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Soil community composition and ecosystem processes
Comparing agricultural ecosystems with natural ecosystems

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Abstract. Soil organisms play principal roles in several ecosystem functions, i.e. promoting plant productivity, enhancing water relations, regulating nutrient mineralisation, permitting decomposition, and acting as an environmental buffer. Agricultural soils would more closely resemble soils of natural ecosystems if management practices would reduce or eliminate cultivation, heavy machinery, and general biocides; incorporate perennial crops and organic material; and synchronise nutrient release and water availability with plant demand. In order to achieve these goals, research must be completed to develop methods for successful application of organic materials and associated micro-organisms, synchronisation of management practices with crop and soil biota phenology, and improve our knowledge of the mechanisms linking species to ecosystem processes.

1. Introduction

Jackson (1995) suggests that modern agriculture operates in a ‘paradigm of ignorance.’ This concept is appropriate for the discipline of soil ecology, which has been recognised as a scientific discipline for only 20 years. Some have labelled soil ecology as a ‘last frontier’ (Andre et al., 1994). About 10% of soil species have been identified (Hawksworth and Mound, 1991). Of the world species, insects, fungi and nematodes are three groups that have not been identified fully (Table 1). Our knowledge of soil organisms has been limited by our ability to extract organisms from soil efficiently and by an ability to appropriately identify juvenile stages. Furthermore, microbiology and soil biology are often ignored by ecologists. Consequently, modern studies of soil and sediment ecology are several steps behind those of other subdisciplines of ecology. Many aspects of decomposer ecology are not well characterised for terrestrial soil or sediments in lakes, streams or oceans. Soil and sediment ecologists are still completing the taxonomy and systematics of soil organisms, revealing life history strategies, and just beginning to understand relationships between organisms and their contribution to ecosystem function (Crossley et al., 1992). One exception is that of earthworms and nitrogen-fixing bacteria whose relationship to ecosystem function has been known for decades. This apparent lack of knowledge does not, however, diminish the importance of soil organisms. Evolutionary and geological

Table 1. Numbers of species in the world.

Organism group	Described species ($\times 10^3$)	Estimated species ($\times 10^3$)	% of estimated species described
Dicot plants	170		
Monocot plants	50		
Ferns	10		
Mosses and liverworts	17		
Fish	19	21	95
Birds	9	9.1	99
Mammals	4	4	100
Reptiles and amphibians	9	9.5	95
Algae	40	60	67
Protozoa	30	100	30
Nematodes	15	500	3
Bacteria	3	30	10
Viruses	5	130	4
Fungi	69	1,500	5
Insects	800	2,000–10,000	0.08–0.4

Source: Hawksworth and Mound (1991).

evidence suggests that soil organisms have considerably longer histories on earth than organisms that have received more attention such as mammals and vascular plants (Main, this volume; Van Noordwijk and Ong, this volume). Their longevity alone suggests they play an essential role(s) in ecosystem function.

This paper will introduce the discipline of soil ecology, with an emphasis on characterising members of the soil community (Table 2) and their respective roles in ecosystem function. Second, approaches to design and management of soil communities to optimise ecosystem function will be discussed.

Table 2. Hierarchy of size and abundance of organisms inhabiting soil.

Class	Example(s)	Biomass (g m^{-2})	Length (mm)	Populations (m^{-2})
Microflora	Bacteria, fungi, algae, actinomycetes	1–100	n.a.[a]	10^6–10^{12}
Microfauna	Protozoa	1.5–6.0	0.005–0.2	10^6–10^{12}
Mesofauna	Nematodes, arthropods, enchytraeids, mites, springtails	0.01–10	0.2–10	10^2–10^7
Macrofauna	Insects	0.1–2.5	10–20	10^2–10^7
Megafauna	Earthworms	10–40	≥ 20	0–10^3

[a] Not applicable.

Source: Dindal (1990) and Lal (1991).

Finally, research priorities will be summarised. Most discussion will focus on nematodes, springtails (Collembola), and mites because they predominate in total numbers, biomass and species of fauna in soil (Harding and Studdart, 1974; Samways, 1992).

2. Soil food web

Mesofauna occupy all trophic levels within the soil food web (Figure 1) and affect primary production directly by root-feeding and indirectly through their contribution to decomposition and nutrient mineralisation (Crossley et al., 1992). In soil, the basic food web structure is similar to other food webs by containing primary producers, consumers and detritivores. Numbers and biomass per volume of soil organisms decrease by orders of magnitude from bottom to top positions in the food chain. In contrast to other food webs, soil food webs tend to have longer food chains, greater incidences of omnivory, and possibly greater complexity than other food webs. Further, all fauna depend on primary producers (e.g. for litter).

Plants and organic debris provide habitats for soil organisms. Plants affect soil biota directly by generating inputs of organic matter above- and below-ground and indirectly by the physical effects of shading, soil protection and uptake of water and nutrients by roots. Energy and nutrients obtained by plants eventually become incorporated in detritus that provide the resource base of a complex soil food web. Plant roots, for example, exude amino acids and sugars that serve as a food source for micro-organisms (Curl and Truelove, 1986). Soil micro- and mesofauna are often aggregated spatially which is probably indicative of the distribution of favoured resources, such as plant roots and organic debris (Swift et al., 1979; Goodell and Ferris, 1980; Barker and Campbell, 1981; Noe and Campbell, 1985; Griffiths, 1994).

Three basic energy pathways exist in soil: those of roots, bacteria and fungi (Moore et al., 1988). The root pathway includes primary herbivores such as pathogenic fungi, bacteria, nematodes, protozoa and their consumers. These organisms decrease primary productivity by altering uptake of water and nutrients, and may create abnormalities in root morphology and/or physiology. The bacterial pathway includes saprophytic and pathogenic bacteria and their respective consumers (e.g. protozoa, bacterial-feeding nematodes). The fungal pathway includes saprophytic, mycorrhizal and pathogenic fungi and their respective consumers (e.g. fungal-feeding nematodes, oribatid mites and springtails). The root, bacterial, and fungal pathways unite at levels higher in the food chain, i.e. omnivores and predators. Many microarthropods and nematodes are omnivores and feed on a variety of food sources, such as algae, fungi, bacteria, small rotifers, enchytraeids and small nematodes. Soil mesofauna are often categorised by specific feeding behaviours and are often depicted as microbial-feeders. However, many organisms are at least capable of feeding of other trophic groups. As a result, omnivory in soil communi-

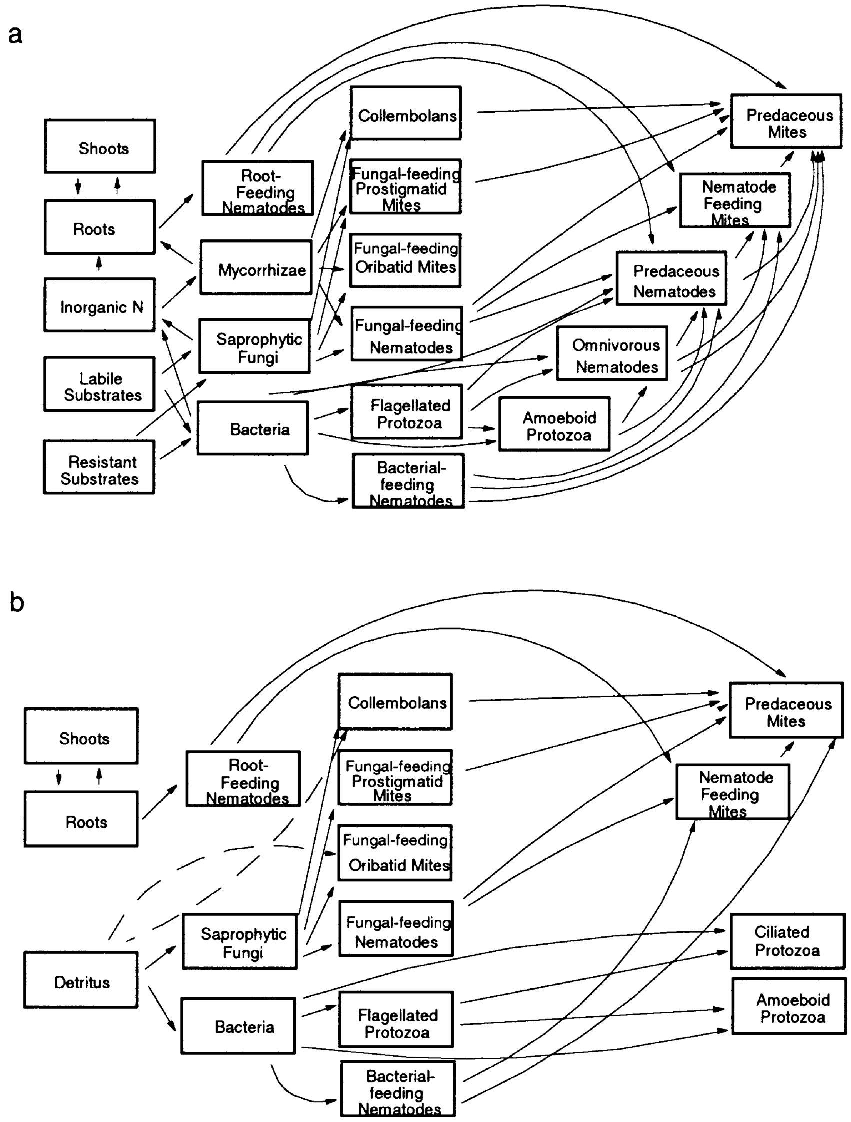

Figure 1. Soil food webs for a) grassland and b) cultivated wheat. Solid and dashed lines represent potential feeding relationships that were and were not quantified, respectively. *Source:* After Moore and de Ruiter (1991).

ties may be more prevalent than assumed previously (Walter, 1987; Walter et al., 1986, 1988; Walter and Ikonen, 1989; Mueller et al., 1990; Bengtsson et al., 1995). Predators include secondary, tertiary and quarternary consumers, including certain nematodes, beetles, fly larvae, centipedes, spiders and mites. Some mesofauna, such as nematodes and protozoa, may serve as predators or prey depending on the other species in the community (Griffiths, 1994; Yeates and Wardle, 1996). Soil microarthropods can be important predators on small arthropods and their eggs (e.g. proturans, pauropods, enchytraeids), nematodes, and on each other (Dindal, 1990).

Soil food web structure varies with geography and climate. In North America, shortgrass prairie (*Bouteloua gracilis*), lodgepole pine (*Pinus contorta* ssp. *latifolia*), and mountain meadow (*Agropyron smithii*) have similar food web structure (Hunt et al., 1987; Ingham et al., 1989). Although structure is conserved, relative abundance of organisms within trophic or functional groups may vary by ecosystem type. In Poland, bacterial-feeders and root-feeding nematodes are most abundant in agricultural soils, omnivory is more common in grasslands than agriculture, and fungal-feeders are relatively more abundant in forest than agricultural soils (Table 3). In contrast, relative numbers of organisms in each functional group differ in Swedish soils. For example, ratios of organisms in fungal to bacterial pathways are greatest in fertilised barley (*Hordeum vulgare* L.) followed in descending order by meadow fescue (*Festuca pratensis* L.) and lucerne ley (*Medicago sativa* L.) (Beare, 1997). In the Netherlands, disturbances such as cultivation and addition of mineral fertilisers eliminate certain functional groups such as predacious nematodes, omnivorous nematodes, and mycorrhizae that would otherwise be present in undisturbed grasslands (Figure 1). Furthermore, testate amoebae are reduced in abundance by at least 50% in agricultural compared to natural ecosystems (Foissner, 1997). Other organisms, such as the Enchytraeidae are less sensitive to cultivation than seasonal changes in climate (van Vliet et al., 1995).

Soil organisms vary in size by several orders of magnitude (Table 2). Microflora and microfauna are the smallest in size and most abundant. Mesofauna are moderate in size and abundance. Mesofauna generally do not have the ability to reshape the soil and, therefore, are forced to use existing

Table 3. Number of nematode genera per trophic group (percent of mean abundance), species diversity, species richness, and numbers of nematodes in soils of Poland.

Trophic Group	Annual crop (rye, potato)	Perennial crop (alfalfa)	Grassland	Forest
Bacterial-feeders	9–15 (41)	15–16[a]	8–18 (29)	11–18 (39)
Fungal-feeders	2–4 (16)	4[a]	1–4 (6)	2–5 (21)
Root-feeders	6–11 (37)	11[a]	9–14 (38)	7–11 (23)
Omnivores/predators	2–7 (6)	11–14[a]	7–17 (27)	2–8 (18)
Species diversity[b]	3.1–4.2	–[a]	3.9–4.9	3.2–4.3
Species richness	33–34	87–100	74	34–68
Mean no. nematodes[c]	3.5–5.0	–[a]	2.3–3.3	2.3–3.7

[a] Not available
[b] Shannon’s index of diversity
[c] 10^6 per m^2
Source: After Wasilewska (1979).

pore spaces, water cavities or channels for locomotion within soil. Most microfauna and mesofauna inhabit soil pores of 25–100 µm diameter. Protozoa (flagellates and small amoebae) occupy pores as small as 8 µm diameter (Griffiths, 1994). Macrofauna and megafauna are the largest and least abundant per unit area. Their size exceeds that of many soil pores and pore necks. Therefore, their movement and activity re-form soil and create burrows or channels.

Habitable pore space (voids of sufficient size and connectivity to support mesofauna) accounts for a small portion of total pore space (Hassink et al., 1993). Microfaunal community composition becomes increasingly dominated by smaller animals as average pore volume decreases (as in compacted soil or soils dominated by fine clays). Within the habitable pore space, microbial and mesofaunal activity are influenced by the balance between water and air. Maximum aerobic microbial activity occurs when 60% of the pore volume is filled with water (Linn and Doran, 1984). Saturation (water-logging) and drought are detrimental to soil faunal communities, because these conditions result in anaerobiosis and dehydration, respectively. Microbes and small fauna (e.g. nematodes, protozoa) depend on water films to live and move through the soil system (Griffiths, 1994; Lavelle et al., 1995). In aerobic environments, nematodes are more abundant when amoebae are present as food. This suggests that amoebae feed on bacteria in pores inaccessible to nematodes and then emerge to act as food for nematodes (Foster and Dormaar, 1991; Griffiths, 1994).

3. Soil function

The ‘first-link’ hypothesis can partly explain the origin of biodiversity in soil but the relationship between biodiversity on soil function remains untested (Lavelle et al., 1995). The hypothesis originated from observed changes in structure of earthworm communities along thermo-latitudinal gradients and extrapolation of observed patterns to plants based on the similarities observed in the general function of both drilosphere and rhizosphere systems (Lavelle et al., 1995). Janzen (1985) asserts that ‘plants wear their guts on the outside’; they produce exudates that trigger microbial activity and subsequent mineralisation of nutrients. In guts of earthworms, intestinal mucus and movement of soil through the gut are functional equivalents of root exudates and elongation through soil, respectively. It has been demonstrated that the mutualistic digestion system of earthworms becomes increasingly more efficient with increasing temperatures (Lavelle et al., 1995). It is assumed that increased temperatures in soils give roots access to a greater volume of nutrient resources because of more efficient mutualisms between soil microflora and plant roots. This would be the first link of a cascade process in which the species richness in the food web of consumers and decomposers would become larger in the tropics than in colder temperate or arctic areas.

In some geographic areas, richness of species composition in grassland and forest soils exceeds that of arable soils with annual crops (Table 3). In contrast, Wardle (1995) reports several cases in which conventional agricultural practices stimulate diversity. For example, the diversity of nematode genera in soils within asparagus (*Asparagus officinale* L.) systems was not affected by management practices such as addition of sawdust mulch, cultivation or herbicide applications. Soil-associated beetle diversity, however, was increased significantly by mulching and (sometimes) high weed densities.

Disturbance certainly plays a role in altering diversity. Perhaps intermediate disturbance promotes macrofaunal diversity, and extreme or lack of disturbance reduces diversity relative to undisturbed systems (Petraitis et al., 1989; Hobbs and Huenneke, 1992). The 'intermediate disturbance hypothesis' (Connell, 1978) could explain why some groups of organisms are more abundant in no-till (i.e. intermediate disturbance) than either conventionally-tilled (i.e. extreme disturbance) or old-field (i.e. no disturbance) systems (Wardle, 1995). If disturbance is common or harsh, only a few taxa that are resistant to disruption will persist (Petraitis et al., 1989). If disturbance is mild or rare, soil communities will approach equilibrium and be dominated by a few taxa that can out-compete all other taxa. However, attainment of steady-state equilibrium in agricultural or natural ecosystems is rare (Richards, 1987). There is little data to support this hypothesis but temporal patterns in diversity appear consistent with patterns detected during natural succession in plant communities (Whittaker, 1975).

Perhaps, it is more important to mimic the diversity of ecosystem function observed in natural systems than to mimic diversity of community composition (Main, this volume; Van Noordwijk and Ong, this volume). For example, an index of trophic diversity may serve as a measure of functional diversity in soil communities (Figure 2). Reducing the frequency of cultivation (Hendrix et al., 1986) and including perennial crops in agricultural systems (Wasilewska, 1979; Freckman and Ettema, 1993; Neher and Campbell, 1994) are two ways to increase trophic diversity in arable soils. Use of a trophic diversity index assumes that greater diversity (an integration of taxa richness and evenness) of trophic groups in soil food webs and longer food chains correspond with improved ecosystem function. In order to test the validity of such assumptions, it is important to identify ecological functions of soil and how soil organisms are involved in those functions. To date, five ecological functions of soil have been identified (*sensu* Larson and Pierce, 1991):

- promote plant growth;
- receive, hold and release water;
- recycle carbohydrates and nutrients through mineralisation;
- transfer energy in the detritus food chain; and
- act as an environmental buffer.

Individual taxa may have multiple functions and several taxa appear to have similar functions. However, taxa may not necessarily be redundant because

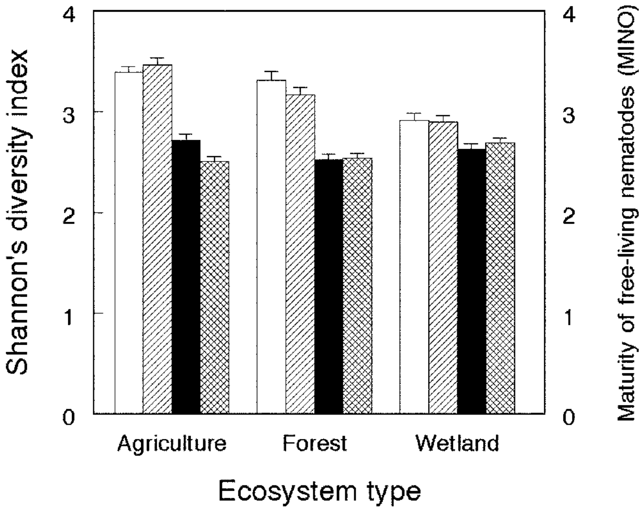

Figure 2. Means and standard errors of two measures of nematode community composition: 1) trophic diversity in disturbed (open bars) and undisturbed (hatched bars) and 2) successional maturity of free-living nematodes in disturbed (solid bars) and undisturbed (stippled bars) soils of North Carolina, USA. Undisturbed is defined as 10+ year-old pastures, 30+ year-old forests, and functioning wetlands. Disturbed is defined as annually cultivated arable soils, one to three year-old forests and wetlands converted to agricultural production. *Source:* Neher et al. (unpubl. data).

taxa performing the same function are often isolated spatially, temporally, or by microhabitat preference (Beare et al., 1995). Ettema (1998) suggests that the extent of nematode functional redundancy in soil has been greatly overestimated. Although redundancy of single functions is common, distinct physiological and environmental requirements drive species of the same functional group to play widely different roles in soil ecosystem processes.

3.1. *Promoting plant growth*

Growth may be enhanced for plants in soils containing multiple functional groups. For example, in North American grasslands containing blue gamma grass (*Bouteloua gracilis*), soil food webs containing primary decomposers and microbial grazers had greater primary productivity than systems limited to only primary decomposers (Ingham et al., 1985). Increases in plant growth have been observed for plants grown in soil containing protozoa and/or nematodes (Verhoef and Brussaard, 1990; Griffiths, 1994; Alphei et al., 1996). In glasshouse experiments, blue gamma grass withdrew more nitrogen from fertilised soil in the presence of amoebae than in their absence (Zwart et al., 1994). Protozoan grazing is necessary to release nitrogen from bacterial biomass for plant uptake (Clarholm, 1985). Finally, shoot production was enhanced 1.5 times in birch (*Betula pendula*) and 1.7 times in Scots pine

(*Pinus sylvestris*) when seedlings were grown in soils containing a more complex food web (bacterial-feeding nematodes, fungal-feeding nematodes, omnivores, springtails and oribatid mites) than when grown in simple systems containing only bacterial- and fungal-feeding nematodes (Setälä et al., 1995).

Based on a simulation model of shortgrass prairie (Hunt et al., 1987), 14% of nitrogen extracted by plants is accounted for by predation of bacteria by amoeba (Zwart et al., 1994). Having similar carbon, nitrogen and phosphorus content as their prey, protozoa incorporate only 10–40% of prey carbon, respire the remaining carbon, and excrete excess (20–60%) nitrogen and phosphorus into soil mostly as inorganic forms that can be assimilated by plants (Griffiths, 1994; Zwart et al., 1994).

Soil fauna not only alter the availability of nutrients for plants, but also alter relative distributions of carbon and nitrogen within plants. For example, plants grown in soils with only protozoa have less carbon in shoots and more carbon in roots than plants grown without protozoa. The opposite pattern was observed for plants grown in soils containing only nematodes (Alphei et al., 1996). Soil fauna generally affect amounts of nitrogen in roots more than in shoots (Alphei et al., 1996). One method of protozoa affecting nitrogen supply to roots is by consuming *Rhizobium* spp. and, consequently, reducing nodulation in the rhizospheres of common garden bean (*Phaseolus vulgaris*) (Zwart et al., 1994).

The effect of soil fauna on plant growth cannot be attributed entirely to an increased supply of nutrients to plants because nutrient leaching may also increase in the presence of soil fauna (Alphei et al., 1996). Protozoa may further stimulate plant growth by altering concentrations of plant hormones (e.g. auxin, tryptophan) in the rhizosphere and/or suppressing pathogenic bacteria (Jentschke et al., 1995; Alphei et al., 1996). Hormonal substances may derive directly from protozoa or indirectly from lysis of bacterial cells grazed by protozoa.

3.2. *Receiving, holding and releasing water*

Dawson and Pate, Hatton and Nulsen, and Dunin et al. (this volume) stress the importance of water in plant physiology and hydrogeology in designing agricultural systems that mimic nature. Soil serves as an interface between plants and geology. Soil water may have positive or negative impacts on soil organisms. Soil microbial and megafaunal populations improve water infiltration by altering soil physical structure. For example, bacteria produce polysaccharide adhesives and fungi produce thread-like hyphae that bind soil particles into stable aggregates and reduce potential soil losses by erosion (Gupta and Germida, 1988; Eash et al., 1994; Beare, 1997). Enchytraeidae (van Vliet et al., 1995) and earthworms (Edward and Bohlen, 1996) create burrows to improve infiltration and improve aeration. Van Vliet et al. (1995) hypothesise that enchytraeids have more influence on soil structure in agricultural fields than in forested areas.

As matric potential in soils declines to about –3 or –6 bars, bacterial respiration declines rapidly and is negligible at –20 bars (Griffin, 1981). Fungi often tolerate matric potential in excess of –30 bars, conditions unsuitable for growth of most bacteria except actinomycetes such as *Strepomyces* spp. Under these dry conditions, diseases caused by fungal pathogens, such as *Fusarium culmorum* on wheat (*Triticum aestivum*), become more severe. *F. culmorum* thrives at matric potentials that reach –100 bars at the surface and –30 bars in the rhizosphere (Griffin, 1981). Other fungi such as the take-all pathogen on wheat, *Gaeumannomyces graminis*, may predominate in irrigated soils (Griffin, 1981).

Ecosystem processes relate directly to the water content in soil. For example, a negative linear relationship occurs between relative nitrogen mineralisation and the logarithm of water potential. Decomposition of organic matter is also influenced by soil matric potential. An initial rapid decrease in decomposition within the –0.3 to –10 bar range is followed by another region where decomposition decreases linearly with decreasing water availability. The role of most bacteria is probably minimal once soils reach –15 bar water potential resulting in actinomycetes (filamentous, gram- positive bacteria) and fungi being the major decomposers in soils. Dry soils reduce the ability of substrate molecules to diffuse to the bacterial cell and the ability of bacteria to move to new substrates (Sommers et al., 1981). At the other extreme, water potential influences decomposition where saturated conditions result in the depletion of oxygen (O_2) and the development of anaerobic conditions. Under these conditions, anaerobic bacteria are the predominant organisms responsible for decomposition. Comparison of decomposition rate to soil water potential must incorporate metabolic shifts that occur in the transition from aerobic to anaerobic conditions. In the former, carbon dioxide (CO_2) is the major end product and in the latter, CO_2 may underestimate microbial activity because methane (CH_4) and other reduced carbon compounds may be significant end-products under saturation (Sommers et al., 1981).

3.3. *Recycling carbohydrates and nutrients through mineralisation*

Fauna may contribute directly to mineralised forms of nitrogen by excretion of ammonium (e.g. nematodes and protozoans) or nitrate (e.g. springtails) (Anderson et al., 1983; Ingham et al., 1985; Teuben and Verhoef, 1992; Darbyshire et al., 1994; Griffiths, 1994). As reservoirs of nutrients, microflora and microfauna also contribute indirectly to mineralisation. Net increases in nitrogen concentration in soil caused by mesofauna grazing on microbes have been demonstrated in petri dish experiments (Trofymow and Coleman, 1982). Nutrients immobilised in microbes are mineralised and subsequently become available to plants (Seastedt et al., 1988; Söhlenius et al., 1988).

Model simulations of soil food webs estimate that 97 and 99% of total nitrogen flux can be attributed to the bacterial pathway in integrated farming and conventional farming systems, respectively (Beare, 1997). Griffiths (1994) estimates from several independent food web studies that protozoa, especially amoebae, are responsible for 20–40% of net nitrogen mineralisation under field conditions. Estimates of protozoan contribution to net nitrogen mineralisation vary by geographic location and farming system. For example, protozoa are estimated to mineralise about 54 and 90 kg of nitrogen per year in no-till and conventionally tilled soils (Beare, 1997). In The Netherlands, protozoa mineralise approximately 30 and 43 kg of nitrogen per year in conventional and integrated farming trials (Beare, 1997). These estimates likely underestimate total contributions to net mineralisation by protozoa because bacteria simultaneously mobilise nutrients rapidly (Griffiths, 1994).

In addition to protozoa, bacterial-feeding and predatory nematodes are estimated to contribute (directly and indirectly) about 8 to 19% of nitrogen mineralisation in conventional and integrated farming systems (Beare, 1997). Although counter-intuitive, predatory nematodes sometimes demonstrate stronger relationships with the amount of microbial food source than the abundance of microbial-feeding fauna, which may serve merely as a conduit by which resources pass from the bottom to top trophic levels (Wardle and Yeates, 1993).

Protozoa may out-compete nematodes for consumption of bacteria because they have much shorter generation times (one to two days compared to four to seven days) (Griffiths, 1994). However, it is assumed that nematodes and protozoa do not compete directly. Although the abundance of protozoa may correlate inversely with numbers of nematodes, nematodes are thought to have a stimulating effect on protozoa (Alphei et al., 1996) by increasing bacterial production (Griffiths, 1994). This hypothesis is supported by faster accumulation of ammonium from cultures containing bacteria, ciliates and nematodes than only bacteria and ciliates (Griffiths, 1994). When protozoa are active in absence of nematodes, nitrate is the major ion leached and is accentuated in the presence of earthworms (Alphei et al., 1996). Mites may stimulate amoebal numbers by increasing the availability of bacteria and decreasing numbers of nematodes in the presence of a large abundance of amoebae (Griffiths, 1994). The latter hypothesis is supported by evidence that nitrogen mineralisation is increased by amoebae feeding on flagellates in the presence of mites (Griffths, 1994), or increased nitrate leaching with protozoa and earthworms (Alphei et al., 1996). The presence and abundance of earthworm activity have also been linked to increased leaching of inorganic nitrogen in field and laboratory conditions (Filser et al., 1995). Soil oxidation state was correlated positively with nitrate leaching in conventionally tilled soils (Doran, 1980). In no-till soils, both nitrification and denitrification were greater in surface soil (0–5 cm) compared to conventionally tilled soils, with the reverse pattern at greater depths (5–21 cm) (Beare, 1997).

The bacterial pathway is not always the dominant force in net nitrogen mineralisation. In Sweden, fungal contributions to nitrogen immobilisation are about 3.5 times more than bacterial contributions (Beare, 1997). It is likely that fungal-feeding microarthropods are more important in mobilising nitrogen from surface residues through grazing in no-till soils than bacteria and their consumers (Beare, 1997).

Not only may soil fauna stimulate net mineralisation of nutrients but they may also promote nutrient immobilisation. In Sweden, more nitrogen was immobilised in surface applied than buried straw in soils cropped to meadow fescue or lucerne. Perhaps competition for available nitrogen occurred between plant roots and residue-borne decomposers (Beare, 1997). Furthermore, phosphorus is immobilised in the presence of nematodes and more so when both protozoa and nematodes are present (Alphei et al., 1996). Earthworms may temporarily immobilise nutrients in microbes while they pass through the earthworm gut (Filser et al., 1995). The relative balance of nutrient mineralisation and immobilisation is not solely a function of soil faunal activities but also depends on the presence of nitrifying bacteria and the mobility of nutrients ions and loading of exchange surfaces (Alphei et al., 1996).

3.4. *Transferring energy in the food chain*

Bacteria (including actinomycetes), fungi, algae and protozoa are primary decomposers of organic matter. Nematodes, large protozoa, springtails and mites feed on microbes in contact with decaying organic matter, but not on the organic matter itself. Microbial-grazing mesofauna affect growth and metabolic activities of microbes and alter community composition, thus regulating decomposition rate of organic matter (Wasilewska et al., 1975; Trofymow and Coleman, 1982; Whitford et al., 1982; Yeates and Coleman, 1982; Seastedt, 1984). Protozoa alter the composition and activity of the microbial community by selectively grazing on small, slow-growing cells which act to maintain taxonomic and metabolic diversity of microflora. It is assumed that this type of grazing preference maintains a bacterial population in a ‘youthful’ state and maintains decomposition activity (Griffiths, 1994). Amoebae apparently have a stimulatory effect when added to bacterial cultures based on evidence of increased respiration, ammonification and siderophore production (Griffiths, 1994). Other fauna have indirect effects on decomposition. For example, microarthropods and Enchytraeidae fragment detritus and increase surface area for further microbial attack (Berg and Pawluk, 1984; Van Vliet et al., 1995). Subsequently, protozoa re-inoculate new substrates by phoretic transport or excretion of viable bacteria (Griffiths, 1994). Examples of invertebrate-microbe mutualisms are prevalent in soil. For instance, most soil invertebrates (e.g. termites and earthworms) do not seem to possess suitable enzymes to directly digest most resources in soil, such as cellulose, lignin, tannin and humic complexes. Instead, the enzymes seem to be produced by ingested microbes rather than by the invertebrate itself (Lavelle et al., 1995).

Carbon and nitrogen dynamics are tightly linked in terrestrial ecosystems suggesting that classic food web theory is insufficient to analyse relations between food web structure and ecosystem processes. Food web structure may influence decomposition rate even if trophic interactions are controlled by the rate of detritus input (Bengtsson et al., 1995). An increased number of trophic levels would increase decomposition rate given that consumers do not influence each others consumption rate or mortality (Bengtsson et al., 1995). This hypothesis is supported by several laboratory studies (Setälä and Huhta, 1991; Bengtsson et al., 1995).

Perhaps ecosystem function depends more on the presence and abundance of particular functional groups rather than complexity of food webs or biodiversity alone (Andrén et al., 1995). The ‘snow chain’ hypothesis predicts a succession of decomposer organisms that respond to changes in substrate quality. This hypothesis is analogous to the addition of snow chains to tires when making the transition from clear to snow-covered roads. Evidence of succession occurs among soil animals. Initially, a peak of enchytraeids and bacterial-feeding nematodes are present. Once the substrate is decomposed somewhat and changed qualitatively, numbers of microarthropod and nematode omnivores and predators increase with a subsequent decline in numbers of bacterial-feeding nematodes and enchytraeids (Andrén et al., 1995).

In desert ecosystems containing creosote-bush (*Larrea tridentata*), food webs with additional trophic groups correspond with faster rates of decomposition than food webs with fewer trophic groups (Whitford et al., 1982). Decomposition rates were slower for systems without mites (treated with the insecticide, chlordane) than with mites (no insecticide). Without mites, nematode grazing may have decreased the decomposition rate. The presence of mites reduced nematode populations and released microbial populations from predation, which resulted in faster decomposition rates. Consequently, predatory mites maintain nematode grazer populations at levels that presumably increase microbial activity and decomposition rates.

3.5. *Acting as an environmental buffer*

Soils act as an environmental buffer physically, chemically and biologically. Physically, soils may filter materials such as pesticides and fertiliser through its porous matrix and reduce the transfer of leachates into ground and surface water. Fulvic and humic acids of organic matter play a major role in the binding of pesticides in soil. Pesticides, or their degradation intermediates, can also be polymerised or incorporated into humus by the action of soil microbial enzymes (Bollag et al., 1992). Additional chemical buffering functions of soil are responsible for regulating the availability of nutrients by cation exchange capacity (principally influenced by organic matter and clay content), serve as a sink for carbon dioxide, and are a source of alleopathic chemicals. Carbon compounds are stored in plant, microbe and animal bodies, in debris and in abiotic carbonate compounds. During decomposition processes, respiration releases carbon dioxide as a by-product. Cultivation releases carbon dioxide to the atmosphere, both through burning of fossil fuels to run the tractor and disturbing the soil, which increases decomposition rates.

Soil microbes, especially fungi, may secrete allelopathic substances that suppress germination of seeds or make seeds unpalatable to predators (Janzen, 1977). This has been demonstrated in the California chaparral with *Adenostoma fasiculatum* (Wicklow, 1981). Fire eliminates the alleopathic effect temporarily. However, it returns after re-establishment of the microbial community. Agronomists have utilised fire to manage soil fungal pathogens of wheat, barley and rice.

The presence of particular groups of organisms has been associated with the suppression of plant disease. First, the springtails *Proisotoma minuta* and *Onychiurus encarpatus* consume the soilborne fungal plant pathogen *Rhizoctonia solani* which causes damping-off disease on cotton seedlings. Springtails prefer feeding on the fungal pathogen in soil compared to the biocontrol fungi *Laetisaria arvalis*, *Trichoderma harzianum*, and *Gliocladium virens* (Curl et al., 1988). Springtail species can also distinguish and graze selectively on different species of vesicular-arbuscular mycorrhizae (Thimm and Larink, 1995). Second, amoebae of the *Vampyrellidae* perforate conidia of *Cochliobolus sativus* on barley (Old, 1967). Protozoa have been reported to play an active role in disease suppression by consuming pathogenic nematodes, bacteria and fungi (Zwart et al., 1994). Generally, plant pathogens have faster growth rates than protozoan predators, so it is unlikely that protozoa will suppress plant pathogens completely in soil. However, for crops grown in liquid media, this balance may tip the other way (Zwart et al., 1994). Finally, abundances of the bacterium *Pseudomonas fluorescens* increase and may act as a biocontrol agent of the take-all pathogen *Gaeumannomyces gramminis* under conditions of no-till, continuous wheat production (Ryder et al., 1990).

4. Designing and maintaining soil communities for optimum function

Modern agricultural methods have replaced or substituted natural and seasonal patterns of ecological processes with inorganic materials. These substitutions of nature are likely to have environmental and ecological costs due to the loss of natural cycles among organisms and their environment through time. The paucity of studies quantifying these costs compels some scientists to declare that generalisations such as ‘conventional farming destroys life in the soil’ or ‘ecofarming stimulates soil life’ are not supported by adequate evidence (Foissner, 1992; Wardle, 1995; Giller et al., 1997).

Regardless, we have evidence that increased detrital food webs containing more groups of organisms are associated with faster decomposition and nutrient turnover rates (Setälä et al., 1991) and increased primary production (Setälä and Huhta, 1991). Balanced with organisms that immobilise nutrients, the net effect is regulation of nutrient availability to plants and other organisms. We cannot conclude that soil biodiversity *causes* ecosystem function because there is insufficient evidence to support this claim.

To better mimic nature, soil ecosystems must be designed and managed to foster food webs containing multiple functional groups or taxa (i.e. complex community) and be relatively mature successionally. This can be achieved by incorporating four types of activities:

- reduction or elimination cultivation, heavy machinery and general biocides;
- incorporating perennial crops and organic material;
- synchronising nutrient release and water availability with plant demand; and
- monitoring biological activity.

4.1. *Reduction or elimination of cultivation, use of heavy machinery and general biocides*

Decomposition rates are sensitive to physical disturbances such as cultivation. For example, decomposition rates are 1.4 to 1.9 times faster in conventionally tilled than in no-till soils with surface residues (Beare, 1997). Fungi are more likely to regulate decomposition of surface-applied residues in no-till soils and bacteria regulate decay rates in incorporated residues in conventionally tilled soils (Beare, 1997).

Soils managed by conventional, reduced, or no tillage practices have distinct biological and functional properties (Doran, 1980; Hendrix et al., 1986). Plant residue is distributed throughout the plough layer in fields managed with conventional tillage. Under these conditions, organisms with short generation times, small body size, rapid dispersal and generalist feeding habits thrive (Steen, 1983). These soils are dominated by bacteria and their predators such as bacterial-feeding nematodes and astigmatid mites (Andrén and Lagerlöf, 1983; Yeates, 1984; Hendrix et al., 1986; Beare et al., 1992; Beare, 1997) and are considered to be in an early stage of succession. Many microarthropods have omnivorous feeding habits in systems which are cultivated frequently (Beare et al., 1992). Alternatively, reduced tillage leaves most of the previous crop residue on the soil surface and results in changes in physical and chemical properties of the soil (Blevins et al., 1983). Surface residues retain moisture, dampen temperature fluctuations, and provide a continuous substrate that promotes fungal growth. Furthermore, the dominance of fungi in early stages of decay of surface residues can be explained by the initially high lignin to nitrogen ratio. Bacteria move in as secondary colonisers after decay is initiated (Beare, 1997). Relative abundance of fungi and their consumers in no-till soils represent a more mature successional state, more closely resembling undisturbed natural ecosystems (Yeates, 1984; Boström and Söhlenius, 1986; Hendrix et al., 1986; Holland and Coleman, 1987; Walter, 1987; Neher and Campbell, 1994; Beare, 1997).

Sometimes agricultural disturbances, such as cultivation, do not reduce soil biodiversity. Instead, cultivation appears to affect species composition but not diversity and more so for macrofauna than microfauna (Wardle, 1995).

Diversity of microfauna is mostly unresponsive to cultivation and there is no general trend for macrofauna. Some species are effected negatively, and others positively, by cultivation (Wardle, 1995). The lack of response of the diversity of groups of small organisms to cultivation may reflect their slight overall response to cultivation or possibly their poorer taxonomic resolution in most studies.

Soil fumigation with general biocides has short and/or long-term impacts on soil community composition and abundance. Biocides may either impact the microbes or fauna directly with toxic effects or indirectly through reduced vegetation or other non-target effects (Andrén and Lagerlöf, 1983). Methyl bromide and benomyl have direct toxic effects on nematodes and earthworms, respectively (Yeates et al., 1991; Ettema and Bongers, 1993; Edwards and Bohlen, 1996). Phenoxy acetic acid herbicides (e.g. 2,4-D, 2,4,5-T, MCPA) do not depress soil fauna directly with toxic effects, but indirectly through reduced vegetation and smaller additions of organic matter to soil (Andrén and Lagerlöf, 1983). Conversion of continuous hop (*Humulus lupulus*) production to a cereal rotation of winter wheat (*Triticum aestivum*) and spring barley (*Hordeum vulgare*) demonstrate the long-lasting effects of intensive biocide input, especially fungicides with copper, which accumulate and remain in soil for more than three years (Filser et al., 1995). Heavy metals, such as copper, eliminate sensitive species such as earthworms and the springtails *Folsomia quadrioculata* and *Isotomiella minor*. Other springtails tolerate heavy metals and increase in dominance, for example *Mesaphorura krausbaueri* and *Onychiurus armatus* (Filser et al., 1995). Broad-spectrum insecticides such as chlorpyrifos, isofenphos, and aldicarb are toxic to non-target insects, such as predaceous and parasitic arthropods (Koehler, 1992; Potter, 1993). Insecticides are usually more toxic than herbicides or fungicides and disturb soil protozoa critically, i.e. populations often do not fully recover within 60 days (Foissner, 1997). Edwards and Bohlen (1996) and Neher and Barbercheck (1998) provide more thorough reviews of effects of biocides on soil community composition.

Benefits of eliminating general biocides are illustrated by two case studies (Ingham, 1998) involving strawberry (*Fragaria* × *Ananassa* Duch.). The first study was in California, USA, where strawberries are grown as an annual crop in monoculture. Annual applications of methyl bromide were used to decrease the population density of certain root pathogens. However, there were major environmental costs. For example, nitrate leached into ground water reaching concentrations of 150 ppm (3 ppm is toxic to humans). Natural disease suppression was lost which may partly be explained by a 50-fold reduction in numbers of bacterial species. A remediation program was implemented to reverse the apparent environmental problems. Spent mushroom compost (high fungal content) was applied to soil at a rate of 60 tons per hectare. Abundances of microflora and microfauna increased and a balance of fungi and bacteria (and their respective consumers) returned to the soil after four to five years, accompanied by nitrate leaching and increased natural disease suppression

(Ingham, 1998). The second study was in Costa Rica where strawberries were grown as perennials. Disease management was maintained and pesticides replaced by transplanting strawberry seedlings in plugs containing compost colonised by a mixture of bacteria, fungi and their respective consumers. This compost promoted the establishment of a complex food web defined as a balance of bacteria and fungi, and their respective grazers. This practice transfers a relatively complex soil food web to the field and obviates the need to manipulate the entire field (Ingham, 1998). In the long-term, managing soil to achieve relatively balanced fungal and bacterial components will reduce fertiliser requirements because soil organisms will maintain processes of nutrient mineralisation and decomposition at sustainable levels.

4.2. *Incorporating perennial crops and organic matter*

Introduction of perennial crops into agricultural systems has several advantages. Root growth is more extensive and less ephemeral than with annual crops and supports a soil community with many omnivores and predators. Soil community composition with perennial crops resembles that of natural ecosystem soils more closely than is the case with annual crops (Ferris and Ferris, 1974; Wasilewska, 1979; Freckman and Ettema, 1993; Neher and Campbell, 1994). Differences between soils with perennial (e.g. meadow fescue) and annual (e.g. barley) crops may be less pronounced for perennial crops younger than three years old than with more mature crops (Boström and Söhlenius, 1986). Furthermore, perennial plants restore function in water infiltration and reduce compaction and, thus, increase rooting depth.

Organic matter can be added to soil as crop residues, urban sludge, manure, green manure, cover crops or compost. Addition of organic matter to soil has multiple benefits. First, organic matter adds nutrients and cation exchange sites to retain nutrients. Second, organic matter increases porosity to soil (Andrén and Lagerlöf, 1983). Third, organic matter includes microbes and microbial grazers (Andrén and Lagerlöf, 1983; Weiss and Larink, 1991) which restore ecosystem processes such as decomposition, nutrient mineralisation and disease suppression. For example, populations of fungal-feeding nematodes (Weiss and Larink, 1991), potworms (enchytraeids), springtails and sometimes mesostigmatid mites increase with applications of manure which provide a better substrate for growth (Andrén and Lagerlöf, 1983). However, there are exceptions, as in Dutch polder soil (van de Bund, 1970).

Although it is difficult to separate their individual effects, concurrent additions of organic matter and elimination of general biocides have the benefit of allowing omnivores and predaceous species to increase in prevalence, which promotes natural disease suppression. In these cases, natural community interactions such as competition, antagonism, competitive exclusion and niche partitioning must be understood for effective results. There is a fine balance between disease suppressive agents and pathogens. Some pathogenic fungi may be stimulated initially by additions of organic residues.

Caution is advised when considering simple solutions to disease and nutrient management. For example, application of mycorrhizal fungi is often considered a favourable practice. A parallel good practice is the promotion of fungal-feeding nematodes, which are usually less abundant than root-feeding or bacterial-feeding species in agricultural soils. However, fungal-feeding organisms such as springtails, nematodes and mites may actually reduce the beneficial effect of promoting mycorrhizae by consuming mycorrhizae. Despite the reduced benefit of mycorrhizae, the plant-fungus symbiosis remains given the soil food web contains interactions among saprophytic microbes and their faunal grazers to ensure efficient mobilisation of nutrients in the rhizosphere (Setälä, 1995).

As with any practice, there are risks associated with applications of organic matter. For example, high doses of manure or sludge fertilisers can harm mesofauna because of toxicity (e.g. anhydrous ammonia), high osmotic pressure due to salt accumulation (Andrén and Lagerlöf, 1983), or heavy metal accumulation (Weiss and Larink, 1991). The repellent nature of ammonium can affect soil invertebrates adversely (Potter, 1993). However, potential for toxic effects can be decreased by applying composted manure or sludge (Ott et al., 1983). One must consider the period of time material is composted prior to incorporating it into soil. For example, the plant-pathogenic fungus *Rhizoctonia solani* may cause damping-off disease in soil when fresh or immature compost material high in cellulose content is added. However, in aged compost, cellulose is degraded and the biocontrol fungus *Trichoderma* spp. can grow and parasitise the pathogen effectively, thus suppressing disease (Chung et al., 1988).

4.3. *Synchronising nutrient and water availability with plant demand*

Fertiliser addition affects soil microflora and indirectly impacts soil mesofauna by changing their food resources (Weil and Kroontje, 1979). Additions of nitrogen may acidify soil and, consequently, inhibit microbial growth and activity. Nitrogen may also affect the quality of microbes as a food source for mesofauna (Darbyshire et al., 1994). Booth and Anderson (1979) grew two species of fungi in liquid media with 2, 20, 200, or 2000 ppm nitrogen and determined the fecundity of the springtail *Folsomia candida* while feeding on the fungi. Fecundity increased with increasing nitrogen content up to 200 ppm, although *F. candida* did not show a preference for feeding on fungi with a greater or lesser nitrogen content.

The effect of fertilisation on microarthropod species diversity and abundance within taxa, and the subsequent impact on decomposition and nutrient mineralisation processes, are not well understood. For example, synthetic fertilisers increase nematode diversity but applications of manure decrease nematode diversity (Wasilewska, 1989). Applications of synthetic nitrogen fertiliser on Swedish arable soils growing spring barley (*Hordeum distichum*

L.) changed community composition but not numbers and biomass of nematodes, springtails and mites (Andrén et al., 1988).

Appropriate timing of water is important for disease management. For example, frequent irrigation episodes may increase potential of root rot diseases caused by *Phytophthora* spp. The reproductive biology of *Phytophthora* spp. is stimulated by changes in the matric potential of soil (Duniway, 1983). Water drainage stimulates production of asexual spores such as sporangia, whereas subsequent saturation (i.e. irrigation event) stimulates the sporangia to germinate indirectly by producing multiple zoospores that are flagellated and may move great distances in surface water (Figure 3). Phytophthora root rots have been well documented world-wide, including those on jarrah (*Eucalyptus marginata*) and *Banksia* in Australia and on many vegetable and tree crops in the US (Erwin et al., 1983).

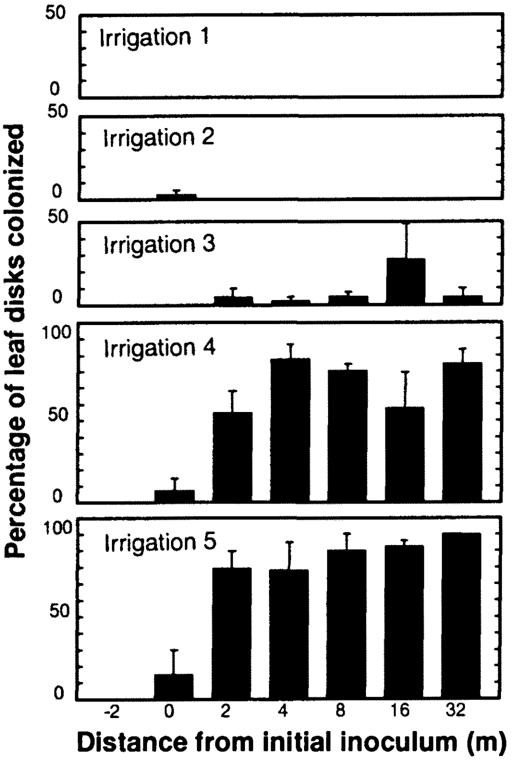

Figure 3. Percentages of tomato leaf disks colonised during five successive irrigations plotted as a function of the distance from the point source where *Phytophthora parasitica* was buried in irrigation furrows. Means for four replicate furrows and standard errors are shown. *Source:* Neher and Duniway (1992).

4.4. *Monitoring biological activity*

The successional status of a soil community may reflect the history of disturbance. Succession in cropped agricultural fields begins with depauperate soil after cultivation and clearing of native vegetation which acts like an island to which organisms migrate. First, opportunistic species, such as bacteria and their predators, are colonists of soil. Subsequently, fungi and their predators migrate into the area (Boström and Söhlenius, 1986). Microarthropods, such as springtails, mites and fly maggots can colonise nearly bare ground and rise quickly in population density. Top predator microarthropods, such as predaceous mites and nematodes, become established later and may have a function similar to keystone predators in other community food webs (Elliott et al., 1988). Finally, macro- and megafauna such as earthworms, millipedes, slugs, centipedes, wood lice, sow bugs and pill bugs join the soil community (Strueve-Kusenberg, 1982).

Succession can be interrupted at various stages by agricultural practices, such as cultivation and applications of fertiliser and pesticides (Ferris and Ferris, 1974; Waskilewska, 1979). The quantification of successional stage using a ‘maturity index’ (Bongers, 1990) proves promising as a monitoring tool of community composition and function (Freckman and Ettema, 1993; Neher and Campbell, 1994; Neher et al., 1995; Neher and Barbercheck, 1998). Maturity indices are based on the principles of succession and relative sensitivity of various taxa to stress or disruption of the successional pattern. Maturity indices, based on life strategy characteristics, were developed originally for nematode communities, but have potential for adaptation to other groups of organisms. Interpretation of maturity indices depends on the type of ecosystem (Figure 2). Successional maturity was greater in older forests (> 30 years) and functional wetlands than young forests (< 3 years) and wetlands converted to conventionally tilled agriculture, respectively (Figure 2). The opposite pattern was observed for agricultural soils, where successional maturity was greater in conventionally tilled soil with annual crops (i.e. disturbed) than permanent pastures (i.e. undisturbed). Indices that describe associations within biological communities, such as a maturity index, are less variable than measures of abundance of a single taxonomic or functional group, and are more statistically reliable as measures of ecosystem condition (Neher et al., 1995; Neher and Campbell, 1996). Because index values for New Zealand (Yeates, 1994) and the US (Neher and Campbell, 1996) were greater than those published in European studies, it is suggested that biogeography may be a confounding factor in interpreting index values. Maturity and trophic diversity indices measure different aspects of soil communities and, together, are complementary.

5. Essential research

Our challenge is to understand concepts and mechanisms that mimic nature, qualitatively and quantitatively, at appropriate spatial (centimetres to hectares), ecological (population, community, ecosystem and landscape) and temporal (seconds to centuries) scales. Most studies have focused on single factors in an effort to reveal underlying mechanisms, resulting in a lack of understanding of how multiple and interacting environmental and biotic factors affect soil biodiversity, nutrient cycling, pest populations and plant productivity. Future research should include studies on productivity of soil animals under various management systems, the analysis of single factors to elucidate causative mechanisms, and studies on the relationship between soil animals, crop production and sustained yield (Foissner, 1992). Holistic systems and their dynamics must be understood to effectively design agricultural systems in concordance with nature. With this information, we should be able to tailor agricultural practices to positively affect beneficial soil organisms and the functions they perform to optimise crop productivity. To achieve the ultimate goal of designing and managing agricultural systems as mimics of nature, the following research goals must be achieved.

5.1. *Methods for successful application of compost materials and/or biocontrol agents*

Simple techniques are usually favoured but may also disregard ecological interactions among organisms, added and between those added and those already existing in the soil. Basic natural history and fundamental niche requirements must be understood at the individual and population level. At the community level, potential competitive exclusion, predation and/or antagonism by organisms already occupying that niche or utilising the resources must be considered. At the ecosystem level, methods to optimise the role that soil organisms play in nutrient cycling, energy flow, and disease management must be evaluated.

5.2. *Timing of management implementation*

While many studies have examined the impact of additions or removals of materials, they have not considered the seasonal impacts or time lags that occur between implementation and response, whether the treatment is biotic or abiotic. By understanding appropriate temporal relationships, nutrient and water supplements can be scheduled according to plant and soil community use. Interactions of intra- and interspecific crop phenology and root architecture relative to soil community composition and function must be integrated to avoid intense competition for nutrients between microbes and plants.

5.3. *Explicit relationships between soil organisms and ecosystem function*

Current understanding is limited to trophic or functional group resolution. However, resolution at a species-level is desirable. Additionally, a more thorough understanding of the sequence of community succession relative to soil function dynamics would be useful in making long-term predictions of community composition associated with ecologically sound agricultural systems.

6. Conclusions

Clearly, soil microbes and fauna play important roles in ecosystem function. Unfortunately, many modern agricultural practices correspond with a decline in abundance and alter the composition of soil communities, which subsequently impacts ecological processes. Interruption to the cycling of carbon, nitrogen, phosphorus and/or water prevents crops from obtaining all requirements for primary productivity. Production deficiencies are replaced by fossil-fuel based inputs that eventually replace natural cycles and processes. To restore ecosystem functions of soil organisms, agricultural systems must be designed to reduce or eliminate cultivation, heavy machinery, and general biocides. In addition, systems should incorporate perennial crops and increase soil organic material. In order to achieve these goals, more research is needed to determine the impact of multiple and interacting management practices on biodiversity, nutrient cycling, decomposition, pest populations, and their concurrent impact on agricultural productivity. With this information, we can maximise our ability to tailor agricultural practices to optimise crop productivity while positively affecting beneficial soil organisms and the functions they perform.

7. References

Alphei J, Bonkowski M and Scheu S (1996) Protozoa, Nematoda and Lumbricidae in the rhizosphere of *Hordelymus europaeus* (Poaceae): faunal interactions, response of microorganisms and effects on plant growth. Oecologia 106: 111–126

Anderson RV, Gould WD, Woods LE, Cambardella C, Ingham RE and Coleman DC (1983) Organic and inorganic nitrogenous losses by microbivorous nematodes in soil. Oikos 40: 75–80

Andre HM, Noti MI and Lebrun P (1994) The soil fauna: the other last biotic frontier. Biodiversity and Conservation 3: 45–56

Andrén O, Bengtsson J and Clarhom M (1995) Biodiversity and species redundancy among litter decomposers. In: Collins HP, Robertson GP and Klug MJ (eds) The Significance and Regulation of Soil Biodiversity, pp 141–151. Kluwer Academic Publishers, Dordrecht, The Netherlands

Andrén O and Lagerlöf J (1983) Soil fauna (microarthropods, enchytraeids, nematodes) in Swedish agricultural cropping systems. Acta Agriculturae Scandinavica 33: 33–52

Andrén O, Paustian K and Rosswall T (1988) Soil biotic interactions in the functioning of agroecosystems. Agriculture, Ecosystems and Environment 24: 57–67

Barker KR and Campbell CL (1981) Sampling nematode populations. In: Zuckerman BM Rohde RA (eds) Plant Parasitic Nematodes, Vol III, pp 451–474. Academic Press, New York, NY

Beare MH (1997) Fungal and bacterial pathways of organic matter decomposition and nitrogen mineralization in arable soil. In: Brussaard L and Ferrera-Cerrato R (eds) Soil Ecology in Sustainable Agricultural Systems, pp 37–70. Lewis Publishers, Boca Raton, LA

Beare MH, Coleman DC, Crossley DA Jr, Hendrix PF and Odum EP (1995) A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. In: Collins HP, Robertson GP and Klug MJ (eds) The Significance and Regulation of Soil Biodiversity, pp 5–22. Kluwer Academic Publishers, Dordrecht, The Netherlands

Beare MH, Parmelee RW, Hendrix PF, Cheng W, Coleman DC and Crossley DA Jr (1992) Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecological Monographs 62: 569–591

Bengtsson J, Zheng DW, Agren GI and Persson T (1995) Food webs in soil: an interface between population and ecosystem ecology. In: Jones C and Lawton J (eds) Linking Species and Ecosystems, pp 159–165. Chapman and Hall, New York

Berg NW and Pawluk S (1984) Soil mesofaunal studies under different vegetative regimes in North Central Alberta. Canadian Journal of Soil Science 64: 209–223

Blevins RL, Smith MS, Thomas GW and Fry WW (1983) Influence of conservation tillage on soil properties. Journal of Soil and Water Conservation 38: 301–304

Bollag JM, Myers CJ and Minard RD (1992) Biological and chemical interactions of pesticides with soil organic matter. Science Total Environment 123/124: 205–217

Bongers T (1990) The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83: 14–19

Booth RG and Anderson JM (1979) The influence of fungal food quality on the growth and fecundity of *Folsomia candida* (Collembola: Isotomidae). Oecologia 38: 317–323

Boström S and Söhlenius B (1986) Short-term dynamics of nematode communities in arable soil: Influence of a perennial and an annual cropping system. Pedobiologia 29: 345–357

Chung YR, Hoitink HAH and Lipps PE (1988) Interactions between organic-matter decomposition level and soilborne disease severity. Agriculture, Ecosystems and Environment 24: 183–193

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310

Clarholm M (1985) Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. Soil Biology and Biochemistry 17: 181–187

Crossley DA Jr, Mueller BR and Perdue JC (1992) Biodiversity of microarthropods in agricultural soils: relations to processes. Agriculture, Ecosystems and Environment 40: 37–46

Curl EA and Truelove B (1986) The Rhizosphere. Springer-Verlag, New York, NY, 288 pp

Curl EA, Lartey R and Peterson CC (1988) Interactions between root pathogens and soil microarthropods. Agriculture, Ecosystems and Environment 24: 249–261

Darbyshire JF, Davidson MS, Chapman SJ and Ritchie S (1994) Excretion of nitrogen and phosphorus by the soil ciliate *Colpoda steinii* when fed the soil bacterium *Arthrobacter* sp. Soil Biology and Biochemistry 26: 1193–1199

Dindal DL (1990) Soil Biology Guide. John Wiley, New York, NY, 1349 pp

Doran JW (1980) Soil microbial and biochemical changes associated with reduced tillage. Soil Science Society of America Journal 44: 765–771

Duniway JM (1983) Role of physical factors in the development of *Phytophthora* diseases. In: Erwin DC, Bartnicki-Garcia S and Tsao PH (eds) *Phytophthora*: Its Biology, Taxonomy, Ecology, and Pathology, pp 175–187. American Phytopathological Society, St Paul, MN

Eash NS, Karlen DL and Parkin TB (1994) Fungal contributions to soil aggregation and soil quality. In: Doran JW, Coleman DC, Bezdicek DF and Stewart BA (eds) Defining Soil Quality for a Sustainable Environment, pp 221–228. SSSA Special Publication No. 35, Madison, Wisconsin

Edwards CA and Bohlen PJ (1996) Biology and Ecology of Earthworms, 3rd ed. Chapman and Hall, London

Elliott ET, Hunt HW and Walter CE (1988) Detrital food web interactions in North American grassland ecosystems. Agriculture, Ecosystems and Environment 24: 41–56

Erwin DC, Bartnicki-Garcia S and Tsao PH (1983) *Phytophthora*: Its Biology, Taxonomy, Ecology, and Pathology. American Phytopathological Society, St Paul, MN, 392 pp

Ettema CH (1998) Soil nematode diversity: species coexistance and ecosystem function. Journal of Nematology 30: 159–169

Ettema CH and Bongers T (1993) Characterisation of nematode colonisation and succession in disturbed soil using the Maturity Index. Biology and Fertility of Soils 16: 79–85

Ferris VR and Ferris JC (1974) Inter-relationships between nematode and plant communities in agricultural ecosystems. Agro-Ecosystems 1: 275–299

Filser J, Fromm H, Nagel RF and Winter K (1995) Effects of previous intensive agricultural management on microorganisms and the biodiversity of soil fauna. Plant and Soil 170: 123–129

Foissner W (1992) Comparative studies on the soil life in ecofarmed and conventionally farmed fields and grasslands of Austria. Agriculture, Ecosystems and Environment 40: 207–218

Foissner W (1997) Protozoa as bioindicators in agroecosystems, with emphasis on farming practices, biocides, and biodiversity. Agriculture, Ecosystems and Environment 62: 93–103

Foster RC and Dormaar JF (1991) Bacteria-grazing amoebae in situ in the rhizosphere. Biology and Fertility of Soils 11: 83–87

Freckman DW and Ettema CH (1993) Assessing nematode communities in agroecosystems of varying human intervention. Agriculture, Ecosystems and Environment 45: 239–261

Giller KE, Beare MH, Lavelle P, Izac A-MN and Swift MJ (1997) Agricultural intensification, soil biodiversity and agroecosystem function. Applied Soil Ecology 6: 3–16

Goodell P and Ferris H (1980) Plant-parasitic nematode distributions in an alfalfa field. Journal of Nematology 12: 136–141

Griffin DM (1981) Water potential as a selective factor in the microbial ecology of soils. In: Parr JF, Gardner WR and Elliott LF (eds) Water Potential Relations in Soil Microbiology, pp 141–151. Soil Science Society of America, Special Publication No. 9, Madison, Wisconsin

Griffiths BS (1994) Soil nutrient flow. In: Darbyshire J (ed) Soil Protozoa, pp 65–91. CAB International, Wallingford, Oxon, UK

Gupta VVSR and Germida JJ (1988) Distribution of microbial biomass and its activity in different soil aggregate size classes as affected by cultivation. Soil Biology and Biochemistry 20: 777–786

Harding DJL and Studdart RA (1974) Microarthropods. In: Dickinson DH and Pugh GJF (eds) Biology of Plant Litter Decomposition, pp 489–532. Academic Press, New York, NY

Hassink J, Bouwman LA, Zwart KB and Brussaard L (1993) Relationships between habitable pore space soil biota and mineralization rates in grassland soils. Soil Biology and Biochemistry 25: 47–55

Hawksworth DL and Mound LA (1991) Biodiversity databases: the crucial significance of collections. In: Hawksworth DL (ed) The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture, pp 17–29. CAB International, Wallingford, UK

Hendrix PF, Parmelee RW, Crossley DA Jr., Coleman DC, Odum EP and Groffman PM (1986) Detritus food webs in conventional and no-tillage agroecosystems. BioScience 36: 374–380

Hobbs RJ and Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6: 324–337

Holland EA and Coleman DC (1987) Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology 68: 425–433

Hunt HW, Coleman DC, Ingham ER, Ingham RE, Elliott ET, Moore JC, Rose SL, Reid CPP and Morley CR (1987) The detrital food web in a shortgrass prairie. Biology and Fertility of Soils 3: 57–68

Ingham ER (1998) Managing the soil foodweb to benefit plant growth: care and feeding of soil microherds. Journal of Nematology 29: 585

Ingham ER, Coleman DC and Moore JC (1989) An analysis of food-web structure and function in a shortgrass prairie, a mountain meadow, and a lodgepole pine forest. Biology and Fertility of Soils 8: 29–37

Ingham RE, Trofymow JA, Ingham ER and Coleman DC (1985) Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecological Monographs 55: 119–140

Jackson W (1985) New Roots for Agriculture. University of Nebraska Press, Nebraska, 150 pp

Janzen D (1977) Why fruits rot, seeds mold, and meats spoil. American Naturalist 111: 691–713

Janzen D (1985) Natural history of mutualism. In: Boucher DH (ed) Biology of Mutualism. Ecology and Evolution, pp 40–99. Oxford University Press, New York, NY

Jentschke G, Bonkowski M, Godbold DL and Scheu S (1995) Soil protozoa and forest tree growth: non-nutritional effects and interactions with mycorrhizae. Biology and Fertility of Soils 20: 263–269

King KL and Hutchinson KJ (1976) The effects of sheep stocking intensity on the abundance and distribution of mesofauna in pastures. Journal of Applied Ecology 13: 41–55

Kitazawa Y (1971) Biological regionality of the soil fauna and its function in forest ecosystem types. In: Proceedings of the Brussels Symposium 1969, Ecology and Conservation No. 4. Productivity of Forest Ecosystems, pp 485–498. UNESCO

Koehler HH (1992) The use of soil mesofauna for the judgement of chemical impact on ecosystems. Agriculture, Ecosystems and Environment 40: 193–205

Lal R (1991) Soil conservation and biodiversity In: Hawksworth DL (ed) The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture, pp 89–104. CAB International, London, UK

Larson WE and Pierce FJ (1991) Conservation and enhancement of soil quality. In: IBSRAM Proceedings 12 (2). Evaluation for Sustainable Land Management in the Development World. Volume 2. Bangkok, Thailand. International Board for Soil Research and Management

Lavelle P, Lattaud C, Trigo D and Barois I (1995) Mutualism and biodiversity in soils. Plant and Soil 170: 23–33

Linn DC and Doran JW (1984) Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. Soil Science Society of America Journal 48: 1267–1272

Moore JC and de Ruiter PC (1991) Temporal and spatial heterogeneity of trophic interactions within below-ground food webs. Agriculture, Ecosystems and Environment 34: 371–397

Moore JC, Walter DE and Hunt HW (1988) Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Annual Review of Entomology 33: 419–439

Mueller BR, Beare MH and Crossley DA Jr (1990) Soil mites in detrital food webs of conventional and no-tillage agroecosystems. Pedobiologia 34: 389–401

Neher D and Duniway JM (1992) Dispersal of *Phytophthora parasitica* in tomato fields by furrow irrigation. Plant Disease 76: 582–586

Neher DA and Campbell CL (1994) Nematode communities and microbial biomass in soils with annual and perennial crops. Applied Soil Ecology 1: 17–28

Neher DA and Campbell CL (1996) Sampling for regional monitoring of nematode communities in agricultural soils. Journal of Nematology 28: 196–208

Neher DA and Barbercheck ME (1998) Diversity and role of soil mesofauna. In: Collins W (ed) Importance of Biodiversity in Agroecosystems, Lewis Publishers, Chelsea, Michigan (in press)

Neher DA, Peck SL, Rawlings JO and Campbell CL (1995) Measures of nematode community structure for an agroecosystem monitoring program and sources of variability among and within agricultural fields. Plant and Soil 170: 167–181

Noe JP and Campbell CL (1985). Spatial pattern analysis of plant-parasitic nematodes. Journal of Nematology 17: 86–93

Old KM (1967) Effects of natural soil on survival of *Cochliobolus sativus*. Transactions of the British Mycological Society 50: 615–624

Ott P, Hansen S and Vogtmann H (1983) Nitrates in relation to composting and use of farmyard manures. In: Lockeretz W (ed) Environmentally Sound Agriculture, pp 145–154. Praeger, New York, NY

Petraitis PS, Latham RE and Niesenbaum RA (1989) The maintenance of species diversity by disturbance. Quarterly Review of Biology 64: 393–418

Potter DA (1993) Pesticide and fertiliser effects on beneficial invertebrates and consequences for thatch degradation and pest outbreaks in turfgrass. In: Racke KD and Leslie AR (eds) Pesticides in Urban Environments: Fate and Significance, pp 331–343. ACS Symposium Series No. 522, American Chemical Society, Washington, DC

Richards BN (1987) The Microbiology of Terrestrial Ecosystems. Longman Scientific and Technical, New York, New York, 399 pp

Ryder MH, Brisbane PG and Rovira AD (1990) Mechanisms in the biological control of take-all of wheat by rhizosphere bacteria. In: Hornby D (ed) Biological Control of Soil-Borne Plant Pathogens, pp 123–130. CAB International, Wallingford, UK

Samways MH (1992) Some comparative insect conservation issues of north temperate, tropical and south temperate landscapes. Agriculture, Ecosystems and Environment 40: 137–154

Seastedt TR (1984) The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29: 25–46

Seastedt TR, James SW and Todd TC (1988) Interactions among soil invertebrates, microbes and plant growth in the tallgrass prairie. Agriculture, Ecosystems & Environment 24: 219–228

Setälä H (1995) Growth of birch and pine seedlings in relation to grazing by soil fauna on ectomycorrhizal fungi. Ecology 76: 1844–1851

Setälä H and Huhta V (1991) Soil fauna increase *Betula pendula* growth: laboratory experiments with coniferous forest floor. Ecology 72: 665–671

Setälä H, Tyynismaa M, Martikainen E and Huhta V (1991) Mineralisation of C, N and P in relation to decomposer community structure in coniferous forest soil. Pedobiologia 35: 285–296

Söhlenius B, Boström S and Sandor A (1988) Carbon and nitrogen budgets of nematodes in arable soil. Biology and Fertility of Soils 6: 1–8

Sommers LE, Gilmour CM, Wildung RE and Beck SM (1981) In: Parr JF, Gardner WR and Elliott LF (eds) Water Potential Relations in Soil Microbiology, pp 97–117. Soil Science Society of America, Special Publication No. 9, Madison, Wisconsin

Steen E (1983) Soil animals in relation to agricultural practices and soil productivity. Swedish Journal of Agricultural Research 13: 157–165

Strueve-Kusenberg R (1982) Succession and trophic structure of soil animal communities in different suburban fallow areas. In: Bornkamm R, Lee JA and Seaward CRD (eds) Urban Ecology, pp 89–98. Blackwell Scientific, Oxford, UK

Swift CJ, Heal OW and Anderson JC (1979). Decomposition in Terrestrial Ecosystems. University of California, Berkeley, California, 372 pp

Teuben A and Verhoef HA (1992) Direct contribution by soil arthropods to nutrient availability through body and faecal nutrient content. Biology and Fertility of Soils 14: 71–75

Thimm T and Larink O (1995) Grazing preferences of some Collembola for endomycorrhizal fungi. Biology and Fertility of Soils 19: 266–268

Trofymow JA and Coleman DC (1982) The role of bacterivorous and fungivorous nematodes in cellulose and chitin decomposition in the context of a root/rhizosphere/soil conceptual model. In: Freckman DW (ed) Nematodes in Soil Ecosystems, pp 117–138. University of Texas, Austin

Van de Bund CF (1970) Influence of crop and tillage on mites and springtails in arable soil. Netherlands Journal of Agricultural Science 18: 308–314

Van Vliet PCJ, Beare MH and Coleman DC (1995) Population dynamics and functional roles of Enchytraeidae (Oligochaeta) in hardwood forest and agricultural ecosystems. Plant and Soil 170: 199–207

Verhoef HA and Brussard L (1990) Decomposition and nitrogen mineralization in natural and agro-ecosystems: The contribution of soil animals. Biogeochemistry 11: 175–211

Walter DE (1987) Trophic behaviour of (mycophagous) microarthropods. Ecology 68: 226–229

Walter DE and Ikonen EK (1989) Species, guilds, and functional groups: taxonomy and behaviour in nematophagous arthropods. Journal of Nematology 21: 315–327

Walter DE, Hudgens RA and Freckman DW (1986) Consumption of nematodes by fungivorous mites, *Tyrophagus* spp. (Acarina: Astigmata: Acaridae). Oecologia 70: 357–361

Walter DE, Hunt HW and Elliott ET (1988) Guilds or functional groups? An analysis of predatory arthropods from a shortgrass steppe soil. Pedobiologia 31: 247–260

Wardle DA (1995) Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. Advances in Ecological Research 26: 105–185

Wardle DA and Yeates GW (1993) The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: evidence from decomposer food-webs. Oecologia 93: 303–306

Wardle DA, Yeates GW, Watson RN and Nicholson KS (1995) The detritus food-web and the diversity of soil fauna as indicators of disturbance regimes in agro-ecosystems. Plant and Soil 170: 35–43

Wasilewska L (1979) The structure and function of soil nematode communities in natural ecosystems and agrocenoses. Polish Ecological Studies 5: 97–145

Wasilewska L (1989) Impact of human activities on nematodes. In: Charholm C and Bergstrom L (eds) Ecology of Arable Land, pp 123–132. Kluwer Academic, Dordrecht, The Netherlands

Wasilewska L, Jakubczyk H and Paplinska E (1975) Production of *Aphelenchus avenae* Bastian (Nematoda) and reduction of mycelium of saprophytic fungi by them. Polish Ecological Studies 1: 61–73

Weil RR and Kroontje W (1979) Effects of manuring on the arthropod community in an arable soil. Soil Biology and Biochemistry 11: 669–679

Weiss B and Larink O (1991) Influence of sewage sludge and heavy metals on nematodes in an arable soil. Biology and Fertility of Soils 12: 5–9

Whitford WG, Freckman DW, Santos PF, Elkins NZ and Parker LW (1982) The role of nematodes in decomposition in desert ecosystems. In: Freckman DW (ed) Nematodes in Soil Ecosystems, pp 98–115. University of Texas, Austin

Wicklow DT (1981) Interference competition and the organization of fungal communities. In: Wicklow DT and Carroll GC (eds) The Fungal Community: Its Organization and Role in the Ecosystem, pp 351–375. Marcel Dekker, New York, NY

Whitaker RH (1975) Communities and Ecosystems. 2nd ed. Macmillian, New York, 385 pp

Yeates GW (1984) Variation in soil nematode diversity under pasture with soil and year. Soil Biology and Biochemistry 16: 95–102

Yeates GW (1994) Modification and qualification of the nematode maturity index. Pedobiologia 38: 97–101

Yeates GW and Wardle DA (1996) Nematodes as predators and prey: relationships to biological control and soil processes. Pedobiologia 40: 43–50

Yeates GW and Coleman DC (1982) Nematodes in decomposition. In: Freckman DW (ed) Nematodes in Soil Ecosystems, pp 55–80. University of Texas, Austin

Yeates GW, Bamforth SS, Ross DJ, Tate KR and Sparling GP (1991) Recolonization of methyl bromide sterilized soils under four different field conditions. Biology and Fertility of Soils 11: 181–189

Zwart KB, Kuikman PJ and VanVeen JA (1994) Rhizosphere protozoa: their significance in nutrient dynamics. In: Darbyshire J (ed) Soil Protozoa, pp 93–121. CAB International, Wallingford, Oxon, UK