.

Understanding organic N cycling may also be of significance in other areas of grassland agriculture, especially in relation to promoting plant diversity. Whilst the capacity of plants to take up organic N directly appears to be ubiquitous, there is emerging evidence that plants vary in their capacity to take up different chemical forms of N, showing species-specific preferential uptake of either organic or inorganic N. So far, species-specific differences have been demonstrated most clearly in arctic tundra (McKane *et al.*, 2002) and in alpine communities (Miller & Bowman 2002, 2003). Studies of grassland plants also indicate a degree of preferential uptake of different forms of N by some species, albeit under laboratory

conditions (Weigelt *et al.*, 2005). These findings are potentially significant since the existence of species-level differences in the preference of plants to take up chemical forms of N could provide a mechanism for plants to efficiently partition a limited soil N pool, thereby facilitating species coexistence and the maintenance of plant diversity (McKane *et al.*, 2002) (Figure 1). The implication here, therefore, is that managing to promote diversity of N forms in soil could contribute to the maintenance of plant diversity, a key objective of sustainable grassland management. A similar model could also be envisaged for P, which similarly occurs in many forms in soil, both organic and inorganic (Turner *et al.*, 2004). It is important to stress, however, that evidence for this is still lacking and work is urgently needed to test the importance of resource partitioning for plant communities in both natural and agricultural settings.

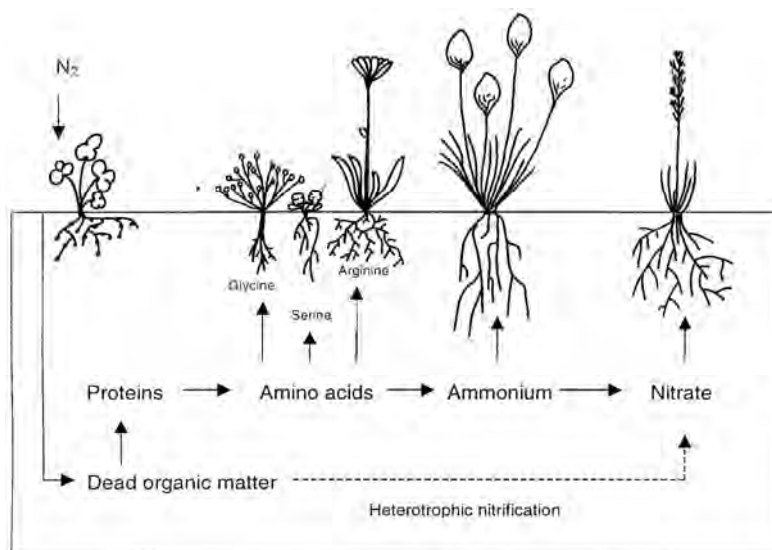


Figure 1 Schematic diagram showing how individual plant species might access different chemical forms of N enabling species to coexist in terrestrial ecosystems (redrawn from Bardgett, 2005)

The above studies all suggest that direct uptake of DON by plants could be of importance for nutrient cycling and vegetation structure in grassland, but especially in unfertilised grassland systems, which are the cornerstone of sustainable agriculture. However, there is still much more work to be done in this area. This point was recently emphasised by Jones *et al.* (2005) who argued that experimental approaches used to assess whether DON is important may be compromised because of the use of inappropriate methods for comparing and quantifying plant available inorganic and organic soil N pools. In addition, they argued that experiments aimed at quantifying plant DON capture, which typically use dual-labelled (N-15, C-13) organic N tracers, often do not consider important aspects such as isotope pool dilution, differences in organic and inorganic N pool turnover times, bi-directional DON flows at the soil-root interface, and the differential fate of the ^{15}N and ^{13}C in the tracer compounds. Based upon experimental evidence, they hypothesised that DON uptake from the soil may not contribute largely to N acquisition by plants but may instead be primarily involved in the recapture of DON previously lost during root exudation. In summary, the jury is still out and

further work is needed to establish the importance of amino acids as plant N acquisition pathway in grassland systems.

Case 2: Links between grazers, plants and soil microbes

Grazing animals are integral to grassland agriculture, and it has long been recognised that they can have important effects on both the productivity and vegetation composition of grassland (Bardgett & Wardle, 2003). However, only recently have ecologists started to consider how grazers can influence decomposer communities, and the consequences of this for grassland production and livestock carrying capacity. A central tenant of ecology is that grazers can actually increase plant production when at intermediate densities (McNaughton, 1985). This is especially the case in areas of high soil fertility, such as productive grassland ecosystems, where the phenomena is referred to as *compensatory growth* (De Mazancourt *et al.*, 1999). Various mechanisms have been proposed to explain this, especially the priming of soil nutrient cycling through the recycling of plant material as animal waste - which is nutrient replete - rather than through a plant litter pathway (Bardgett *et al.*, 1998). Recent studies, however, point to other mechanisms that involve soil microbes and roots that could be of high significance for sustainable management.

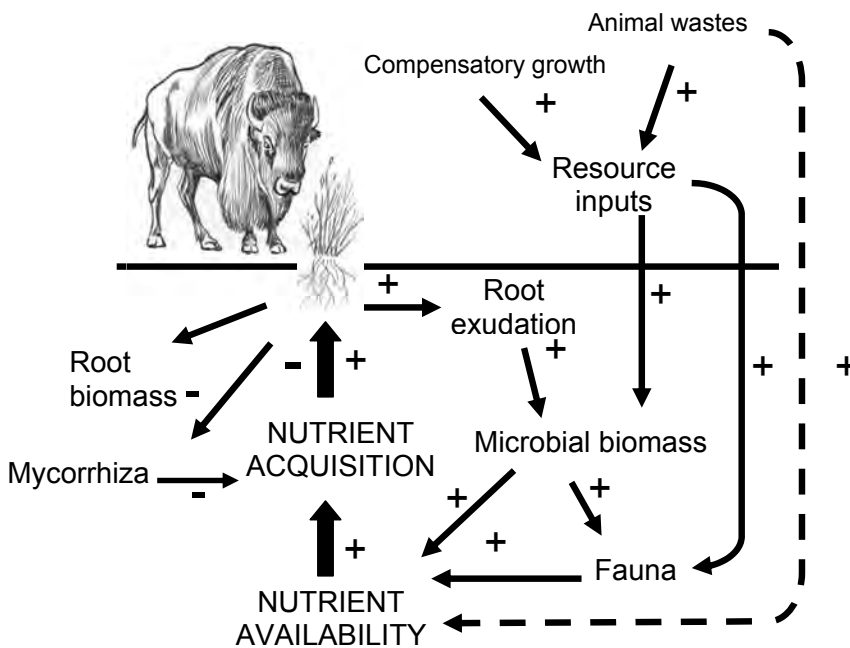


Figure 2 Schematic diagram of the effects of herbivory on producer-decomposer feedbacks in fertile grasslands that result from changes in the quantity of resources returned to the soil. These mechanisms are commonest in nutrient rich grasslands, where dominant plant species benefit from herbivory through positive feedbacks between herbivores, plants and soil biota, and through preventing colonisation by later successional plants that produce poorer litter quality (redrawn from Bardgett & Wardle, 2003).

It is well known that plants allocate large proportions of their assimilated C to root exudation, which may stimulate the growth and activity of heterotrophic microbes in the rhizosphere. A number of studies have shown that defoliation of grassland plants actually leads to short-term pulse of root exudation, which has the effect of stimulating microbial activity in the rhizosphere (Mawdsley & Bardgett, 1997; Guitian & Bardgett, 2000; Paterson & Sim, 1999; Murray *et al.*, 2004). In turn, this has been shown to also increase population densities of animals in the root zone that feed on microbes, such as bacterial and fungal-feeding nematodes (Mikola *et al.*, 2001, Hokka *et al.*, 2004). This is of relevance to sustainable agriculture because such positive effects of defoliation on rhizosphere organisms can feedback positively to the plant through enhanced soil N availability (Bardgett *et al.*, 1998). This was recently demonstrated by Hamilton & Frank (2001) who showed that simulated defoliation of the grazing tolerant grass *Poa pratensis* led to increased leaf photosynthesis and root exudation of recently assimilated ^{13}C , which stimulated microbial biomass in the root zone. This in turn increased soil N availability and plant N acquisition, which ultimately benefited plant growth. It was proposed that such mechanisms could explain, in part, the compensatory response of grasses to grazing in high fertility grasslands (Hamilton & Frank, 2001) (Figure 2). There does appear to be much inter-species variability in the response of plants to defoliation (Guitian & Bardgett, 2000, Hokka *et al.*, 2004). Also, responses are likely to vary with growth stage of the plant. However, what these findings collectively suggest is that physiological responses of plants to grazing have the potential to stimulate rhizosphere processes that ultimately feedback positively on plant nutrition and plant productivity (Bardgett & Wardle, 2003). Understanding the nature of such feedbacks between soil microbes, plants, and their consumers is clearly of high significance for sustainable grassland management, since nutrient cycling processes in unfertilised grasslands will be in part reliant on them. The challenge is thus to encourage such positive feedback mechanisms in sustainable grassland systems.

Case 3: Managing grassland to promote linkages between soil and plant diversity

The final example that I wish to consider is the potential for soil biodiversity to influence vegetation diversity in grassland. A key aim of sustainable management is the promotion of botanical diversity, and recent studies point to an important role for soil organisms in achieving this goal. This is perhaps best illustrated by using recent studies on mycorrhizal fungi, which are well known to benefit the performance of their host plants. However, whilst mycorrhizal fungi associate with the majority of plants within any community, they confer different degrees of benefit on certain plant species, thereby directly influencing the structure of plant communities. One of the first studies to illustrate this experimentally was by Grime *et al.* (1987) who assembled diverse grassland communities in microcosms and allowed them to develop in the presence and absence of arbuscular mycorrhizal (AM) fungi. The presence of AM fungi led to a shift in plant community composition, reducing the dominance of grass in favour of several subordinate herb species that benefited most from AM fungal infection. The net effect of this was a significant increase in plant species diversity due to a relaxation of plant competitive interactions. Positive effects of AM fungi on plant diversity have also been shown to occur in the field, due again to the promotion of subordinate species in the community (Gange *et al.*, 1993). Several mechanisms have been proposed to explain increases in plant diversity resulting from AM fungal infection. Allen (1991) suggested that mycorrhizal fungi might increase plant diversity due to spatial heterogeneity of fungal infectivity in field soil, allowing mycotrophic (i.e. species that depend on mycorrhizal associations) and non-mycotrophic species to coexist in patches of high and low inoculum. Alternatively, Grime *et al.* (1987) suggested that AM fungi increase plant diversity through

inter-plant transfers of carbon and nutrients via hyphal links, which lead to more even distribution of resources within the plant community, reducing the ability of certain species to monopolise resources. The net effect of such nutrient distribution would be more equitable competitive interactions between plant species, promoting species coexistence and greater plant diversity. This view is also consistent with findings of Van der Heijden (2004) who found that AM fungi promoted seedling establishment in perennial grassland by integrating emerging seedlings into extensive hyphal networks and by supplying nutrients, especially P, to the seedlings. AM fungi therefore act as a symbiotic support system that promotes seedling establishment and reduces recruitment limitation in grassland (Van der Heijden, 2004).

Variations in AM fungal diversity are also likely to strongly affect plant diversity in grassland. This was tested by Van der Heijden *et al.* (1998b), who manipulated the number of native AM species (1-to-14 species) in experimental grassland units containing 15 plant species. They found that plant diversity and productivity were positively related to AM fungal diversity. This effect was thought to be due to an increase in AM hyphal length in the more diverse treatments, enabling more efficient exploitation and partitioning of soil P reserves, thereby relaxing plant competition and increasing plant productivity.

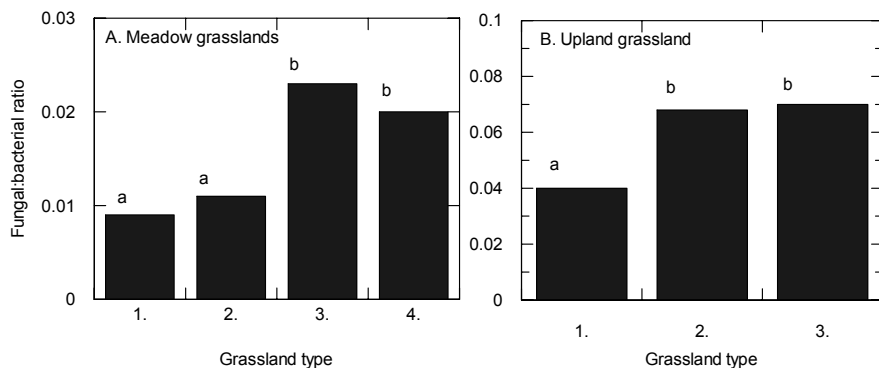


Figure 3 Effects of management intensity on fungal-to-bacterial biomass ratios measured using PLFA. (A). Gradient of declining management intensity on meadow grasslands in northern England, characterised by long-term reductions in fertiliser use and livestock density, classified as: (1) improved meadow; (2) very modified meadow; (3) slightly modified meadow, and (4) unmodified meadow. (B). Gradient of three upland grassland types of varying management intensity across ten sites in different biogeographic areas of the UK, from: (1) improved *Lolium - Cynosurus* grassland; (2) semi-improved *Festuca - Agrostis - Galium* grassland, *Holcus - Trifolium* sub-community, and; (3) unimproved *Festuca - Agrostis - Galium* grassland. Values are means and bars with the same letter are not significantly different (data from Bardgett & McAlister, 1999; and Grayston *et al.*, 2004).

What is clear from the above studies is that AM fungi have the potential to promote plant diversity in grassland, and also more efficient exploitation of nutrients within the plant-soil system. The challenge therefore is to develop management strategies that are specifically aimed at encouraging the growth of these fungi in grassland soil, with a view to enhancing plant diversity and nutrient exploitation. Recent literature shows that there is much scope to do this. In particular, studies of gradients of management intensity in temperate grasslands reveal that soils of traditionally managed, unfertilised grasslands have fungal-dominated food

webs, with a high component of AM fungi, whereas intensive systems, characterised by high levels of fertiliser use, high grazing pressures, and reduced soil organic matter content, consistently have bacterial-dominated soil food webs (Yeates *et al.*, 1997, Bardgett & McAlister, 1999; Donnison *et al.*, 2000, Grayston *et al.*, 2001, 2004) (Figure 3). Furthermore, field manipulation studies reveal that seeding of particular plant species, for example legumes, can positively influence the growth of fungi in soils (Smith *et al.*, 2003), thereby increasing opportunities for plant-soil interactions that positively influence nutrient cycling and plant diversity in grassland. In sum, there is clearly much scope to manage grassland to promote plant-soil microbial interactions that are central to sustainable management.

Conclusions

This paper provides insights into fast developing areas of ecological science that offer scope for enhancing efficient cycling of nutrients in sustainable grassland systems. The work that I have presented has not yet been integrated into practical agriculture. However, what I have hopefully shown is that there is much scope to alter grassland management systems to optimise biotic interactions between plants, their grazers, and soil microbes, to increase the efficiency of nutrient cycling and plant nutrition in unfertilised, low input systems. Much work is still to be done, but the rapid development of this area of research suggests that integration of below-ground ecology into sustainable grassland management is not far away.

References

- Allen, M. F. (1991). *The Ecology and Mycorrhizae*. Cambridge University Press, Cambridge.
- Bardgett, R. D. (2005). *The Biology of Soil: A Community and Ecosystem Approach*. Oxford University Press.
- Bardgett, R. D. & E. McAlister (1999). The measurement of soil fungal:bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate grasslands. *Biology and Fertility of Soils*, 19, 282-290.
- Bardgett, R. D. & D. A. Wardle (2003). Herbivore mediated linkages between above-ground and belowground communities. *Ecology*, 84, 2258-2268.
- Bardgett, R. D., D. A. Wardle & G. W. Yeates (1998). Linking above-ground and below-ground food webs: how plant responses to foliar herbivory influence soil organisms. *Soil Biology and Biochemistry*, 30, 1867-1878.
- Bardgett, R. D., T. Streeter & R. Bol (2003). Soil microbes compete effectively with plants for organic nitrogen inputs to temperate grasslands. *Ecology*, 84, 1277-1287.
- Chapin, F.S., L. Moilanen & K. Kielland (1993). Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature*, 361, 150-15.
- De Mazancourt, C., M. Loreau & L. Abbadie (1999). Grazing optimization and nutrient cycling: potential impact of large herbivores in a savannah system. *Ecological Applications*, 9, 784-797.
- Donnison, L. M., G. S. Griffith, J. Hedger, P. J. Hobbs & R. D. Bardgett (2000). Management influences on soil microbial communities and their function in botanically diverse haymeadows of northern England and Wales. *Soil Biology and Biochemistry*, 32, 253-263.
- Gange, A. C., V. K. Brown & G. S. Sinclair (1993). Vesicular-arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. *Functional Ecology*, 7, 616-622.
- Grayston S. J., C. D. Campbell, R. D. Bardgett, J. L. Mawdsley, C. D. Clegg, K. Ritz, B. S. Griffiths, J. S. Rodwell, S. J. Edwards, W. J. Davies and D. J. Elston (2004). Assessing shifts in soil microbial community structure across a range of grasslands of differing management intensity using CLPP, PLFA and community DNA techniques. *Applied Soil Ecology*, 25, 63-84.
- Grayston, S. J, G. Griffiths, J. L. Mawdsley, C. Campbell & R. D. Bardgett (2001). Accounting for variability in soil microbial communities of temperate upland grasslands. *Soil Biology and Biochemistry*, 33, 533-551.
- Grime, J. P., J. M. Mackey, S. H. Hillier & D. J. Read (1987). Floristic diversity in a model system using experimental microcosms. *Nature*, 328, 420-422.
- Guitian, R. & R. D. Bardgett (2000). Plant and soil microbial responses to defoliation in temperate semi-natural grassland. *Plant and Soil*, 220, 271-277.
- Hamilton, E.W. & D. A. Frank (2001). Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology*, 82, 2397-2402.
- Henry, H.A.L. & R. L. Jefferies (2003). Plant amino acid uptake, soluble N turnover and microbial N capture in soils of a grazed Arctic salt marsh. *Journal of Ecology*, 91, 627-636.

- Hodge, A., J. Stewart, D. Robinson, B. S. Griffiths & A. H. Fitter (1998). Root proliferation, soil fauna and plant nitrogen capture from nutrient-rich patches in soil. *New Phytologist*, 139, 479-494.
- Hodge, A., J. Stewart, D. Robinson, B. S. Griffiths & A. H. Fitter (1999). Plant, soil fauna and microbial responses to N-rich organic patches of contrasting temporal availability. *Soil Biology and Biochemistry*, 31, 1517-1530.
- Hokka, V., J. Mikola, M., Vestberg & H. Setälä (2004). Interactive effects of defoliation and an AM fungus on plants and soil organisms in experimental legume-grass communities. *Oikos*, 106, 73-84.
- Jones D.L. & K. Kielland (2002). Soil amino acid turnover dominates the nitrogen flux in permafrost-dominated taiga forest soils. *Soil Biology and Biochemistry*, 34, 209-219.
- Jones, D.L., J. R. Healey, V. B. Willett, J. F. Farrar & A. Hodge (2005). Dissolved organic nitrogen uptake by plants—an important N uptake pathway? *Soil Biology and Biochemistry*, 37, 413-423
- Kielland, K. (1994). Amino acid absorption by arctic plants: implication for plant nutrition and nitrogen cycling. *Ecology*, 75, 2373-2383.
- Lipson, D.A. & R. K. Monson (1998). Plant-microbe competition for soil amino acids in the alpine tundra: effects of freeze-thaw and dry-rewet events. *Oecologia*, 113, 406-414.
- Mawdsley, J. L. & R. D. Bardgett (1997). Continuous defoliation of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) and associated changes in the microbial population of an upland grassland soil. *Biology and Fertility of Soils*, 24, 52-58.
- McKane, R.B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E. Giblin, K. Kielland, B. L. Kwiatkowski, J. A. Laundre & G. Murray (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 413, 68-71
- McNaughton, S. J. (1985). Ecology of a grazing system: the Serengeti. *Ecological Monographs*, 55, 259-294.
- Mikola, J., G. W. Yeates, G. M. Barker, D. A. Wardle & K. I. Bonner (2001). Effects of defoliation intensity on soil food-web properties in an experimental grassland community. *Oikos*, 92, 333-343.
- Miller, A. E. & W. D. Bowman (2002). Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition by nitrogen form? *Oecologia*, 130, 609-616.
- Miller, A. E. & W. D. Bowman (2003). Alpine plants show species-level differences in the uptake of organic and inorganic nitrogen. *Plant and Soil*, 250, 283-292.
- Murray, P. J., N. Ostle, C. Kenny & H. Grant (2004). Effect of defoliation on patterns of carbon exudation from *Agrostis capillaris*. *Journal of Plant Nutrition and Soil Science*, 167, 487-493.
- Näsholm, T., K. Huss-Danell & P. Högberg (2000). Uptake of organic nitrogen in the field by four agriculturally important plant species. *Ecology*, 81, 1155-1161.
- Owen, A. G. & D. L. Jones. (2001). Competition for amino acids between wheat roots and rhizosphere microorganisms and the role of amino acids in plant N acquisition. *Soil Biology and Biochemistry*, 33, 651-657.
- Paterson, E. & A. Sim (1999). Rhizodeposition and C-partitioning of *Lolium perenne* in axenic culture by nitrogen supply and defoliation. *Plant and Soil*, 216, 155-164.
- Raab, T. K., D. A. Lipson & R. K. Monson (1999). Soil amino acid utilization among species of the cyperaceae: plant and soil processes. *Ecology*, 80, 2408-2419.
- Schimel, J. P. & F. S. Chapin (1996). Tundra plant uptake of amino acid and NH₄⁺ nitrogen in situ: plants compete well for amino acid N. *Ecology*, 77, 2142-2147.
- Smith, R. S., R. S. Shiel, R. D. Bardgett, D. Millward, P. Corkhill, G. Rolph & P. J. Hobbs (2003). Diversification management of meadow grassland: plant species diversity and functional traits associated with change in meadow vegetation and soil microbial communities. *Journal of Applied Ecology*, 40, 51-64.
- Streeter, T. C., R. Bol & R. D. Bardgett (2000). Amino acids as a nitrogen source in temperate upland grasslands: the use of dual labelled (¹³C, ¹⁵N) glycine to test for direct uptake by dominant grasses. *Rapid Communications in Mass Spectrometry*, 14, 1351-1355.
- Turner, B. L., R. Baxter, N. Mahieu, S. Sjögersten & B. Whitton (2004). Phosphorus compounds in subarctic Fennoscandian soils at the mountain birch (*Betula pubescens*)-tundra ecotone. *Soil Biology and Biochemistry*, 36, 815-823.
- Van der Heijden, M. G. A. (2004). Arbuscular mycorrhizal fungi as support systems for seedling establishment in grassland. *Ecology Letters*, 7, 293-303.
- Van der Heijden, M.G.A., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, R. Boller, A. Wiemken & I. R. Sanders (1998b). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, 396, 69-72.
- Weigelt, A., R. Bol & R. D. Bardgett (2005). Preferential uptake of soil nitrogen forms by grassland plant species. *Oecologia*, 142, 627-635.
- Yeates, G.W., R. D. Bardgett, R. Cook, P. J. Hobbs, P. J. Bowling & J. F. Potter (1997a). Faunal and microbial diversity in three Welsh grassland soils under conventional and organic management regimes. *Journal of Applied Ecology*, 34, 453-471.