Chapter 9

Relevance of Interactions amongst Soil Microorganisms to Soil Biological Fertility

Wendy M. Williamson[1] and David A. Wardle[2]
[1] *Landcare Research, PO Box 69, Lincoln, New Zealand*
[2] *Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, U.K.*

1. INTRODUCTION

In this chapter we discuss trophic interactions within the soil food web, with emphasis on soil microorganisms, and how these interactions influence the release of plant-available nutrients. The theme is that soil fertility is causally linked to interactions between soil biotic components and is exemplified by the interdependence and non-random location of plants and soil organisms. We use a conceptual model of detritus decomposition divided into bacterial and fungal energy channels to illustrate how non-random interactions, such as substrate quality and the presence of plant roots, influence soil fertility. Finally, an ecological perspective summarises land management effects on nutrient cycling and identifies key mechanisms that control the fertility of soil in managed systems.

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2. NON-RANDOM LOCATION OF SOIL ORGANIC MATTER

Organic matter is not randomly located within soil. For example, sulfur bacteria can align themselves along the crystal planes of sulfur-containing clay minerals (Edwards *et al.* 2000). Such specific biotic and abiotic interactions will act as primary foci for the accumulation of soil organic matter, the build up of which will provide microbial habitats, promote microbial activity and spatially segregate processes that soil microorganisms mediate. The associations of soil microorganisms in specific microhabitats within the soil matrix can be deduced from the locations of ATP and enzyme activity. Ladd (1972) found ATP and active enzymes located with the fine clay fraction and in fragments of plant material (Figure 1), suggesting that clay minerals and organic matter serve as hotspots for biological activity in soil. It is also of interest that as water-stable soil particles become smaller, the C-to-N ratios decrease. This is indicative of plant residues (which are characterised by higher C-to-N ratios) disappearing from the soil organic matter and being replaced by microbial biomass (Ahmed and Oades 1984). Chemotactic foraging behaviour of plant roots and soil microbes is dependent on this non-random location of organic matter hotspots for the establishment of chemical gradients that induce plant and microbial responses of attraction or repulsion (Ahmed and Oades 1984, Tinker 1984). Spatially distinct patches of organic matter enhances nutrient uptake by plants to a greater extent than when the organic matter is homogeneously distributed through the soil, with enhanced root growth localised within patches (Bonkowski *et al.* 2000).

While many soil microbes are adapted for rapid growth in the presence of plant roots (see Chapter 5 this volume), a large number survive outside the rhizosphere. Organisms that live outside the rhizosphere inhabit a much harsher environment and the patches of organic matter they occupy comprise less than 5% of the soil volume (Griffiths 1994). These zones are characterised by low microbial metabolic activity, with spores, cysts and dormancy dominating the physiological and morphological status of the community (Tinker 1984). However, the microorganisms that are active in this zone are likely to determine the direction that plant roots will follow, since the active microbes will utilise resources spatially removed from the root, establishing concentration gradients to which plants and soil flora and fauna respond. Free-living organisms tend to be dominated by K-selected species (which are characterised by low metabolic activity) and while they may have specific enzymatic capabilities to fix N or utilise complex substrates, competition for C probably limits their effectiveness (Tinker 1984). Therefore, away from the plant roots, plant-available nutrients are bound up in complex organic matter, and the soil environment is effectively a nutrient-poor matrix dotted with discrete islands rich in organic matter and biotic activity that are connected by chemical gradient bridges.

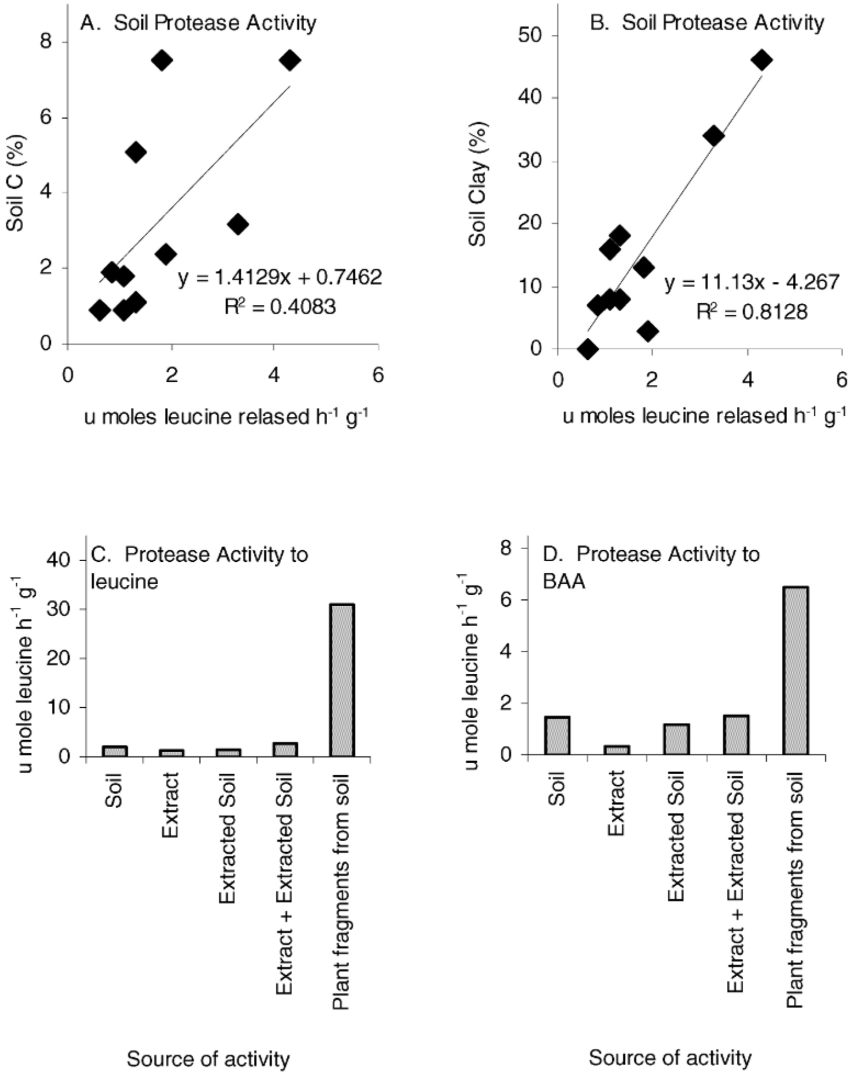

Figure 1 Activity and location of soil enzymes as a response to presence of plant litter in the soil. (A,B) Correlation of soil protease activity (expressed as µmoles leucine released from Z-phenylalanyl leucine per hour per g soil dry weight) with (A) organic C content of the soil (%) and (B) clay content of soil (%). (C, D) The protease activity towards either (C) Z-phenylalanyl leucine or (D) benzoyl arginine amide (BAA), expressed as µmoles leucine released per hour per g soil dry weight, from specific fraction of soil. Derived from (Ladd 1972).

3. ENERGY CHANNELS AND SOIL FOOD WEBS

The magnitude of microbial response to soil fertility tends to be variable. This variability is best illustrated by microbial responses to different crop management systems (perennial vs annual), where the magnitude of the response varies with microbial attributes measured and crop management (Figure 2). The microbial responses are thought to be due to differential utilisation of detritus by specific fractions of the soil microbial biomass.

Plants give rise to primary and secondary detritus. The primary detritus originates directly from the plant and comprises the litter (dead roots, branches, leaves, flowers etc.) and simple carbon-containing substances secreted into the rhizosphere (rhizodeposition), whereas secondary detritus originates from the plant consumers and the organisms that utilise the primary detritus. The microflora acts as both source and sink of plant-available nutrients, and is the priming agent responsible for the breakdown of organic materials in soil.

Moore and Hunt (1988) partitioned the below-ground ecosystem into the root and detritus energy channels, and the latter further partitioned into bacterial-based and fungal-based energy channels (Figure 3). The bacterial-based energy channel is characterised by the rapid turnover of organic matter and is dominated by bacterial metabolism (r-selected organisms). The fungal-based energy channel is associated with more stable organic matter, and has slow but relatively steady transformation of nutrients (K-selected organisms). The primary driving force behind the two energy channels is the soil invertebrate community, which has considerable habitat and food overlap facilitated through resource partitioning and body size limitation (Moore and Hunt 1988). Resource partitioning involves the utilisation of one resource by different species or groups of organisms that are spatially and/or temporally segregated. Preferential grazing of fungal spores and hyphae (young vs old) by different species of microarthropods is an example of resource partitioning.

Bacteria and the processes that they mediate dominate the bacterial-based energy channel. This energy channel typically has a strong association of active protozoa and nematodes, which utilise the microflora as a resource and are dependent on available water for motility. This interaction between the microfauna and microflora of the bacterial-based energy channel is highly relevant to the sustained biological fertility of soil. For example, protozoa are effective at releasing significant quantities of mineral N into the soil environment, especially in the rhizosphere; a 5% increase in protozoa numbers led to a 21% increase in mineral N, while a

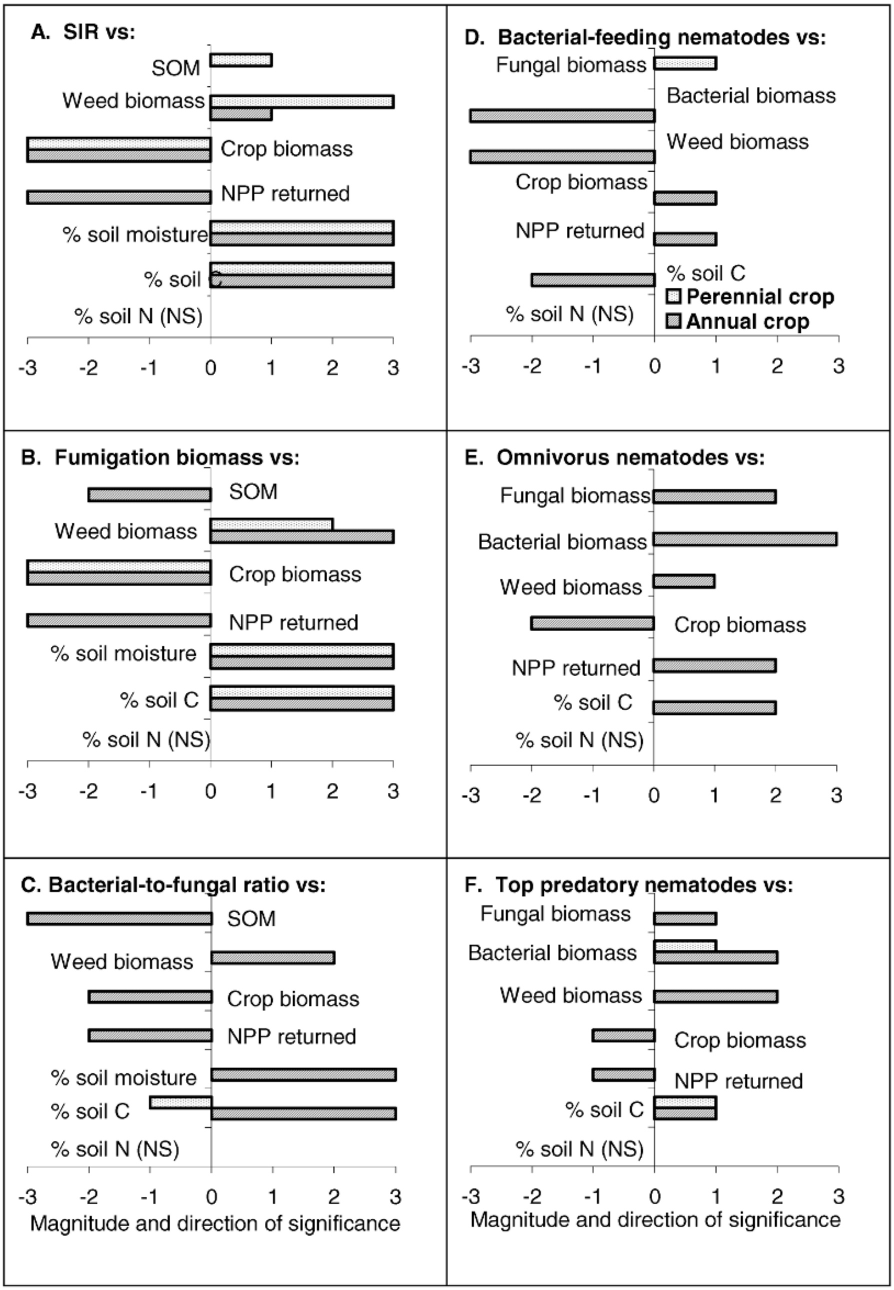

Figure 2 Levels of significance of correlation between below-ground properties in two cropping systems (one annual: maize (Zea mays L.) and one perennial: asparagus (Asparagus officinale L)) bars within the panels represent the strength between a range of belowground

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properties and (A) substrate induced respiration (SIR); (B) microbial biomass (fumigation incubation method); (C) bacterial-to-fungal ratio; (D) bacterial-feeding nematodes; (E) omnivorous nematodes; and (F) top feeding nematodes. The numbers beneath axis represent: 1 = correlation significant at 0.05; 2 = correlation significant at 0.01; 3 = correlation significant at 0.001, NA = not significant. Positive and negative values represent positive and negative correlations respectively. Derived from (Wardle et al. 1999) for A, B, C and from (Yeates et al. 2000) for D, E, F.

50% increase in protozoa translated into about 73% more mineral N (Griffiths 1994). It is estimated that 30 to 70% of ingested microbial-N is excreted by soil microfauna (Griffiths 1994). Increased nematode biomass production occurs in the presence of both bacteria and protozoa; protozoa enter pore spaces unsuitable for nematodes and consume bacteria (Elliott *et al.* 1980), but may then be consumed by nematodes. It appears that the presence of protozoa and nematodes is successful at reducing the loss of nutrients from soil because microfaunal grazing synchronises N mineralisation with plant uptake of available N (Bonkowski *et al.* 2000).

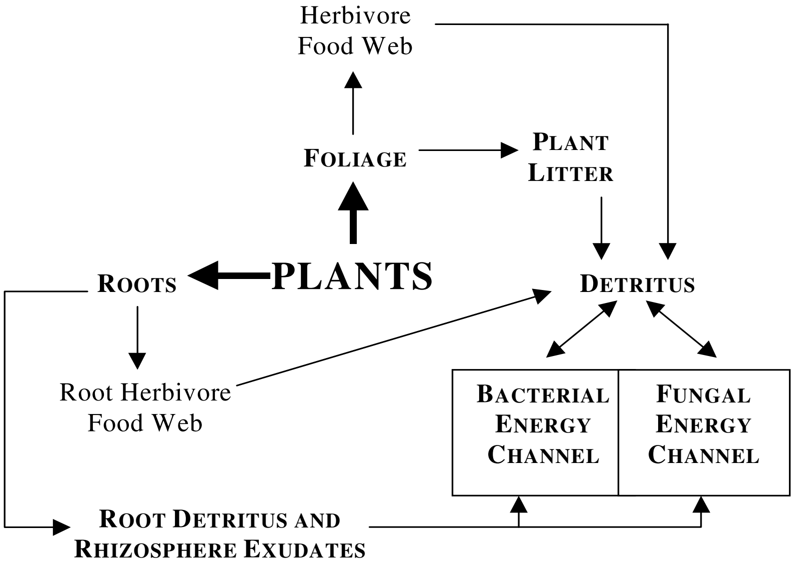

Figure 3 Schematic representation of the conceptual model for the energy channels derived from plants, indicating the dichotomy of bacterial-based and fungal-based energy channels from the detritus compartment.

Grazing by protozoa directly affects the morphological characteristics of the soil bacterial community. Medium-sized bacterial cells dominate the population when protozoan grazing is low. However, as the grazing pressure increases, situations and only small and large bacteria resit grazing (Hahn and Hofle 1999). The protozoan grazing effect is due to smaller sized bacteria being able to occupy pore spaces that are too small for protozoa to enter or that have a pore neck size that limits protozoan access. Alternatively, small bacteria may aggregate into multicellular communities that have an effective size unsuitable for protozoan ingestion (Shapiro 1995). Some large bacteria may escape initial grazing pressure and as a result of reduced competition rapidly grow too large for subsequent protozoan grazing (Hahn and Hofle 1999).

With regard to the fungal-based energy channel, fungal-invertebrate interactions are typified by microarthropod grazing on fungal mycelium and spores. Selective grazing by microarthropods can alter fungal community structure, and therefore strongly influence the dynamics of litter decomposition through feeding interactions that preferentially promote intraspecific and interspecific fungal activity (Newell 1984). The fungal-based energy channel is usually favoured by low disturbance (e.g. no-till systems), with more nutrients immobilised in the fungal biomass than when bacterial-based energy channels are favoured.

4. INTERACTIONS OF THE SOIL FOOD WEB

Microbial growth is promoted when interactions between the soil microflora and soil invertebrates. The soil invertebrate community has three functional compartments, micropredators, litter transformers and ecosystem engineers (Lavelle *et al.* 1995), which operate within and between trophic levels by a network of interactions. Micropredators are the small invertebrates (protozoa, nematodes and microarthropods) whose activity is dependent on the body size of their prey or nutrition gained from them. Prey size tends to determine the detritus energy channels with which the micropredators are principally associated.

Litter transformers have two direct effects on the soil ecosystem. Firstly, they are responsible for comminutation of litter. This disrupts cellular integrity and greatly increases the surface area of the resource available for microbial attack by mechanical and enzymatic means. Secondly, the litter transformers' faecal pellets represent dynamic sites of concentrated organic matter that are strongly associated with microbial activity and are collectively referred to as the external rumen (Lavelle *et al.* 1995).

Ecosystem engineers, such as earthworms and termites, build more permanent organo-mineral structures. These structures provide additional habitats for soil fauna and microorganisms. The ecosystem engineers develop strong mutualistic interactions with the microflora in their gut cavities, allowing macrofauna with low digestive capabilities to consume food that would otherwise be unsuitable. The gut environment is essentially one of an unlimited aqueous phase, with temperature, moisture and pH conditions conducive for microbial metabolism and reproduction, and greatly favours bacterial-based energy channel processes (Daniel and Anderson 1992).

5. RESOURCES FOR THE SOIL FOOD WEB

Resource (residue) quality alters during decomposition. Decomposition is affected by the biotic and abiotic factors that influence microbial activity and associated interactions (Wardle 2001). Therefore, even though organic matter is not randomly located in soil, the direction and magnitude of biotic responses to substrate quality and soil fertility are often difficult to predict (Figure 2).

The addition of plant and animal residues to soil tends to increase soil enzyme activity by two mechanisms. First, enhanced microbial activity in response to residue addition is typified by increased activity of the bacterial-based energy channel. Second, residue-associated enzymes, some of which retain activity for a considerable period of time, enhance decomposition by reducing the direct energy expenditure by the microflora (Dick and Tabatabai 1993). In addition to soil physical factors that affect enzyme activity (such as pH, temperature and presence of inhibitory compounds), vegetation type and vegetation quality are principal determinants of soil enzyme activity (Dick and Tabatabai 1993).

The rhizosphere is a principal functional unit in regulating biological soil fertility, and is typified by increased bacterial activity due to more readily available C from roots and root exudates. Rhizosphere-associated bacteria are more active than those inhabiting non-rhizosphere zones (Lynch and Whipps 1990) and tend be larger (Foster 1988). Further, the doubling time of bacteria in the rhizosphere is less than that in non-rhizosphere soil, and this may be due to higher grazing intensities in the rhizosphere that keep the bacteria in logarithmic growth. For example, *Pseudomonas* spp. can have a generation time of five to six hours near the root tip compared with 77 hours in bulk soil. In contrast, the generation time of *Bacillus* spp. may be 39 hours in the rhizosphere compared with 100 hours when not associated with roots (Anderson 1988). The enhanced microbial activity close to the root is associated with greater protozoan and nematode activity and the microbial and microfaunal populations tend to follow the spatial and temporal root tip growth. There is a reduction in microbial biomass that is correlated with the distance from plant roots. Similarly, the microbial biomass associated with older roots is lower than that of younger more active roots (Newman 1985). These spatial distributions are consistent with the non-random location of microbes in soil.

In the non-rhizosphere soil, fungi dominate the microbial biomass, suggesting that very different interactions occur away from plant roots. The translocation of resources between regions of the same fungal colony, and even between fungi, is considered central to the generalist ability of saprotrophic fungi (Thrower and Thrower 1961, Connolly *et al.* 1999). The ability to translocate nutrients is not a universal feature of fungi, nor is it expressed in an unregulated manner (Thrower and Thrower 1961). While some fungi can only translocate when they encounter nutritionally rich substrates, most can move C from older to younger tissue (Thrower and Thrower 1961). Although it is generally assumed that the fungi translocate nutrients only from decomposing organic matter, Connolly *et al.* (1999) showed that some fungi could extract and subsequently translocate nutrients directly from the mineral horizon to the surface organic matter, which may represent a very important mechanism for spatial dynamics and redistribution of nutrients in the soil. Net-N immobilisation in surface plant residues is directly associated with fungal activity (Frey *et al.* 2000) and reflects the lower turnover of available resource when processes are dominated by fungal-based energy channel processes (i.e. grazed by microarthropods rather than protozoa). This indicates that any mineral N produced in surface litter is initially unavailable to plants and suggests that this pool of N if subsequently translocated may permit fungi to exploit resources of less favourable C-to-N ratios (Frey *et al.* 2000).

Earthworm mucus can be likened to rhizodeposition by plants and gut-associated processes have parallels with those driven by root-elongation (Martin *et al.* 1987). The passage of microbes through the earthworm gut usually alters microbial community structure (Edwards and Fletcher 1988, Daniel and Anderson 1992). The feeding and burrowing activity of earthworms introduces fungi, bacteria and litter fragments to different sites within the soil resulting in temporal and spatial dynamics that the microbes could not have achieved independently (Tiunov and Scheu 2000). In addition, earthworm casts and the faecal pellets of arthropods can be more compact than the surrounding soil (Chauvel *et al.* 1999), which favours bacterial processes over fungal due to the available pore size being smaller. However, fungi rapidly colonise the outside of the pellets and the external rumen process of organic matter breakdown continues (Swift *et al.* 1979).

Competition for soil nutrients means that many organisms increase their competitiveness by inhibiting the growth of other microbes directly through the production of antimicrobial agents (Cain *et al.* 2000). Other mechanisms by which negative interactions between soil microorganisms may work include the production of extracellular agents capable of causing cell lysis (Kope and Fortin 1990), reduction in extracellular polysaccharides (Barrion and Habte 1988) and sequestering of ferric ions, such as action of siderophores (Fogel 1985). Production of extracellular polysaccharides, which help microorganisms resist adverse environmental conditions, have been shown to be substantially reduced through the competitive effects of soil actinomycetes (Barrion and Habte 1988).

6. A PERSPECTIVE OF SOIL BIOLOGICAL FERTILITY

Agricultural intensification, which generally involves the increasing use of mechanical and synthetic inputs and the deliberate reduction of aboveground biodiversity, has important direct and indirect effects on soil function. Decreasing levels of soil organic matter, which may reduce the soil microbial biomass and therefore the biological fertility of the soil, can adversely affect belowground nutrient cycling processes. Although soil organic matter stocks directly determine the fertility of the soil (Tiessen *et al.* 1994), the initial status of a soil's nutrient reserves do not necessarily indicate how responsive a soil will be to cropping pressure. It is the rate at which standing organic matter is lost, rather than the absolute amount of organic matter, that is the key determinant of long-term soil fertility. Soils with higher nutrient contents initially tend to lose a larger proportion of their organic matter than soils of lower status (i.e. a non-linear response), when agricultural intensification occurs (Sparling *et al.* 2000). The constraints on soil microbial activity do not necessarily determine the absolute state of the habitat, but rather, the degree and direction of change in the physical, chemical and biological properties dictates the microbial response to soil management, such as cropping and tillage. In general, increasing cropping pressure or tillage decreases soil organic resources (Davidson and Ackerman 1993) and consequently decreases the metabolic activity of soil microflora and microfauna (Sparling *et al.* 2000).

Agricultural practices that promote soil disturbance, such as tillage, have important effects on soil food web structure, and tend to adversely affect larger-bodied organisms (e.g. earthworms, arthropods) more than smaller animals such as protozoa and nematodes (Wardle 1995). Therefore, soil disturbance by tillage tends to promote the bacterial-based energy channel at the expense of the fungal-based channel and tends to disadvantage larger animals, reducing flow-on benefits from gut-associated mutualistic microbial interactions (Hendrix *et al.* 1986). However, cultivation also generates buried resource islands, which may contribute to greater spatial heterogeneity in soil (Wardle *et al.* 1999).

In low intensity agricultural systems herbicides are frequently used in the place of tillage to control weeds. Indirect effects of herbicides have been postulated as one of the reasons for the differential responses of soil food-web components to no-tillage agriculture (Hendrix and Parmelee 1985). Firstly, the herbicides serve as C substrates for bacteria and promote the bacterial-based energy channel, although these effects are generally likely to be minor (Domsch *et al.* 1983). A more important mechanism of altering the below-ground food web involves the changes in plant community structure brought about by herbicide use. The presence of weeds at moderate levels (but at levels below which are likely to interfere with crop production), results in patches of higher quality litter in the soil (Wardle *et al.* 1995); this in turn has important positive effects on components of the soil biota.

Cropping affects soil fertility partly through altering soil biotic interactions. Such alterations can lead to complex interactions in which only some groups appear to be stimulated. However, other groups may have been stimulated, but are subsequently regulated by higher trophic levels, giving an apparent decreased or neutral response to cropping. For example, in a cropping system Wardle *et al.* (1999) found that increased residue additions (sawdust) to a perennial crop promoted fungal, but not bacterial growth. In this case, resource addition promoted top predatory nematodes, but predation pressure induced by these nematodes resulted in regulation at lower trophic levels, preventing bacteria from showing a positive response towards resource addition even though their turnover rate increased. This indicates the importance of studying several trophic levels of the soil food web when investigating the dynamics of specific soil management practices.

The presence of grazing animals can exert important effects upon the decomposer subsystem as well as on nutrient mineralisation processes carried out by the soil biota (Bardgett *et al.* 1998). These include the return of dung and urine, alteration of plant productivity, allocation of C and nutrients to roots (Seastedt 1985), and the quantity of organic matter returned by the plant (Bardgett *et al.* 1998). Continuous grazing of grasses appears to favour the bacterial-based energy channel over fungal in the short-term (Mawdsley and Bardgett 1997). In the longer-term, the net effect of defoliation may be towards the fungal-based energy channel as rhizodeposition declines and the soil microbial community adapts accordingly, with the long-term effect of defoliation tending to diminish microbial activity (Mikola *et al.* 2001). The difference in the nature of resource input between crop production and livestock-based agricultural systems can also strongly influence the nature of the soil food web and soil fertility. Because grazing systems tend to be based on perennial plant species, they are generally associated with soils with higher levels of organic matter, higher levels of soil microbial biomass, and greater populations of the associated soil animals (Srivastava and Singh 1991). However, grazed grasslands can also support lower populations of smaller soil organisms, relative to cropping systems, such as nematodes, which typify the bacterial-based energy channel (Yeates *et al.* 2000).

In summary, soil management practices that promote the maintenance of organic matter and an active microbial biomass, which may be approached through the proper management of organic residues, can maintain crop production through biological mechanisms regulating the supply of plant-available nutrients. The factors that control soil biological fertility are therefore those that regulate the activity of the soil microbial biomass and the interactions with soil fauna. Decomposition processes and nutrient cycling occur in a defined manner, however the dynamics within different systems will alter the multitude of possible interactions due to differences in substrate quality. Therefore it is difficult to make specific predictions of biological response to different soil management practices. This difficulty is despite the fact that soil processes are initiated and maintained by non-random processes both spatially and temporally.

7. ACKNOWLEDGEMENTS

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