

A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling

M.H. Beare^{1,3}, D.C. Coleman¹, D.A. Crossley Jr¹, P.F. Hendrix² and E.P. Odum¹

¹*Institute of Ecology, University of Georgia, Athens, GA30602, USA and* ²*Department of Crop and Soil Sciences and Institute of Ecology, University of Georgia, Athens, GA 30602, USA.* ³*Current address: New Zealand Institute for Crop and Food Research, Canterbury Agriculture and Science Centre, Private Bag 4704, and Lincoln University, Christchurch, New Zealand*

Key words: biodiversity, biotic interactions, biogeochemistry, detritosphere, drilosphere, functional groups, key-stone species, microsites, nutrient cycling, porosphere, rhizosphere, spatial heterogeneity

Abstract

The significance of biodiversity to biogeochemical cycling is viewed most directly through the specific biogeochemical transformations that organisms perform. Although functional diversity in soils can be great, it is exceeded to a high degree by the richness of soil species. It is generally inferred from this richness that soil systems have a high level of functional redundancy. As such, indices of species richness probably contribute little to understanding the functioning of soil ecosystems. Another approach stresses the value of identifying "keystone" organisms, that is those that play an exceptionally important role in determining the structure and function of ecosystems. Both views tend to ignore the importance of biodiversity in maintaining the numerous and complex interactions among organisms in soils and their contributions to biogeochemical cycling. We describe some of those interactions and their importance to ecosystem function.

Soil organisms alter the physical, chemical and biological properties of soils in innumerable ways. The composition and structure of biotic communities at one hierarchical level can influence the spatial heterogeneity of resource and refuge patches at other hierarchical levels. This spatial heterogeneity is supported by a number of biologically relevant spheres of influence that include the detritosphere, the drilosphere, the porosphere, the aggregatosphere and the rhizosphere. Each has fairly distinct properties that operate at different spatial scales. We discuss how these properties may function in regulating the interactions among organisms and the biogeochemical processes that they mediate. It is through the formation of a spatially and temporally heterogeneous structure that biodiversity may contribute most significantly to the functioning of soil ecosystems.

Real advances in understanding the significance of biodiversity to biogeochemical cycling will come from taking a broader view of biodiversity. Such a view will necessarily encompass many levels of resolution including: 1) the importance of biodiversity to specific biogenic transformations, 2) the complexity and specificity of biotic interactions in soils that regulate biogeochemical cycling, and 3) how biodiversity may operate at different hierarchically arranged spatial and temporal scales to influence the structure and function of ecosystems.

Introduction

Interest in biodiversity has grown rapidly in both public and scientific circles (Wilson, 1988). Increasingly, attention is being drawn to organisms other than those of the vertebrate world (i.e. birds, mammals, and fish). While much of this attention can be attributed to a desire to maintain genetic diversity and to harvest its biochemical potential, the importance of biodiversity

to ecosystem function has been largely overlooked (di Castri and Younes, 1990; Franklin, 1993).

Evaluating the importance of biodiversity to biogeochemical cycling will ultimately depend on how we define biodiversity, and on our ability to characterize it functionally and to identify the critical biotic and abiotic factors that regulate it. Clearly the diversity of soil organisms is vast. Many of these organisms are unknown and perhaps unknowable in a timeframe rel-

evant to their protection. Given that many soil species have been or will be lost before we can act to protect them, and that the risks to species will always be balanced against the benefits of natural resource development, it becomes critical to understand what aspects of biodiversity are important to maintaining ecosystem function.

The dichotomy between functional and descriptive approaches to soil ecology is no more apparent than in the discussion of the significance of soil biodiversity to biogeochemical cycling. The task of joining these approaches is constrained both by our metaphorical view of soil as a 'black box' and the experimental limits it imposes (Paul, 1989). Given the enormous breadth of the subject, we will not attempt to cover all aspects of biodiversity as they relate to biogeochemical cycling. Rather we present a view that incorporates ideas from several levels of resolution. We begin with some examples of specific biogenic transformations in soils, ranging from those that are highly specialized to those that are much more widely distributed. This is followed by an argument which challenges the assumption that soil biota are highly functionally redundant and that much of the organization and function of ecosystems can be attributed to a select group of "keystone" organisms, instead placing greater emphasis on the importance of biotic interactions to biogeochemical cycling. We conclude with a discussion of how biodiversity may operate at different hierarchically arranged spatial and temporal scales to influence the structure and function of ecosystems.

Biodiversity and biogenic transformations

The importance of biodiversity to biogeochemical cycling can be viewed most directly through the specific biogeochemical transformations that organisms perform. Their effects on biogeochemical cycling occur through both direct and indirect means. Though variously defined (Wolters, 1991), for the purposes of this discussion a direct effect is defined as any organism-induced modification that can, without further biological involvement, alter the transformations and transport of elements within soils. The following section reviews the direct effects of plants, bacteria, fungi and fauna on biogeochemical cycling in soils.

Plants

Plants play a critical role in biogeochemical cycling by serving as the primary source of fixed carbonaceous energy and as both a source and a sink of nutrients. Species specific differences in the organic constituents (e.g. cellulose, lignin) and nutrient content of plant tissues as well as patterns of biomass accretion and tissue senescence influence the extent and timing of organic matter decomposition and nutrient release in soil (Swift et al., 1979). These species specific factors apply equally well in agricultural as well as natural ecosystems.

Plants also contribute directly to nutrient cycling through the weathering of primary minerals. This occurs principally through the production of root exudates that lower soil pH or chelate metals, releasing many essential nutrients (e.g. Fe, Ca, K, Mg, and Na) (Likens et al., 1977). Although some studies suggest that mineral weathering rates are lower in soils dominated by coniferous as compared to deciduous vegetation (Knoll and James, 1987), the degree to which species differ in their contributions to mineral weathering and, thus, localized influences on mineral availability is poorly known. The extent to which plant community structure determines, or is determined by, the spatial variation in soil biogeochemical properties, especially mineral nutrient availability, is a subject of much continued research (Grime, 1979; Tilman, 1982).

Bacteria

Soil bacteria are responsible for some of the most specific biogenic transformations in elemental cycles (Alexander, 1977; Paul and Clark, 1989). In the nitrogen cycle, many bacteria are involved in ammonification, but other N transformations are carried out by taxonomically narrow groups of microorganisms. Chemoautotrophic nitrification, for example, is accomplished by relatively few obligate aerobic soil bacteria which oxidize NH_3 to NO_2^- (e.g. *Nitrosomonas*, *Nitrococcus*) and NO_2^- to NO_3^- (*Nitrobacter*). Heterotrophic nitrification is also known for several bacteria (e.g. *Arthrobacter*) and actinomycetes, but probably accounts for relatively low levels of NO_3^- production. Other steps in the N cycle, such as dissimilatory NO_3^- and NO_2^- reduction (e.g. *Mycobacterium*, *Clostridium*) and denitrification (e.g. *Pseudomonas*, *Bacillus*, *Thiobacillus*), are carried out by a few, widely distributed genera (Payne, 1981).

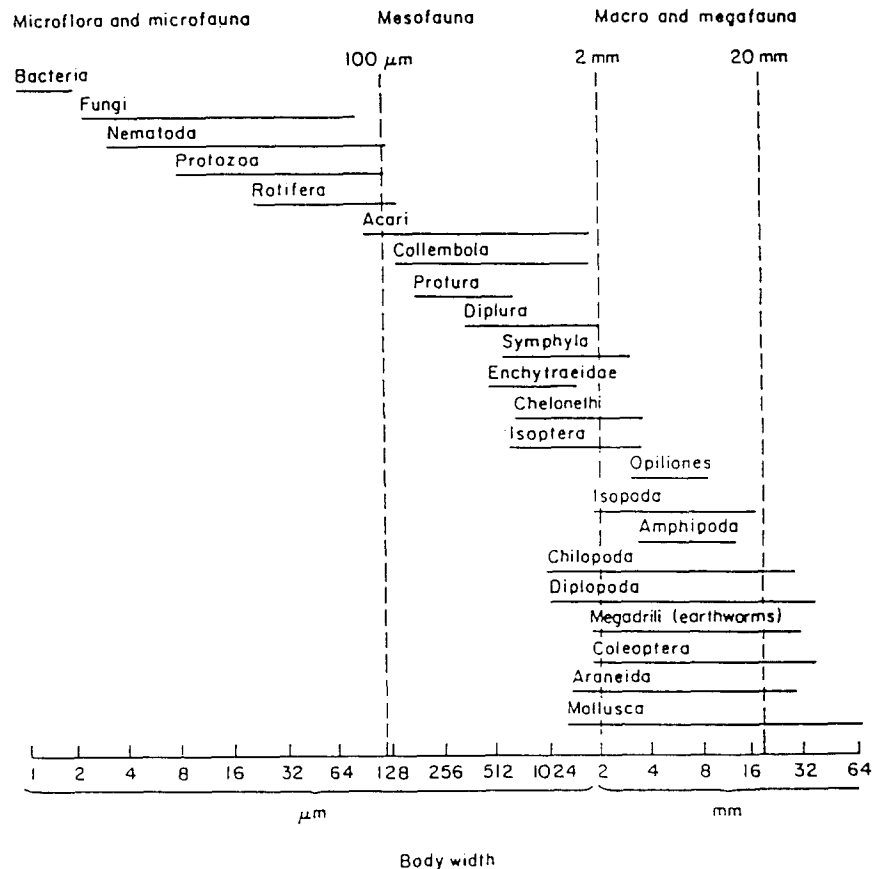


Fig. 1. Size classification of soil organisms by body width (from Swift et al., 1979).

Although biological N_2 -fixation is widely distributed, the bacteria responsible for these transformations are often limited to a fairly narrow range of environmental conditions (Postgate, 1982). Asymbiotic N_2 -fixation is carried out by aerobic (e.g. *Azotobacter*, *Beijerinckia*), microaerophilic (e.g. *Klebsiella*, *Bacillus*) and anaerobic (e.g. *Clostridium*) organotrophic bacteria as well as free-living cyanobacteria that are sometimes abundant in soils. Symbiotic N_2 -fixation is best known for bacterial (*Rhizobium*, *Bradyrhizobium*) associations with legumes and actinomycete (*Frankia*) associations with numerous genera of nonleguminous angiosperms (e.g. *Alnus*, *Casuarina*, *Ceanothus*, *Myrica*).

The role of bacteria in the phosphorus cycle appears somewhat less specialized. Although there are no microbially mediated gaseous fluxes of P, a wide range of soil bacteria (e.g. *Pseudomonas*, *Bacillus*) are involved in the solubilization of inorganic phosphorus. As a group, soil bacteria are important to the short-term immobilization of P and the mineral-

ization of organic phosphorus. Somewhat more specialized groups of bacteria are involved in the transformations of metals in soils. Examples of these transformations include the reduction (e.g. *Bacillus*) and precipitation (e.g. *Chlamydbacteriaceae*) of iron as well as the chemolithotrophic oxidation of Fe^{2+} under acid conditions (*Thiobacillus ferrooxidans*). Other examples of specialization can be found in the sulfur cycle. All microorganisms require sulfur for synthesis of amino acids, but many biogenic transformations of sulfur including the oxidation of inorganic sulfur by chemolithotrophic (e.g. *Thiobacillus*) and photolithotrophic (e.g. *Rhodospirillaceae*) bacteria and dissimilatory reduction of SO_4^{2-} (e.g. *Desulfovibrio*) are limited to few genera and occur under a fairly narrow range of environmental conditions (Bettany and Stewart, 1982).

An area of recent interest involves the organisms and conditions responsible for the production and consumption of methane. Methanogenesis is now attributed to more than 50 known species of bacteria that

are rare in most soils but common in a broad range of anaerobic habitats (Jones, 1991). Their growth and survival depends directly on the activities of associated microflora which enhance methanogenesis through the release of C substrates and the maintenance of reducing conditions, or inhibit it through the production of alternative electron acceptors (i.e. SO_4^{2-} , NO_3^- , Fe^{3+}). Conversely, methane oxidation appears to be limited to relatively few genera of obligate aerobic bacteria (e.g. *Methylobacter*, *Methylococcus*) that are widely distributed in terrestrial ecosystems (Topp and Hanson, 1991). Though principally responsible for regulating fluxes of methane, they may also contribute to ammonium oxidation and O_2 depletion which enhance N_2O production.

Fungi

Fungi are a major component of the soil biomass (Hawksworth, 1991) and are of considerable importance in regulating ecosystem processes (see recent reviews by Cromack and Caldwell, 1992; Dighton and Boddy, 1989; Wainwright, 1992). Though often grouped by their specific enzymatic capabilities, most fungi have broad versatility in their chemoheterotrophic metabolism. Despite this versatility and their prominent role in plant litter decomposition (Cromack and Caldwell, 1992; Kjoller and Struwe, 1982), many fungi maintain more specialized mechanisms for obtaining energy and nutrients (Wainwright, 1992). For example, some species of fungi are able to use other sources of C, ranging from gaseous forms (CO , CO_2 , CH_4) (e.g. Parkinson et al., 1991) and volatile organics (Fries, 1973) to relatively complex compounds such as lignin, humic acids and phenolic acids that are important constituents of soil organic matter (Bååth and Söderström, 1980).

The important role of many fungi (Wainwright, 1992), including ectotrophic mycorrhizal species (Read et al., 1989), in the ammonification of organic N is well established, but their contribution in other areas of the N cycle has received little attention. Nitrification, for example, has long been known for *Aspergillus flavus*, but the broader range of fungal involvement has only recently been described (Killham, 1987). Though autotrophic nitrification by bacteria is often assumed to dominate, the heterotrophic activities of fungi may account for a significant proportion of the nitrification in acid forest soils (e.g. Schimel et al., 1984). The extent of fungal nitrification in other soil systems remains poorly known. In contrast, several genera of

fungi are known to play a role in nitrite reduction (e.g. *Fusarium*, *Acremonium* and *Aspergillus* sp.) though few studies have demonstrated significant levels of complete denitrification in fungi. Early evidence of N_2 -fixation in fungi has not held up to scrutiny though their ability to scavenge combined forms of nitrogen from the atmosphere may be widespread (Wainwright, 1992).

The role of fungi in the oxidation of elemental and reduced forms of inorganic sulfur is now known to be important in soils (Lawrence and Germida, 1988) and numerous genera appear to be involved (Wainwright, 1992). Similar to roots and their mycorrhizal symbionts, some free-living fungi (*Aspergillus* and *Penicillium*) also excrete organic acids and Fe siderophores that solubilize insoluble forms of phosphate (Sollins et al., 1981) and contribute to the weathering of soil minerals (Mehta et al., 1979).

Methylation of halide ions by some wood-rotting fungi in the presence of cellulose represents another specialized biogenic transformation in fungi. Harper (1985) showed that through this process fungi could make a substantial contribution to the global budget of atmospheric chloromethane (CH_3Cl) which is important in regulating stratospheric ozone levels. While chloromethane production has been reported for several species of *Fomes* and *Agaricus bisporus*, this biosynthetic capability is poorly known for most other cellulosic species, especially those of agricultural soils where cellulosic fungi are common (Broder and Wagner, 1988; Harper and Lynch, 1985; Killham et al., 1988).

One particularly important feature of the mycelial growth habit is the ability of fungi to overcome the physical and chemical constraints imposed by soil structure and the patchy distribution of substrates to access and translocate nutrients from regions of enrichment to regions of depletion (Cairney, 1992; Jennings, 1990). The hyphal growth form also allows some fungi to accumulate nutrients and to sequester cytotoxic elements (e.g. Al, Ca, Fe, Mn) away from growing hyphal tips (Cromack and Caldwell, 1992).

Fauna

The effects of soil fauna on soil processes have been described in several recent reviews (Anderson, 1988; Hendrix et al., 1990; Lee and Pankhurst, 1992; Wolters, 1991). From the standpoint of function, soil fauna are most often classified by size (Swift et al., 1979; Fig. 1) into three major groupings; microfauna,

mesofauna and macrofauna. The soil microfauna are composed mainly of protozoa and nematodes, numbering as high as 10^7 m^{-2} and 10^9 m^{-2} , respectively, in some soils (Anderson, 1988). They feed primarily on fungi and bacteria, though predatory and parasitic forms are also abundant. Their direct effects on biogeochemical cycling occur principally through their feeding on and assimilation of microbial tissue and the excretion of mineral nutrients. Due to their high consumption levels, short generation times and fast turnover rates they tend to track the dynamics of bacterial and fungal populations. The importance of bacterial-feeding protozoa to the release of ammonium-N and enhanced N-uptake by plants has been shown in several studies (e.g. Clarholm, 1985; Kuikman and van Veen, 1989). The effects of microbivorous nematodes are more variable, having both stimulatory and inhibitory effects on microbial populations and nutrient release (e.g. Ingham et al., 1985).

Soil mesofauna comprise a diverse assemblage of organisms ranging from soil microarthropods (principally mites and Collembola) to the often abundant but poorly known enchytraeidae. Soil enchytraeids directly affect biogeochemical cycling through their geophagic processing of soil organic matter and changes in the pore size distribution that may affect solute transport and O_2 -availability (Didden, 1990). The direct effects of microarthropods on biogeochemical cycling result from the enhanced mineralization of nutrients during their feeding on soil microflora and fauna and from the comminution of plant detritus and fecal deposition, changing the surface area for microbial attack and the leaching of water-soluble constituents (Seastedt, 1984). Species specific differences in their contributions to biogeochemical cycling are poorly known. Though many microarthropods are fungivorous, others are bacterivorous or predatory, feeding on a number of micro- and mesofaunal groups. Recent studies indicate, however, that many microarthropods are omnivorous, shifting trophic habits as resources change, a characteristic that makes their arrangement into functional groups difficult (Moore et al., 1988; Mueller et al., 1990; Walters et al., 1988).

Soil macrofauna are represented by a morphologically and behaviorally diverse group of organisms that includes millipedes, termites and earthworms. Their direct effects on biogeochemical cycling occur through the comminution and burial of plant detritus, improving the resource availability to microbes and mediating the transfer of solutes and particulates deeper

into the soil profile. They also affect biogeochemical cycling through a physical rearrangement of soil particles, changing the pore size distribution and, as a result, patterns of infiltration and gaseous emission. Effects of earthworms are universally recognized, but soil turnover by ants and termites may be equally important (Lobry de Bruyn and Conacher, 1990).

Of the macrofauna, earthworms provide one of the best examples of the union of functional and taxonomic approaches to biodiversity in soils. The familiar ecological categories of earthworms (Bouché, 1971; Lee, 1959) clearly describe their niche separation within a soil volume. Polyhumic epigeic and epiendogeic species occupy litter and surface soil layers; meso- and oligohumic endogeic species inhabit mineral soil within the rhizosphere and beyond; and anecic species exploit both the surface litter as a source of food and the mineral soil as a refuge. The activities of earthworms within these categories influence biogeochemical processes in various ways. For example, epigeic species facilitate the breakdown and mineralization of surface litter, while anecic species incorporate organic matter deeper into the soil profile and enhance aeration and water infiltration through burrow formation (Lee, 1985).

An alternative to the redundancy-keystone dualism

The examples above represent only a sampling of the rich and varied ways in which organisms contribute directly to biogeochemical transformations in soils. Although their functional diversity can be quite high, it is exceeded to a large degree by the richness of soil species. For this reason, many authors have argued that an accounting of species richness contributes little to understanding ecosystem function, primarily due to the high degree of functional redundancy assumed for many soil species (di Castri and Younes, 1990). It is generally inferred from this that a loss of species will not necessarily be reflected by a change in rates of biologically mediated processes and biogeochemical transformations (Franklin, 1993). Though redundancy in a single function may be common among many soil biota, the suite of functions attributable to any one species is unlikely to be redundant. Furthermore, functionally similar organisms often have different environmental tolerances, physiological requirements and microhabitat preferences (Perry et al., 1989). As such, they are likely to play quite different roles in the soil system.

Many authors have called for an approach to biodiversity protection that targets "keystone" organisms (species and functional groups), that is, those that play exceptionally important roles in maintaining the organization and function of ecosystems. Although there is little doubt that some organisms have an overriding influence on ecosystem processes, the keystone-organism approach has recently been called into question (Mills et al., 1993), due largely to its tendency to disregard the importance of biotic interactions in regulating ecosystem function. Biotic interactions can be either positive (e.g. mutualistic, associative) or negative (e.g. competitive, predatory) in function. The importance of negative interactions to regulating soil processes has been the subject of much research (Coleman et al., 1983; De Ruiter et al., 1993; Santos et al., 1981). Recently, there has been a growing interest in understanding the positive interactions in soils and whether they may confer greater stability and resiliency to ecosystem function (Perry et al., 1989). Taken as a whole, the more complex the biotic interactions, the greater the probability that indirect effects will be important to regulating ecosystem function (Price, 1988). Thus, the diversity that supports these complex interactions will be important to regulating the processes that determine biogeochemical cycling.

For these reasons, an approach that relies less on the redundancy-keystone dualism and more on understanding the complexity and specificity of biotic interactions (Mills et al., 1993) will yield greater returns in determining the significance of biodiversity to ecosystem function. This point is made clearer by reviewing the broad range of biotic interactions in soils that contribute to biogeochemical cycling.

Biodiversity, biotic interactions and indirect effects

Due to their vast diversity, large populations and long evolutionary history, microorganisms have contributed greatly to the rich and complex interactions among soil organisms (Price, 1988). These interactions range from highly specific symbioses to diffuse mutualisms. Mycorrhizal symbioses are among the best known examples of plant-microbe interactions and play a key role in regulating plant productivity and nutrient cycling (Allen, 1992; Barea, 1991). Mycorrhizal fungi are found in 75–80% of all vascular plants species. Although these associations are often assumed to have weak specificity, Molina et al. (1992) have shown that

many are highly specific, emphasizing the importance of diversity to ecosystem function.

Somewhat more complex interactions are found in the tripartite associations of plants, symbiotic VAM fungi and rhizobia that enhance plant nutrient uptake (Allen, 1992). In addition to this well known association, other tripartite interactions such as those involving the N-fixer *Frankia*, the VAM fungus *Glomus*, and *Alnus* trees have been shown to stimulate N₂-fixation and enhance the productivity and P content of host plants in soils of low fertility (Jha et al., 1993). In many cases, one or more of the mutualists have a restricted or obligate relationship with the plant, making these relationships especially sensitive to the loss of species (Janos, 1980; Perry et al., 1989).

Other strictly microbial interactions have also been described. In one particularly intriguing example, Lynch and Harper (1985) described a tripartite association on straw where the activities of fungal cellulases supply simple sugars to an N₂-fixing bacteria. The third partner in the association is a polysaccharide-producing bacterium which helps to maintain the anaerobic environment necessary for nitrogenase activity. While Lynch and Harper (1985) report gains of up to 84 kg N ha⁻¹, incredibly, other bacteria/bacteria associations have been described that may double those gains (Halsall and Gibson, 1986).

There are also important symbiotic interactions between microorganisms and soil fauna. In one prominent example, termites in the subfamily Macrotermitinae culture 'fungus gardens' on leaf cuttings or fecal pellets, harvesting the fungi (*Termitomyces* spp.) as a primary food source (Lee and Pankhurst, 1992). In another example, the pantropical earthworm, *Pontoscolex corethrurus*, primes its symbiotic gut microflora with secreted mucus and water to increase their degradation of ingested organic matter and the release of assimilable metabolites (Barois and Lavelle, 1986). These interactions can have profound effects on the distribution and decomposition of soil organic matter.

Interactions among organisms in the root zone can indirectly affect plant growth and nutrient uptake. The effects of root-infecting pathogens on plant productivity are well known and can have many far-reaching implications for biogeochemical cycling (e.g. Rovira et al., 1990). Though often attributed to microbial antagonism or soil mycostasis, soil fauna are increasingly recognized as potential suppressants of root pathogens. For example, some species of fungivorous amoebae (Charkraborty et al., 1983), nematodes (Barnes et al.,

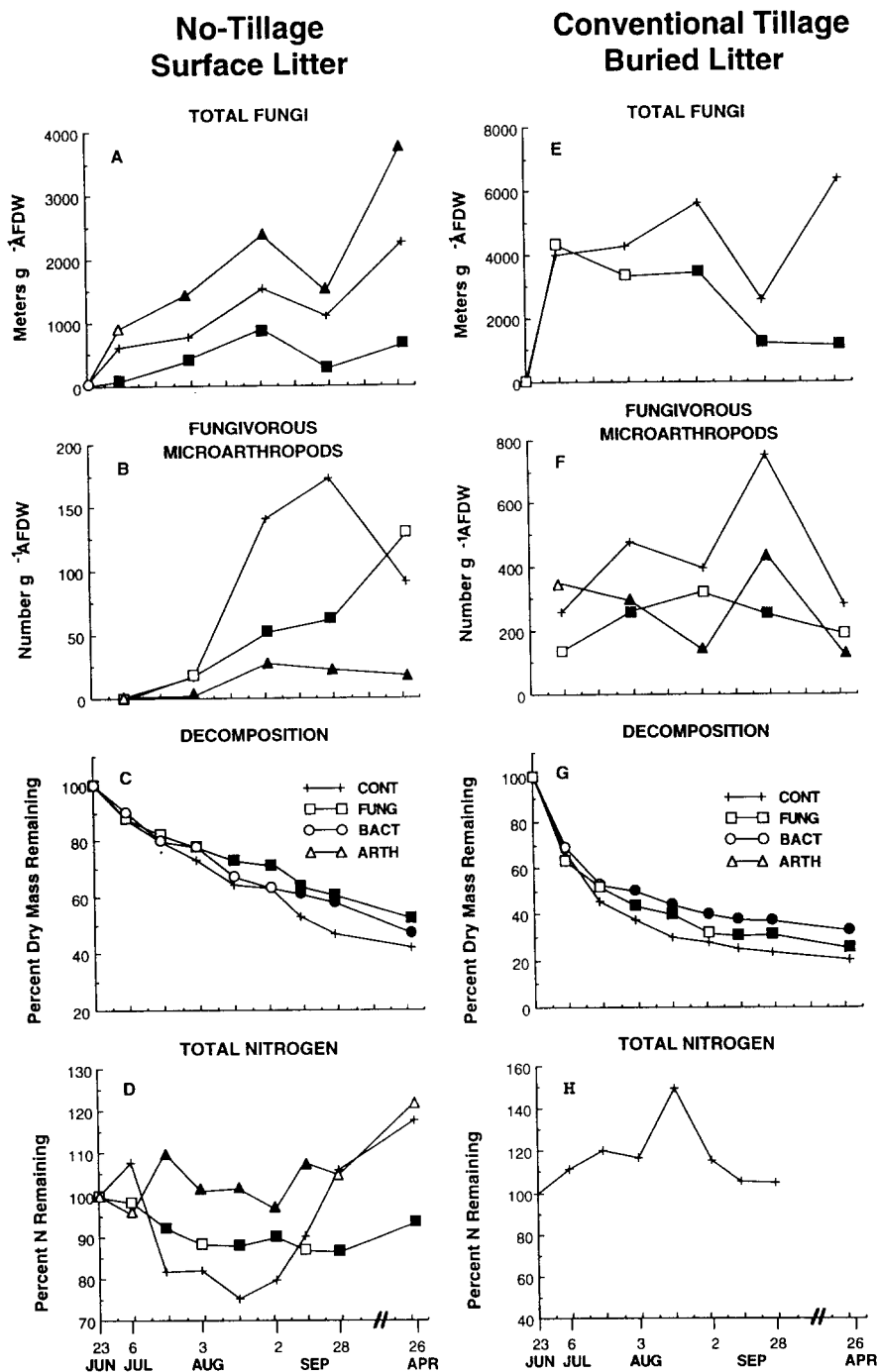


Fig. 2. Effects of biocide treatments on densities of total fungal hyphae, fungivorous microarthropods, and the percentage litter mass and nitrogen remaining in surface and buried *Secale* litter of NT and CT agroecosystems, respectively. Legend abbreviations are: CONT= Control, FUNG=Fungicide, BACT= Bactericide, ARTH=Insecticide. Results of the biotic treatments are shown only where a significant difference (ANOVA/Tukey-Kramer) from controls was detected across dates. Solid symbols show were biotic treatments differed significantly ($p < 0.05$) from controls on each sample date (after Beare et al., 1992).

Plants can also promote heterotrophic interactions in the root zone that increase mineral nutrient availability. For example, the C sources supplied in root exudates can stimulate bacterial growth and CO₂ production. The CO₂ attracts protozoan grazers, enhancing the release of microbial N in the form of NH₄⁺ for plant uptake (Clarholm, 1985).

and P mineralization than the more conservative fungivore nematode interactions. In a related study, Elliott et al. (1980) showed that soil amoebae can be an important trophic link between bacteria and bacterivorous nematodes, increasing nematode growth and C mineralization. Recent studies by Brussaard et al. (1991) provide a further example of the complex interactions that can occur in simple bacteria-bacterivore food chains. Using pre-sterilized soil microcosms reconstituted with increasingly more complex suspensions of soil organisms (bacteria and protozoa plus: bacterivore nematodes, bacterivore mites, or all three) they observed changes in the populations of amoebae and N mineralization rates that were attributed to both stimulatory and competitive interactions between bacterivorous fauna.

Soil mesofauna may have many other important indirect effects on soil processes. For example, the size and composition of microarthropod communities can influence the structure of microbial communities through their dispersal of fungal propagules (Visser, 1985), selective grazing (Newell, 1984) and/or the regrowth of fungi in response to different grazing intensities (Hanlon and Anderson, 1979).

In order to incorporate more of the functionally rich interactions among organisms, several researchers have used a biocide approach to quantify biotic and

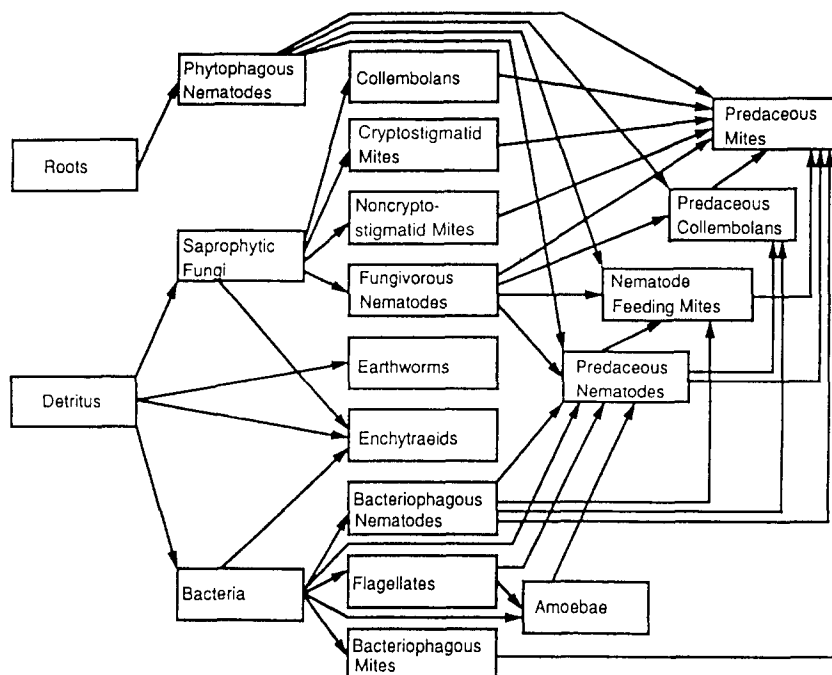


Fig. 3. A diagram of the belowground food web for the Lovinkhoeve experimental farm (from De Ruiter et al., 1993)

process level responses to the selective inhibition of targeted functional groups (e.g. Ingham et al., 1986; Parker et al., 1984). For example, Santos et al. (1981) used biocide exclusions to investigate biotic interactions and the regulation of creosote litter decomposition in desert soils. In general their results showed that nematophagous mites were important in regulating populations of bacterivorous nematodes at levels which maintained higher bacterial activity and greater litter decomposition rates than where bacterivore nematodes were more abundant.

Other examples come from our studies of conventional (CT) and no-tillage (NT) agroecosystems in Georgia. Our research has focused on the hypothesis that rates of litter decomposition and N dynamics are tied to differences in the composition of decomposer communities and their trophic interactions (Beare et al., 1992; Hendrix et al., 1986). Related studies from this site have shown that the composition of fungal (Beare et al., 1993), nematode (Parmelee and Alston, 1986) and microarthropod (Mueller et al., 1990) communities differ between CT and NT soils. Furthermore, Crossley et al. (1992) showed that long-term (14 yr) management of these soils has resulted in a greater decline in the diversity of oribatid mites in CT (5 genera) than in NT (15 genera), as compared to the 24 genera present under pre-cultivation conditions. Alternatively, prostigmatid mites have increased in response to cultivation. In a recent study, biocides were used to investigate the relative importance of fungal and bacterial pathways in decomposer food webs (Beare et al., 1992). In this study, applications of a fungicide reduced fungal densities in surface applied litter in NT, resulting in lower fungivorous microarthropod populations and slower rates of decomposition as compared to untreated controls (Fig. 2). Bacteria appeared to play a greater role in buried litter decomposition in CT soils, though bacterial populations were not strongly regulated by bacterivorous fauna. Exclusion of fungivorous microarthropods revealed their importance in regulating fungal populations and fungal-mediated N immobilization in surface residues of NT as compared to CT. Despite the interesting differences in decomposer pathways there was little evidence of tight linkages between microbivorous fauna and higher trophic levels (e.g. predatory microarthropods) as has been observed in other systems (e.g. Santos et al., 1981).

As shown above, grouping species into functionally related trophic categories is increasingly the preferred approach to integrating information on the diversity of soil biota. Using this approach, conceptual models of

belowground food webs emphasize the diversity and complexity of interactions in soils (Fig. 3; De Ruiter et al., 1993). Model simulations have furthered our understanding of these interactions and their significance to biogeochemical cycling (Hunt et al., 1987; Moore et al., 1988). The importance of integrating biodiversity into models of belowground food webs is discussed in an adjoining review.

Biodiversity and hierarchical scales of influences

Spatiotemporal heterogeneity

Factors such as resource availability, microclimatic conditions, soil solution chemistry and soil structure can significantly influence the size, composition and distribution of soil biotic communities (Wolters, 1991). In turn, characteristics of the soil community structure affect the location and rate of interspecific interactions and biogeochemical transformations in soils, factors which are important to determining the functional properties of ecosystems (Anderson, 1988). Soils can be viewed as being composed of a number of biologically relevant spheres of influence that define much of their spatial and temporal heterogeneity. Examples of these spheres include the detritusphere, the drilosphere, the porosphere, the aggregatusphere and the rhizosphere (Fig. 4). They are formed and maintained by biological influences that operate at different spatial and temporal scales. Although not mutually exclusive, each sphere has fairly distinct properties that regulate the interactions among organisms and the biogeochemical processes that they mediate.

Probably more than any other biological factor, the composition and structure of plant communities determine, directly or indirectly, the physical, chemical and biological properties of soils. Individual plants can have markedly different zones of influence in soils. For example, recent studies by Belsky et al. (1993) and Coleman et al. (1991) in the savanna of East Africa report very different patterns of influence by *Acacia* (*Acacia tortilis*) and Baobab (*Adansonia digitata*) trees on the physical (bulk density), chemical (organic matter, N, P, K, Ca) and biological (mineralizable N, microbial biomass, nematodes and plants) properties of the understory environments extending from the base of these trees. These effects may result from a number of plant specific factors ranging from differences in canopy closure or litter quality and quantity in the aboveground environment to differences

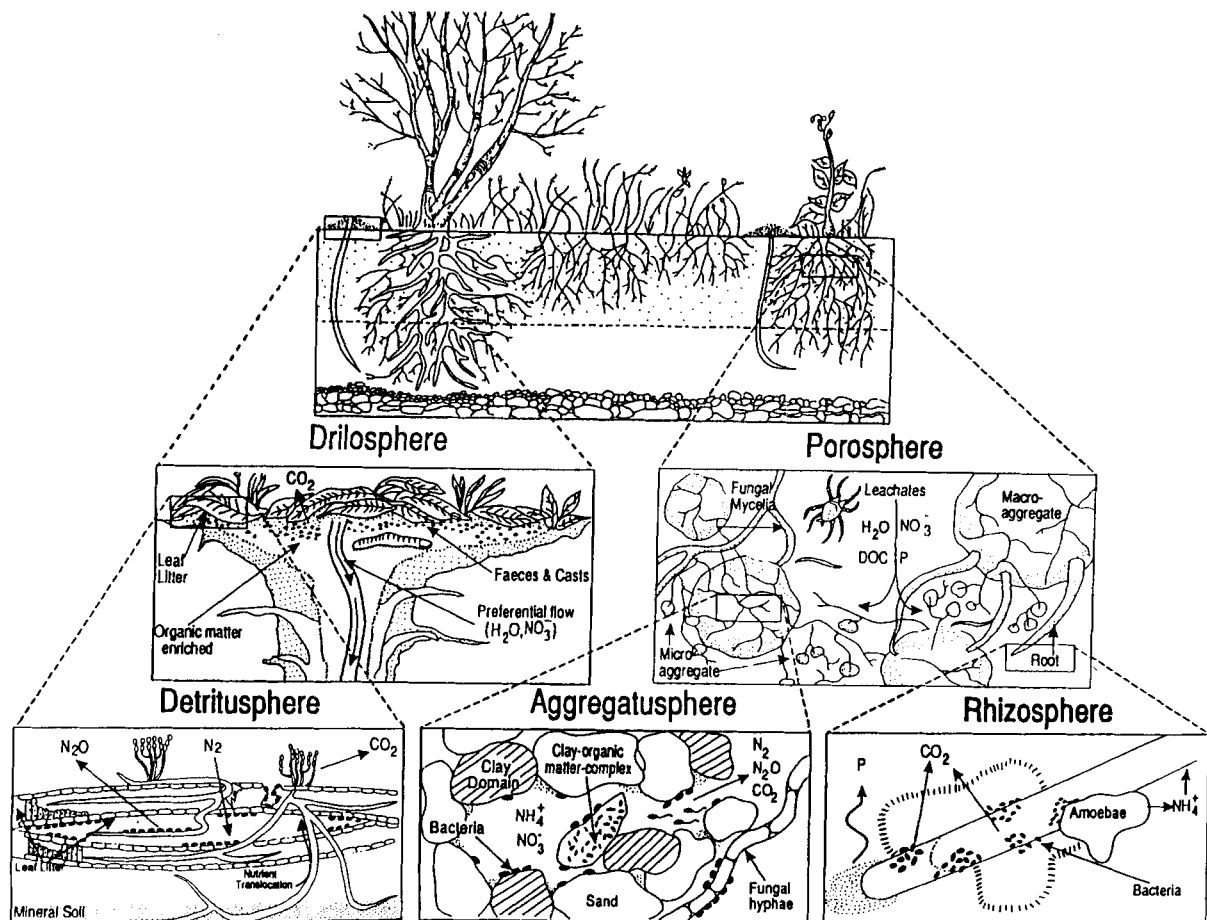


Fig. 4. A hierarchical view of biodiversity as it influences the diversity in structure and function of ecosystems. Several panels were adapted from the descriptions and renderings of Elliott and Coleman (1988), Paul and Clark (1989), Hamilton and Dindal (1983), and Clarholm (1985). The drawing was prepared by Terry Moore.

in root architecture, water use efficiency or nutrient uptake in the belowground environment.

The detritosphere

The diversity and structure of aboveground plant communities can be important to determining spatial and temporal heterogeneity in the detritosphere, i.e. the zone of recognizable plant and animal detritus undergoing decay (Fig. 4). Numerous studies have shown that the structure of decomposer communities is influenced by the chemical composition of plant detritus (Garrett, 1951; Kjølter and Struwe, 1982; Swift et al., 1979). In many cases, distinct communities of soil organisms, such as fungi (Wicklow et al., 1974) or microarthropods (Petersen and Luxton, 1982), can be ascribed to ecosystems of similar vegetational cover. Diversity in microfungal communities often correlates well with the variance in the composition of the plant

community (Christensen, 1989), a relationship that can be tied to the patchy distribution of resources. Perturbations to the soil ecosystem such as over-grazing, cultivation, and fertilizer applications tend to reduce microhabitat heterogeneity and the diversity of corresponding microfungal communities (Boddy et al., 1988; Christensen, 1989; Gochenauer, 1981). The distribution of microhabitat patches (e.g. leaf litter types, twigs) also affects their colonization by fungivorous fauna and the intensity of fungivore grazing, factors that influence rates of fungal regrowth (Bengtsson et al., 1993). Furthermore, microhabitat patches may create a mosaic of aerobic and anaerobic microsites that promote the activities of N_2 -fixing and denitrifying microorganisms in the detritosphere (Aulakh et al., 1991; Lynch and Harper, 1985). Finally, patterns of microbial and faunal colonization and the resulting trophic interactions can influence the magnitude and

timing of nutrient fluxes in litter (Beare et al., 1992; Parker et al., 1984).

Relationships between litter quality (chemical composition), decomposition and mineral nutrient dynamics are well known for single species litter (Melillo et al., 1982; Taylor et al., 1989; Swift et al., 1979). However, in most terrestrial ecosystems residues of different plant species rarely occur in isolation and are often found in close proximity to each other. Some authors have proposed that nutrient releases from rapidly decaying litter stimulate decomposition of adjacent recalcitrant litter (Seastedt, 1984) while others suggest inhibitory compounds such as phenolics and tannins may slow the decomposition of litter mixtures (e.g. Harrison, 1971). Recent studies by Blair et al. (1990) provide support for these hypotheses, showing that interaction between litter types can alter decomposer communities and rates of nutrient release from that predicted by results from single species litter. Similarly, in a study of forest floor processes, Chapman et al. (1988) found that nutrient availability, leaching, heterotrophic activity and selected faunal populations were higher in spruce/pine mixtures, but lower in spruce/alder and spruce/oak forests relative to spruce monocultures. The number and frequency of interacting litter types will depend on the richness of plant species and their patterns of distribution.

The drilosphere

Many soil fauna actively change the size and distribution of plant litter on the soil surface. For example, microarthropods and millipedes fragment plant litter, increasing the surface area for microbial attack and mixing the fragments with other detritus (Anderson et al., 1985; Seastedt, 1984). Macrofauna such as earthworms and termites redistribute plant litter both vertically and horizontally in the soil environment, creating patches of organic matter that are both substrates and refugia for microorganisms and fauna (Lee, 1985). For instance, some earthworms form leaf litter middens around their burrow openings (Hole, 1981) creating a patchwork of organic matter-enriched sites that are heavily colonized by organisms such as saprophytic fungi, oribatid mites, millipedes and enchytraeids (Dózsa-Farkas, 1978; Hamilton and Sillman, 1989). This zone of earthworm influence, including midden litter and the soil volume descending along the burrow wall is often referred to as the "drilosphere" (Hamilton and Dindal, 1983; Lavelle et al., 1989; Fig. 4). Drilosphere soils are enriched in N, P, and humified organic

matter as compared to the surrounding soils. They are also estimated to contain a high percentage of the whole soil N₂-fixing and denitrifying bacteria (Bhatnagar, 1975). However, the nature of these influences differs between species, in accordance with their ecological classification. For example, Shaw and Pawluk (1986) observed that deep burrowing anecic earthworms had effects on the soil fabric that were localized in the drilosphere. But where endogeic species were also present, their activities tended to homogenize the surface soil horizons. Clearly, these interactions can greatly affect the heterogeneity of organisms and processes in soils.

The porosphere

Soil structure can be defined as the arrangement of solids and voids in soils covering a range of sizes from nanometers to centimeters (Oades, 1993). The influences of soil biota span the full range of sizes, affecting the pore size distribution through biopore development and the formation and disruption of soil aggregates. This milieu, termed the "porosphere" (Vannier, 1987) is occupied by organisms ranging from bacteria, protozoa and nematodes inhabiting water-films to microarthropod and mycelial fungi that are aerial inhabitants of larger pores (Fig. 4).

By physically rearranging soil particles, larger soil biota such as plant roots, earthworms and other macrofauna create smooth, cylindrically shaped macropores. These biopores extend considerable distances in the soil, forming channels for the preferential flow of water and nutrients under some conditions. The size and configuration of biopores appears to depend greatly on the species from which they are formed (Lee and Foster, 1991). Probably the best known examples come from the activities of macrofauna, particularly ants, termites and earthworms. Mound-forming ants and termites have pronounced and often patchy effects on soil structure and nutrient cycling (Lobry de Bruyn and Conacher, 1990). The denuded surfaces surrounding many mounds tend to increase surface runoff. However, mounds are also sites of nutrient enrichment due to subsoil nutrients brought to the surface and the storage of plant detritus in their galleries. Some species, notably the western harvester ant (*Pogonomyrmex occidentalis*), enrich their nests with VAM spores that are capable of high levels of endophyte infection (Frieese and Allen, 1993).

As noted previously, the burrowing activities of earthworms differ substantially among species, affecting biopore development and the processes they medi-

ate. For example, where deep burrowing species (e.g. *Allolobophora*) are present, soils have greater total porosity, increasing infiltration rates and the rooting depth of plants over that of soils having only surface-dwelling species (Springett, 1985). Furthermore, removal of earthworms can markedly affect the transport of sediment and nutrients. For instance, Sharpley et al. (1979) observed lower infiltration rates and greater surface transport of water-soluble nutrients (NH_4^+ , NO_3^- , dissolved P) in a pasture where earthworms were removed with a broad-spectrum carbamate biocide as compared to untreated soils. Interestingly, however, plots with earthworms had more than three-fold higher rates of sediment transport than plots without earthworms. Effects of earthworm removals in other ecosystems will undoubtedly depend on the composition of the macrofaunal communities and their specific burrowing and feeding activities.

Macropores also provide sites of concentrated microbial activity and, as such, they are frequently colonized by high numbers of microbivorous microarthropods, nematodes and protozoa (Lee and Foster, 1991). In other cases, microarthropods and perhaps other soil fauna use abandoned biopores as channels for vertical migration in response to changes in moisture availability (Malinda et al., 1982; as cited in Oades, 1993). In undisturbed soils, they can also be sites of concentrated mycorrhizal inocula, increasing rates of mycorrhizal infection and phosphorous availability as compared to plants grown in plowed soils (Evans and Miller, 1988).

Where they persist, macropores can also be sites of preferential root growth, enabling roots to penetrate compacted soils, thereby gaining access to water and solutes that may otherwise be of limited availability (Logsdon and Linden, 1992; Passioura, 1991). Furthermore, burrow walls are often enriched in nutrients, promoting root growth and increasing the potential for nutrient uptake by plants (Kladivko and Timmenga, 1990).

The aggregatusphere

Soil organisms have many wide-ranging effects on soil aggregation that can influence the physical, chemical and biological properties of soils (Lee and Foster, 1991). Aggregates are comprised of a number of hierarchically arranged components, ranging from clay microstructures and fine particulate organic matter to microaggregates (50–250 μm diam) made up of these primary particles and macroaggregates (>250 μm diam) composed of smaller microaggregates (Oades

and Waters, 1991). The aggregatusphere can be defined as encompassing all the organic matter constituents, primary particles and voids that span the complete hierarchical scale (Fig. 4). The primary boundaries of this sphere are those that limit the exchange of biota, solutes and gases across aggregate surfaces, properties that depend on the scale from which they are viewed.

The contributions of soil biota to aggregate formation occur principally through bioturbation. They are most apparent in soils of lower clay content and low shrink-swell capacities where the abiotic effects of wet-dry and freeze-thaw cycles are reduced (Oades, 1993). In many temperate regions the litter-feeding activities of surface-dwelling invertebrates, such as microarthropods, are responsible for large accumulations of particulate and fecal aggregates in surface soils (Rusek, 1985). In other soils, earthworm casts can account for nearly 50% of the macroaggregates (>250 μm diam) in surface horizons (Lee, 1985). The effects of earthworms on the formation of soil aggregates can be highly species specific (Lee and Foster, 1991). Rates of cast production as well as the degree to which they are enriched with organic matter and nutrients also vary among species. For example, James (1991) found that the native *Diplocardia* spp. from a tallgrass prairie in Kansas were responsible for much more of the total cast production and a greater proportion of the total cast-associated organic matter and nutrients than the exotic Lumbricidae. Furthermore, the effects of one organism can modify the influences of another. Hamilton and Dindal (1989), for example, showed that the compost worm *Eisenia fetida* inhibited the feeding of *Lumbricus terrestris* on surface litter, causing a decline in *L. terrestris* populations and the 4 mm water-stable aggregates they form.

When conditioned by drying and the activities of microorganisms, earthworm casts can have higher porosity and greater stability than non-casted aggregates (Lee and Foster, 1991; Shipitalo and Protz, 1988). Several authors have concluded that the stability of earthworm casts is strongly influenced by the quantity and composition of organic matter they contain (Lee, 1985), properties that can be highly species specific. Earthworms affect the stabilization of aggregates both directly, through the rearrangement of particles and the deposition of mucus, and indirectly, through the stimulation of microbial, principally fungal, activity (Marinissen and Dexter, 1990).

Microorganisms are the primary agents of aggregate stabilization. Both fungi and bacteria contribute to the stabilization of soil aggregates through the depo-

sition of extracellular polysaccharides and formation of degraded, aromatic humic materials that form clay-polyvalent metal-organic matter complexes. Though not as persistent, fungi also contribute to aggregate stabilization through hyphal entanglement of particles. The influences of fungi and bacteria on aggregate stabilization vary widely among species and depend considerably on the nature of the available substrates (Aspiras et al., 1971), such as those that may be added or modified in passage through the animal gut (Lee and Foster, 1991) or the products of rhizodeposition (Reid and Goss, 1981). Soil micro- and meso fauna may indirectly influence soil aggregation through their effects, both stimulatory and inhibitory, on the activities of roots and microorganisms, although the mechanisms involved have been little studied (Elliott and Coleman, 1988; Wolters, 1991). Furthermore, both the composition of microbial communities and their contribution to aggregate stabilization can be influenced by the type of landuse management (Beare et al., 1993, 1994b).

Various factors, including the rearrangement of mineral particles and the deposition of polysaccharides may create occluded micropores in aggregates, perhaps restricting the access of some microbivorous fauna to protected sites of microorganisms. For example, Elliott et al. (1980) presented evidence to show that by feeding on bacteria in pores inaccessible to nematodes, protozoa can serve as an important trophic link between bacteria and nematodes in finer-textured soils. Furthermore, Foster and Dormaar (1991) showed that amoebae can extend pseudopodia into narrow pore necks to consume bacteria, possibly confining bacteria to the interiors of aggregates. In selected microsites, organic matter may become sufficiently occluded so as to be protected from microbial decay (Beare et al., 1994a; Elliott, 1986). This represents a potentially important mechanism by which organisms influence the accumulation and storage of soil organic matter. Still, the extent to which protected organic matter may be affected by mode of aggregate formation and stabilization remains largely unknown.

Spatial variability in soil structure has often been attributed to biologically mediated properties. As sites of potentially high C availability and limited O₂ diffusion, water-saturated aggregates can function as anaerobic microsites, supporting high rates of denitrification (Tiedje et al., 1984). Spatially heterogeneous distributions of aggregates coupled with differences in their organochemical composition may explain some of the high spatial variability in N cycling processes (e.g. nitrification, N mineralization) in many soils, par-

ticularly the "hotspots" of denitrification, reported by Robertson et al. (1988), Elliot et al. (1990) and others.

The rhizosphere

The zone of primary root influence can be termed the "rhizosphere" (Fig. 4). It is a temporally and spatially variable environment where the products of rhizodeposition stimulate microbial activity and where microfauna track bacterial and fungal populations, thereby altering the balance between N mineralization and immobilization (Clarholm, 1985; Coleman et al., 1988). The biomass of soil microflora and fauna is usually greater in the rhizosphere than in root-free soil (Bowen and Rovira, 1991), although species diversity does not necessarily parallel this trend. For example, some studies show that fungal species diversity is lower while the morphological diversity of bacteria and actinomycetes is higher in the rhizosphere as compared to soil outside this zone (Bowen and Rovira, 1991). The extent of these effects depend on characteristics of root growth, including their production, turnover and architecture.

Root architecture both influences and is influenced by the physical, chemical and biological properties of soils. Developing root systems respond strongly to soil fertility. The proportion of total plant production allocated belowground and the architecture of the root system (e.g. root length, branching frequency and mycorrhizal development) depend greatly on the distribution and availability of nutrients (Fitter, 1985). Increases in fine root proliferation, slower root turnover, and greater allocations of plant C to mycorrhizal associates tend to occur where nutrients are low or patchily distributed.

Soil structure also influences root architecture. As mentioned previously, abandoned earthworm channels can be paths of preferential root growth and vice versa. Root growth also appears to be influenced by the extent of aggregation in soil, often being greater in soils composed of smaller rather than larger aggregates (e.g. Donald et al., 1987). Roots also influence the stability of aggregates, principally through the deposition of polysaccharides in the rhizosphere and their removal of soil water. These effects can be highly species specific, both increasing and decreasing aggregate stability (Reid and Goss, 1981). As such, they may have fairly localized effects on the aggregation of soils. Furthermore, Jastrow (1987) and Miller and Jastrow (1990) have shown that the formation of water-stable aggregates can be related to the biomass of roots as well as the composition of the plant community.

Differences in root architecture determine the quantity and location of rhizodeposited organic matter (Curl and Truelove, 1986; Feldman, 1988). Roots of different species also vary in the composition of exudates and their rates of deposition. Depending on their source, root exudates can inhibit the growth of phytopathogenic microorganisms and alter the composition of the rhizosphere community. Though not well studied, mycorrhizal symbionts also influence characteristics of root exudates that shape the composition and activity of the rhizosphere community (e.g. Meyer and Linderman, 1986).

Biodiversity and the scale of biogeochemical processes

The fluxes of elements in ecosystems are a product of biogeochemical processes that occur at different hierarchical levels. Anderson (1988) argued that ecosystem-level fluxes are the net effect of processes that occur across a mosaic of microsites, varying in the degree to which they promote or inhibit a given process. He further suggested that any perturbations (e.g. flooding) to the soil system that impose synchrony on the microsite processes will be manifested as fairly distinct flushes of activity (e.g. N mineralization, denitrification), altering the regulatory balance between microsites. While many perturbations will have only relatively transient influences on microsite processes (e.g. extreme wetting or drying) others may markedly alter the mosaic of patches and microsites in soils (e.g. intensive cultivation, forest clearcuts), resulting in a much more persistent effect on the processes they mediate.

Through a hierarchy of interactions, biodiversity in both the aboveground and belowground environments is critical to developing and maintaining the diverse mosaic of resource patches and microsites in soils. The broad array of distinct resource and refuge types (e.g. leaf litter types, fecal pellets, macropores, aggregates) that comprise these patches are a product of diversity at different spatial and temporal scales (e.g. plant communities, macrofaunal communities). Swift (1984) referred to the species assemblages occupying these distinct resources as "unit communities". Due to differences in the colonization of individual patches and the interactions among colonizing species, the diversity of species (and presumably functions) in the total community ("metacommunity") occupying a given resource is expected to be greater than that of any single patch (Wilson, 1992). Although many of the biological interactions that cross different spatial and temporal scales will encourage a diversification of

microsites and microsite processes, others may tend to reduce the discontinuity between patches. For example, the comminution and mixing of leaf litter by some mesofauna, mentioned previously, may serve to fragment patches into a relatively homogeneous mixture, thereby reducing the number of unit communities and eliminating their patchy distribution. In this way, some organisms may reduce the structural and functional diversity in soils by altering the patch mosaic. As a result of these complex interactions, diversity at one hierarchical level (e.g. plant, macrofauna communities) within an ecosystem may influence the diversity of both structure (e.g. species, functional groups) and function (e.g. lignin degradation, N immobilization, denitrification) at other hierarchical levels (e.g. detritusphere, rhizosphere, aggregatusphere). It is through this influence that biodiversity may contribute most significantly to the functioning of soil ecosystems.

In conclusion, advances in understanding the significance of biodiversity to biogeochemical cycling will come from taking a broader view of biodiversity. Such a view will necessarily encompass many levels of resolution from: 1) individual organisms and their specific biogenic transformations to 2) the complex interactions between organisms that have important direct and indirect effects on biogeochemical processes and, finally 3) the influence of biodiversity at one spatiotemporal scale on the diversity of structure and function at other levels of organization.

Acknowledgements

We are grateful for the valuable critiques and suggestions given by our colleagues at the University of Georgia: George Brown, Miguel Cabrera, Ron Carroll, Shuijin Hu and Petra van Vliet. Special thanks are extended to Terry Moore for his artistic contributions to the diagram of hierarchical properties (Fig. 4). The preparation of this review was supported in part by grants from the NSF (BSR-8818302) and USDA-NRI (91-37102-6785).

References

- Alexander M 1977 Introduction to Soil Microbiology. 2nd ed. Academic Press, New York.
- Ali M A, Tribulsi J Y and Abd-Elsamea M E 1981 Antagonistic interactions between *Meloidogyne incognita* and *Rhizobium leguminosarum* on cowpea. Plant Dis. 65, 432-435.

- Anderson J M 1988 Spatiotemporal effects of invertebrates on soil processes. *Biol. Fert. Soils* 6, 216–227.
- Anderson J M, Huish S A, Ineson P, Leonard M A and Splatt P R 1985 Interactions of invertebrates, microorganisms and tree roots in nitrogen and mineral element fluxes in deciduous woodland soils. *In Ecological Interactions in Soil*. Eds. A H Fitter, D Atkinson, D J Read and M B Usher. pp 377–392. Blackwell, Oxford.
- Allen M F 1992 Mycorrhizal Functioning: An Integrative Plant-Fungal Process. Chapman and Hall, New York.
- Aspiras R B, Allen O N, Harris R F and Chester G 1971 The role of microorganisms in the stabilization of soil aggregates. *Soil Biol. Biochem.* 3, 347–353.
- Aulakh M S, Doran J W, Walters D T, Mosier A R and Francis D D 1991 Crop residue type and placement effects on denitrification and mineralization. *Soil Sci. Soc. Am. J.* 55, 1020–1025.
- Bååth E and Söderström B 1980 Degradation of macromolecules by microfungi isolated from different podzolic soil horizons. *Can. J. Bot.* 58, 422–425.
- Barea J M 1991 Vesicular-arbuscular mycorrhizae as modifiers of soil fertility. *Adv. Soil Sci.* 15, 2–40.
- Barois I and Lavelle P 1986 Changes in respiration rate and some physicochemical properties of a tropical soil during transit through *Pontosclex corethrurus* (Glossoscolecidae, Oligochaeta). *Soil Biol. Biochem.* 18, 539–541.
- Barnes G L, Russell C C, Foster W D and McNew R W 1981 *Aphelechu avenae*, a potential biological control agent for root rot fungi. *Plant Dis.* 65, 423–432.
- Beare M H, Cabrera M L, Hendrix P F and D C Coleman 1994a Aggregate-protected and unprotected pools of organic matter in conventional and no-tillage soils. *Soil Sci. Soc. Am. J.* 58, 787–795.
- Beare M H, Hu S, Coleman D C and Hendrix P F 1994b Influences of mycelial fungi on soil aggregation and soil organic matter retention in conventional and no-tillage soils. *Geoderma* (submitted).
- Beare M H, Pohlad B R, Wright D H and Coleman D C 1993 Residue placement and fungicide effects on fungal communities in conventional and no-tillage soils. *Soil Sci. Soc. Am. J.* 57, 392–399.
- Beare M H, Parmelee R W, Hendrix P F, Cheng W, Coleman D C and Crossley D A Jr 1992-Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecol. Monogr.* 62, 569–591.
- Belsky A J, Mwonga A M, Amundson R G, Duxbury J M and Ali A R 1993 Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *J. Appl. Ecol.* 30, 143–155.
- Bengtsson G, Hedlund K and Rundgren S 1993 Patchiness and compensatory growth in a fungus-Collembola system. *Oecologia* 93, 296–302.
- Bettany J R and Stewart J W B 1982 Sulfur cycling in soils. *Proc. Int. Sulfur Inst.* 2, 767–785.
- Bhatnagar T 1975 Lombriciens et humification: Un aspect nouveau de l'incorporation microbienne d'azote induite par les vers de terre. *In Biodégradation et Humification*. Eds. G Kilbertus, O Reisinger, A Mourey and J P Cancela da Fonesca. pp 157–168. Pierron, Sarreguemines, France.
- Blair J M, Parmelee R W and Beare M H 1990 Decay rates, nitrogen fluxes and decomposer communities of single- and mixed species foliar litter. *Ecology* 71(5), 1976–1985.
- Boddy L, Watling R and Lyon A J E 1988 Fungi and ecological disturbance. *Proc. Royal Soc. Edinburgh, B*, 94.
- Bouché M B 1971 Relations entre les structures spatiales et fonctionnelles des écosystèmes, illustrées par le rôle pédobiologique des vers de terre. *In La Vie dans les Sols: Aspects nouveaux, Etudes Experimentales*. Ed. P Pesson. pp 187–209. Gauthier-Villars, Paris.
- Bowen G D and Rovira A D 1991 The rhizosphere, the hidden half. *In Plant Roots. The Hidden Half*. Eds. Y Waisel, A Eshel and U Kafkafi. pp 641–669. Marcel Dekker, New York.
- Broder M W and Wagner G H 1988 Microbial colonization and decomposition of corn, wheat, and soybean residues. *Soil Sci. Soc. Am. J.* 52, 112–117.
- Brussaard L, Kools J P, Bouwman L A and de Ruiter P C 1991 Population dynamics and nitrogen mineralization rates in soil as influenced by bacterial grazing nematodes and mites. *In Advances in Management and Conservation of Soil Fauna*. Eds. G K Veeresh, D Rajagopal and C A Viraktamath. pp 517–523. Oxford and IBH Publishing Co., New Delhi.
- Cairney J W G 1992 Translocation of solutes in ectomycorrhizal and saprotrophic rhizomorphs. *Mycol. Res.* 96, 135–141.
- Charkarborty S, Old K M and Warcup J H 1983 Amobae from a take-all suppressive soil which feed on *Gaeumannomyces graminis tritici* and other soil fungi. *Soil Biol. Biochem.* 15, 17–24.
- Chapman K, Whittaker J B and Heal O W 1988 Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agric. Ecosyst. Environ.* 24, 33–40.
- Christensen M 1989 A view of fungal ecology. *Mycologia* 81, 1–19.
- Clarholm M 1985 Possible roles of roots, bacteria, protozoa and fungi in supplying nitrogen to plants. *In Ecological Interactions in Soil*. Eds. A H Fitter, D Atkinson, D J Read and M B Usher. pp 297–317. Blackwell, Oxford.
- Coleman D C 1985 Through the ped darkly: An ecological assessment of root-soil-microbial-faunal interactions. *In Ecological Interactions in Soil*. Eds. A H Fitter, D Atkinson, D J Read and M B Usher. pp 297–317. Blackwell, Oxford.
- Coleman D C, Reid C P P and Cole C V 1983 Biological strategies of nutrient cycling in soil systems. *Adv. Ecol. Res.* 13, 1–55.
- Coleman D C, Crossley D A Jr, Beare M H and Hendrix P F 1988 Interactions of organisms at root/soil and litter/soil interfaces in terrestrial ecosystems. *Agric. Ecosyst. Environ.* 24, 117–134.
- Coleman D C, Edwards A L, Belsky A J and Mwonga S 1991 The distribution and abundance of soil nematodes in East African savannas. *Biol. Fert. Soils* 12, 67–72.
- Cromack K and Caldwell B A 1992 The role of fungi in litter decomposition and nutrient cycling. *In The Fungal Community, Its Organization and Role in the Ecosystem*. Eds. G C Carroll and D T Wicklow. pp 601–618. Marcel Dekker, Inc., New York.
- Crossley Jr D A, Mueller B R and Perdue J C 1992 Biodiversity of microarthropods in agricultural soils: relations to processes. *Agric. Ecosyst. Environ.* 40, 37–46.
- Curl E A and Truelove B 1986 *The Rhizosphere*. Springer-Verlag, Berlin.
- Curl E A, Gudauskas R T, Harper J D and Peterson C M 1985 Effects of soil insects on populations and germination of fungal propagules. *In Ecology and Management of Soilborne Plant Pathogens*. Eds. C A Parker, A D Rovira, K J Moore, P T W Wong and J F Kollmorgen. pp 20–23. American Phytopathological Society, St. Paul.
- De Ruiter P C, Moore J C, Zwart K B, Bouwman L A, Hassink J, Bloem J, De Vos J A, Marinissen J C Y, Didden W A M, Lebbink G and Brussaard L 1993 Simulation of nitrogen mineralization in the below-ground food web of two winter wheat fields. *J. Appl. Ecol.* 30, 95–106.
- di Castri F and Younes T 1990 Ecosystem function of biological diversity. *Biol. Int. Special Issue N°22*.
- Didden W A M 1990 Involvement of Enchytraeidae (Oligochaeta) in soil structure evolution in agricultural fields. *Biol. Fert. Soils* 9, 152–158.

- Dighton J and Boddy L 1989 Role of fungi in nitrogen, phosphorus and sulphur cycling in temperate forest ecosystems. In *Nitrogen, Phosphorus and Sulphur Utilization by Fungi*. Eds. L Boddy, R Marchant and D J Read. pp 269–298. Cambridge University Press, Cambridge.
- Donald R G, Kay B D and Miller M H 1987 The effect of soil aggregate size on early shoot and root growth of maize (*Zea mays* L.). *Plant and Soil* 103, 251–259.
- Dózsa-Farkas K 1978 Die ökologische Bedeutung des Mikrohabitates für das Vorkommen einiger Enchytraeiden-Arten. *Pedobiologia* 18, 366–372.
- Elliott E T 1986 Aggregate structure and carbon, nitrogen and phosphorus in native and cultivated soils. *Soil Sci. Soc. Am. J.* 50, 627–633.
- Elliott E T, Anderson R V and Coleman D C 1980 Habitable pore space and microbial trophic interactions. *Oikos* 35, 327–335.
- Elliott E T and Coleman D C 1988 Let the soil work for us. *Ecol. Bull.* 39, 23–32.
- Elliot P W, Knight D and Anderson J M 1990 Denitrification in earthworm casts and soil from pastures under different fertilizer and drainage regimes. *Soil Biol. Biochem.* 22, 601–605.
- Evans D G and Miller M H 1988 Vesicular-arbuscular mycorrhizas and the soil-disturbance-induced reduction of nutrient absorption in maize. *New Phytol.* 110, 67–74.
- Feldman L J 1988 The habits of roots. *Bioscience* 38, 612–618.
- Fitter A H 1985 Functional significance of root morphology and root system architecture. In *Ecological Interactions in Soil*. Eds. A H Fitter, D Atkinson, D J Read and M B Usher. pp 87–106. Blackwell, Oxford.
- Foster R C and Dormaar J F 1991 Bacteria-grazing amoebae in situ in the rhizosphere. *Biol. Fertil. Soils* 11, 83–87.
- Franklin J F 1993 Preserving biodiversity: species, ecosystems, or landscapes? *Ecol. Applic.* 3, 202–205.
- Fries N 1973 Effects of volatile organic compounds on the growth and development of fungi. *Trans. Brit. Mycol. Soc.* 60, 1–21.
- Friese C F and Allen M F 1993 The interaction of harvester ants and vesicular-arbuscular mycorrhizal fungi in a patchy semi-arid environment: the effects of mound structure on fungal dispersion and establishment. *Functional Ecol.* 7, 13–20.
- Garrett S D 1951 Ecological groupings of soil fungi: A survey of substrate relationships. *New Phytol.* 50, 149–166.
- Gochenauer S E 1981 Responses of soil fungal communities to disturbance. In *The Fungal Community: Its Organization and Role in the Ecosystem*. Eds. D T Wicklow and G C Carroll. pp 459–479. Marcel Dekker, New York.
- Grime J P 1979 *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester, England.
- Halsall D M and Gibson A H 1986 Comparison of two *Cellulomonas* strains and their interactions with *Azospirillum brasilense* in degradation of wheat straw and associated nitrogen fixation. *Appl. Environ. Microbiol.* 51, 855–861.
- Hanlon R D G and Anderson J M 1979 The effects of Collembola grazing on microbial activity in decomposing leaf litter. *Oecologia* 38, 93–99.
- Hamilton W E and Dindal D L 1983 The vermisphere concept: Earthworm activity and sewage sludge. *Biocycle* 24, 54–55.
- Hamilton W E and Dindal D L 1989 Influence of earthworms and leaf litter on edaphic variables in sewage-sludge-treated soil microcosms. *Biol. Fertil. Soils* 7, 129–133.
- Hamilton W E and Sillman D Y 1989 Influence of earthworms middens on the distribution of soil microarthropods. *Biol. Fertil. Soils* 8, 279–284.
- Harper D B 1985 Halomethane from halide ion - a highly efficient fungal conversion of environmental significance. *Nature* 315, 55–57.
- Harper S H T and Lynch J M 1985 Colonization and decomposition of straw by fungi. *Trans. Brit. Mycol. Soc.* 85, 655–661.
- Harrison A F 1971 The inhibitory effect of oak leaf litter tannins on the growth of fungi in relation to litter decomposition. *Soil Biol. Biochem.* 3, 167–172.
- Hawksworth D L 1991 The fungal dimension of biodiversity: Magnitude, significance, and conservation. *Mycol. Res.* 95, 641–655.
- Hendrix P F, Parmelee R W, Crossley D A Jr, Coleman D C, Odum E P and Groffman P M 1986 Detritus food webs in conventional and no-tillage agroecosystems. *Bioscience* 36, 374–380.
- Hendrix P F, Crossley D A Jr, Blair J M and Coleman D C 1990 Soil biota as components of sustainable agroecosystems. In *Sustainable Agricultural Systems*. Eds. C A Edwards, R Lal, P Madden, R H Miller and G House. pp 637–654. Soil and Water Conservation Society, Ankeny, Iowa.
- Hole F D 1981 Effects of animals in soil. *Geoderma* 25, 75–112.
- Hunt H W, Coleman D C, Ingham E R, Ingham R E, Elliott E T, Moore J C, Rose S L, Reid C P P and Morley C R 1987 The detrital food web in a shortgrass prairie. *Biol. Fertil. Soils* 3, 57–68.
- Ingham R E, Trofymow J A, Ingham E R and Coleman D C 1985 Interactions of bacteria, fungi and their nematode grazers: Effects on nutrient cycling and plant growth. *Ecol. Monogr.* 55, 119–140.
- Ingham E R, Trofymow J A, Ames R N, Hunt H W, Morley C R, Moore J C and Coleman D C 1986 Trophic interactions and nitrogen cycling in a semi-arid grassland soil. *J. Appl. Ecol.* 23, 615–630.
- James S W 1991 Soil nitrogen, phosphorus and organic matter processing by earthworms in tallgrass prairie. *Ecology* 72, 2101–2109.
- Janos D P 1980 Mycorrhizae influence tropical succession. *Biotropica* 12 (Suppl.), 56–64.
- Jastrow J D 1987 Changes in soil aggregation associated with tall-grass prairie restoration. *Am. J. Bot.* 74, 1656–1664.
- Jennings D H 1990 The ability of basidiomycete mycelium to move nutrients through the soil ecosystem. In *Nutrient Cycling in Terrestrial Ecosystems*. Eds. A F Harrison, P Ineson and O W Heal. pp 233–245. Elsevier Science Publishers, Ltd, London.
- Jha D K, Sharma G D and Mishra R R 1993 Mineral nutrition in the tripartite interaction between *Frankia*, *Glomus* and *Alnus* at different soil phosphorus regimes. *New Phytol.* 123, 307–311.
- Jones J W 1991 Diversity and physiology of methanogens. In *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*. Eds. J E Rogers and W B Whitman. pp 39–55. American Society of Microbiology, Washington, DC.
- Killham K 1987 Heterotrophic nitrification. In *Nitrification*. Ed. J Prosser. pp 117–126. Society of General Microbiology, Spec. Public. I.R.L. Press, Oxford.
- Killham K, Sinclair A H and Allison M F 1988 Effect of straw addition on composition and activity of soil microbial biomass. *Proc. R. Soc. Edinburgh* 94B, 135–143.
- Kjoller A and Struwe S 1982 Microfungi in ecosystems: Fungal occurrence and activity in litter and soil. *Oikos* 39, 391–422.
- Kladivko E J and Timmenga H J 1990 Earthworms and agricultural management. In *Rhizosphere Dynamics*. Eds. J E Box and L C Hammond. pp 192–216. ASA Selected Symposium 113, Madison.
- Knoll M A and James W C 1987 Effect of the advent and diversification of vascular plants on mineral weathering through geologic time. *Geology* 15, 1099–1102.

- Kuikman P J and van Veen J A 1989 The impact of Protozoa on the availability of bacterial nitrogen to plants. *Biol. Fert. Soils* 8, 13–18.
- Lavelle P 1983 The structure of earthworm communities. *In* Earthworm Ecology, From Darwin to Vermiculture. Ed. J E Satchell. pp 449–474. Chapman and Hall, London.
- Lavelle P, Barois I, Martin A, Zaidi Z and Schaefer R 1989 Management of earthworm populations in agro-ecosystems: A possible way to maintain soil quality? *In* Ecology of Arable Land. Eds. M Clarholm and I Bergström. pp 109–122. Kluwer Academic Publishers, Dordrecht.
- Lawrence J R and Germida J J 1988 A most probable number method (MPN) for the enumeration of heterotrophic thiosulphate producing sulfur oxidizers in soil. *Soil Biol. Biochem.* 20, 577–578.
- Lee K E 1959 The earthworm fauna of New Zealand. *N.Z. Dept. Sci. Ind. Res. Bull.* 130, 1486.
- Lee K E 1985 Earthworms: Their Ecology and Relationships with Soils and Land Use. Academic Press, Sydney. 411 p.
- Lee K E and Foster R C 1991 Soil fauna and soil structure. *Aust. J. Soil Res.* 29, 745–775.
- Lee K E and Pankhurst C E 1992 Soil organisms and sustainable productivity. *Aust. J. Soil Res.* 30, 855–892.
- Likens G E, Bormann F H, Pierce R S, Eaton J S and Johnson N M 1977 Biogeochemistry of a forested ecosystem. Springer-Verlag, New York. 146 p.
- Lobry de Bruyn L A and Conacher A J 1990 The role of termites and ants in soil modification: A review. *Aust. J. Soil Res.* 28, 55–93.
- Logsdon S L and Linden D R 1992 Interaction of earthworms with soil physical conditions and plant growth. *Soil Sci.* 154, 330–337.
- Lynch J M and Harper S H T 1985 The microbial upgrading of straw for agricultural use. *Phil. Trans. R. Soc. London.* 310 B, 221–226.
- Marinissen J C Y and Dexter A R 1990 Mechanisms of stabilization of earthworm casts and artificial casts. *Biol. Fertil. Soils* 9, 163–167.
- Mehta A P, Torma A E and Murr L E 1979 Effect of environmental parameters on the efficiency of biodegradation of basalt rock by fungi. *Biotechnol. Bioeng.* 21, 875–885.
- Melillo J M, Aber J D and Muratore J F 1982 Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63, 621–626.
- Meyer J R and Linderman R G 1986 Selective influence on populations of rhizosphere or rhizoplane bacteria and actinomycetes by mycorrhizas formed by *Glomus fasciculatum*. *Soil Biol. Biochem.* 18, 191–196.
- Miller R M and Jastrow J D 1990 Hierarchy of root and mycorrhizal fungal interactions with soil aggregation. *Soil Biol. Biochem.* 22, 579–584.
- Mills L S, Soulé M E and Doak D F 1993 The keystone-species concept in ecology and conservation. *Bioscience* 43, 219–224.
- Molina R, Massicotte H and Trappe J M 1992 Specificity phenomena in mycorrhizal symbioses: Community-ecological consequences and practical implications. *In* Mycorrhizal Functioning: An Integrative Plant-Fungal Process. Ed. M F Allen. pp 357–423. Chapman and Hall, New York.
- Moore J C, Walter D E and Hunt W H 1988 Arthropod regulation of micro- and mesobiota in belowground detrital food webs. *Annu. Rev. Entomol.* 33, 419–439.
- Mueller B R, Beare M H and Crossley D A Jr 1990 Soil mites in detrital food webs of conventional and no-tillage agroecosystems. *Pedobiologia* 34, 389–401.
- Newell K 1984 Interactions between two decomposer basidiomycetes and collembola under sitka spruce: Distribution, abundance and selective grazing. *Soil Biol. Biochem.* 16, 227–234.
- Oades J M 1993 The role of biology in the formation, stabilization and degradation of soil structure. *Geoderma* 56, 377–400.
- Oades J M and Waters A G 1991 Aggregate hierarchy in soils. *Aust. J. Soil Res.* 29, 815–828.
- Parker L W, Santos P F, Phillips J and Whitford W G 1984 Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan desert annual, *Lepidium lasiocarpum*. *Ecol. Monogr.* 54, 339–360.
- Parkinson S M, Jones R, Meharg A A, Wainwright M and Killham K 1991 The quantity and fate of carbon assimilated from $^{14}\text{CO}_2$ by *Fusarium oxysporum* grown under oligotrophic and near oligotrophic conditions. *Mycol. Res.* 95, 1345–1349.
- Parmelee R W and Alston D 1986 Nematode trophic structure in conventional tillage and no-tillage agroecosystems. *J. Nematol.* 18, 403–407.
- Passioura J B 1991 Soil structure and plant growth. *Aust. J. Soil Res.* 29, 717–728.
- Paul E A 1989 Soils as components and controllers of ecosystem processes. *In* Toward a More Exacting Ecology. Eds. P J Grubb and J B Whittaker. pp 353–374. Blackwell Scientific Publications, Oxford.
- Paul E A and Clark F E 1989 Soil Microbiology and Biochemistry. Academic Press, San Diego.
- Payne J W 1981 Denitrification. Wiley Press, New York.
- Perry D A, Amaranthus M P, Borchers J G, Borchers S L and Brainerd R E 1989 Bootstrapping in ecosystems. *Bioscience* 39, 230–237.
- Petersen H and Luxton M 1982 A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* 39, 288–388.
- Price W P 1988 An overview of organismal interactions in ecosystems in evolutionary and ecological time. *Agric. Ecosyst. Environ.* 2, 369–377.
- Postgate J R 1982 Fundamentals of Nitrogen Fixation. Cambridge University Press, London.
- Read D J, Leake J R and Langdale A R 1989 The nitrogen nutrition of mycorrhizal fungi and their host plants. *In* Nitrogen, Phosphorus and Sulphur Utilization by Fungi. Eds. L Boddy, R Marchant and D J Read. pp 269–298. Cambridge University Press, Cambridge.
- Reid J B and Goss J M 1981 Effects of living roots of different plant species on the aggregate stability of two arable soils. *J. Soil Sci.* 32, 521–541.
- Robertson G P, Huston M A, Evans F C and Tiedje J M 1988 Spatial variability in a successional plant community: Patterns of nitrogen availability. *Ecology* 69, 1517–1524.
- Rovira A D, Elliot L F and Cook R J 1990 The impact of cropping systems on rhizosphere organisms affecting plant health. *In* The Rhizosphere. Ed. J M Lynch. pp 386–436. John Wiley, New York.
- Rusek J 1985 Soil microstructures - contributions of specific organisms. *Quaest. Entomol.* 21, 497–514.
- Santos P F, Phillips J and Whitford W G 1981 The role of mites and nematodes in early stages of buried litter decomposition in a desert. *Ecology* 62, 664–669.
- Seastedt T R 1984 The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* 29, 25–46.
- Schimel J P, Firestone M K and Killham K 1984 Identification of heterotrophic nitrification in a Sierra forest soil. *Appl. Environ. Microbiol.* 48, 802–806.
- Sharpley A N, Syers J K and Springett J A 1979 Effect of surface-casting earthworms on the transport of phosphorus and nitrogen in surface runoff from pasture. *Soil Biol. Biochem.* 11, 459–462.
- Shaw C and Pawluk S 1986 The development of soil structure by *Octolasion tyrtaeum*, *Aporrectodea turgida* and *Lumbricus terrestris* in parent materials belonging to different textural classes. *Pedobiologia* 29, 327–339.

- Shipitalo M J and Protz R 1988 Factors influencing the dispersibility of clay in worm casts. *Soil Sci. Soc. Am. J.* 52, 764–769.
- Sollins P, Cromack K Jr, Li C Y and Fogel R 1981 Role of low-molecular-weight organic acids in the inorganic nutrition of fungi and higher plants. *In The Fungal Community, Its Organization and Role in the Ecosystem*. Eds. D T Wicklow and G C Carroll. pp 607–619. Marcel Dekker, Inc., New York.
- Springett J A 1985 Effects of introducing *Allolobophora longa* Ude on root distribution and some soil properties in New Zealand pastures. *In Ecological Interactions in Soil*. Eds. A H Fitter, D Atkinson, D J Read and M B Usher. pp 399–405. Blackwell, Oxford.
- Swift M J 1984 Microbial diversity and decomposer niches. *In Current Perspectives in Microbial Ecology*. Eds. M J Klug and C A Reddy. pp 8–16. American Society of Microbiology, Washington, DC.
- Swift M J, Heal O W and Anderson J M 1979 Decomposition in Terrestrial Ecosystems, *Studies in Ecology*. Vol 5. Blackwell, Oxford.
- Taylor B R, Parkinson D and Parsons W F J 1989 Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. *Ecology* 70, 97–104.
- Tiedje J M, Sextone A J, Parkin T B, Revsbech N P and Shelton D R 1984 Anaerobic processes in soil. *Plant and Soil* 76, 197–212.
- Tilman D 1982 Resource competition and community structure. Princeton University Press, Princeton, New Jersey.
- Topp E and Hanson R S 1991 Metabolism of radiatively important trace gases by methane-oxidizing bacteria. *In Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*. Eds. J E Rogers and W B Whitman. pp 71–90. American Society of Microbiology, Washington, D C.
- Vannier G 1987 The porosphere as an ecological medium emphasized in Professor Gilarov's work on soil animal adaptations. *Biol. Fertil. Soils* 3, 39–44.
- Visser S 1985 Role of the invertebrates in determining the composition of soil microbial communities. *In Ecological Interactions in Soil*. Eds. A H Fitter, D Atkinson, D J Read and M B Usher. pp 297–317. Blackwell, Oxford.
- Wainwright M 1992 The impact of fungi on environmental biogeochemistry. *In The Fungal Community, Its Organization and Role, in the Ecosystem*. Eds. G C Carroll and D T Wicklow. pp 601–618. Marcel Dekker, Inc., New York.
- Walters D E, Hunt W H and Elliott E T 1988 Guilds or functional groups? an analysis of predatory arthropods from a shortgrass prairie soil. *Pedobiologia* 31, 247–260.
- Wicklow M C, Bollen W B and Denison W C 1974 Comparison of soil microfungi in 40 year-old stands of pure alder, pure conifer, and alder-conifer mixtures. *Soil Biol. Biochem.* 6, 73–78.
- Wilson D S 1992 Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* 73, 1984–2000.
- Wilson E O 1988 Biodiversity. National Academy Press, Washington, D C.
- Wolters V 1991 Soil invertebrates - Effects on nutrient turnover and soil structure - a review. *Z. Pflanzenernähr. Bodenkd.* 154, 389–402.