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## «SOIL COMMUNITY COMPOSITION AND ECOSYSTEM PROCESSES»

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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 synchronize 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*

**1-** 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' (André et al. 1994).  About 10% of soil species have been identified (Hawksworth & 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 sub-disciplines 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 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.

**2-**This paper will intoduce 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.  Finally, research priorities will be summarised.   Most discussions will focus on nematodes, springtails (Collembola) and mites because they predominate in total numbers, biomass and species of fauna in soils (Harding & Studdart 1974; Samways, 1992).

### *Table 1.*  **Numbers of species in the world**

| Organism group | Describes species (X $10^3$) | Estimated species (X $10^3$) | % of estimated species described |
|---|---|---|---|
| Dicot plants | 170 | | |
| Monocot plants | 50 | | |
| Ferns | 10 | | |
| Moses and liverworts | 17 | | |
| Fish | 19 | | |
| Birds | 9 | 21 | 95 |
| 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 | 0,08-0,04 |

*Source:* Hawksworth and Mound (1991).

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

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| 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 | 1,0-6,0 | 0,005-02 | $10^6$-$10^{12}$ |
| 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 | $\geq$20 | 0=$10^3$ |

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[a] Not applicable
*Source:* Dindal (1990) and Lal (1991).

## 2. *Soil food web*

**3-** Mesofauna occupy all trophic levels within the soil food web (Fig. 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).

**4-** Plant 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 source 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 & 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;

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Goodell & Ferris, 1980; Barker & Campbell, 1981; Noe & Campbell, 1985; Griffiths, 1994)

**5-** 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 spring tails). 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 communites may be more prevalent than assumed previously (Walter, 1987; Walter et al. 1986, 1988; Walter & Ikonen 1989;Mueller et all. 1990; Bengtsson et al. 1995). Predators include secondary, tertiary and quaternary 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 & 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).

**6-** 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 types. 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 agriculture soils (table 3). In constrast 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.)* (Baere, 1997). In the Netherlands, disturbances such as cultivation and addition of mineral fertilisers eliminate certain functional groups such as predacious nematodes, omnivorus 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 Vielt et al. 1995).

*Table 3*   Number of nmatode genera per trophic (percent) of mean abundance), species diversity, species richness, and numbers of nematodes in soil in 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 | 2-4 (16) | 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] | 3.9-4.93.2-4.3 | |
| Species richness | 33-34 | 87-100 | 74 | 34-68 |
| Mean no. nematodes | 3.5-5.0 | _[a] | 2.3-3.32.3-3.7 | |

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

**7-** 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 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.

**8-** 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 & Doran 1984). Saturation (water-logging) and drought are detrimental to soil faunal communities, because these conditions result in anaerobiosis and dehydratation, 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 & Dormaar 1991; Griffiths 1994).

### 3. *Soil function*

**9-** 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.

**10-** 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 nematodes genera in soils within asparagus *(Asparagus officinalis 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.

**11-** Disturbance certainly plays a role in altering diversity.  Perhaps intermediate disturbance promotes macrofungal diversity, and extreme or lack of disturbance reduces diversity relative to undisturbed systems (Petraitis et al. 1989: Hobbs & 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-fields (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 appproach 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).

**12-** Perhaps, it is more important to mimic the diversity of ecosystem functions observed in natural systems than to mimic diversity of community composition (Main, this volume;Van Noordwijk & Ong, this volume). For example, an index of trophic diversity may serve as a measure of functional diversity in soil communities (Fig. 2).  Reducing the frequency  of cultivation (Hendrix et al. 1986) and including perennial crops in agricultural systems (Wasilewska 1979; Freckman & Ettema 1993; Neher & 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 functions. 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 & Pierce 1991):

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

**13-** Individual taxa may have multiple functions and several taxa appear to have similar functions. However, taxa may not necessarily be redundant because taxa performing the same function are often isolated spatially, temporally, or by microhabitat preference (Beare et al. 1995). Ettma (1998) suggests that the extent of nematode functional redundancy in soil has been greatly over-estimated. Although redundancy of single functions is common, distinct physiological and environmental requirements drive species of the same functional group to play widely diffrent roles in soil ecosystem processes.

### 3.1 *Promoting plant growth*

**14-** Growth may be enhanced for plants in soils containing multiple functional groups.  For example, in North America 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 (Verrhoef & Brusaard 1990; Griffiths 1994; Alphei et al 1996). In glasshouse experiments, blue gamma grass withdrew more nitrogen from fertilised soil in the presence of amoebea 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

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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).

**15-** 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 amoebae (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).

**16-** 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 obseerved 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 rhizopheres of common garden bean *(Phaseolus vulgaris)* (Zwart et al. 1994).

**17-** 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.; 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*

18- 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

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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 soils 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 inflitration and improve aeration. Van Vliet et al. (1995) hypothesise that enchytraeids have more influence on soil structure in agricultural fileds than in forested areas.

**19-** 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 *Streptomyces 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).

**20-** 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 decomposing where saturated conditions result in the depletion of oxygen ($O_2$) and the development of anaerobic conditions. Under these conditions, anaerobic bacteria are predominant organisms responsible for decomposition. Comparison of decomposition rate to soil water

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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 reduces carbon compounds may be significant end-products under saturation (Sommer et al. 1981).

### 3.3 *Recycling carbohydrates and nutrients through mineralisation*

**21-** 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 1994; 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 subsequently become available to plants (Seastedt et al. 1988; Söhlenius et al. 1998),

**22-** Model simulations of soil food web estimate that 97% and 99% of total nitrogen flux can be attributed to bacterial pathway in integrated farming and conventional farming systems, respectively (Neare 1997).  Grifftiths (1994) estimates from independant 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 90kg of nitrogen per year in no-till and conventionally tilled soils (Beare 1997). In The Netherlands, protozoa mineralise approximately 30 to 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)

**23-** In addition to protozoa, bacterial-feeding and predatory nematodes are estimated to contribute (directly and indirectly) abour 8 to 19% of nitrogen mineralisation in conventional and integrated farming systems (Baere 1997). Although counter-intuitive, predatory nematodes sometimes demonsrate 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).

**24-** 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 (Griffiths 1994) or increased nitrate leaching with prorozoa and earthworms (Alphei et al. 1996). The presence and abundance of earthworm activity have also been linked to increased leaching in 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).

**25-** The bacteria pathway is not always the dominant force in net nitrogen mineralisation. In Sweden, fungal contributions to nitrogen immobilisation is 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).

**26-** Not only may soil fauna stimulate net mineralisation of nutrients but they may also promote nutrient immobilisaion. In Sweden, more nitrogen was immobilised in surface applied than burried straw in soils cropped to meadow fescue or lucerne. Perhaps competition for available nitrogen occured 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*

**27-** 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 reinoculate 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

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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).

**28-** 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 199l; Bengtsson et al. 1995)

**29-** 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 enchytreids and bacterial-feeding nematodes are present. Once the substrate is decomposed somewhat and changes 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).

**30-** In desert ecosystems containing creosote-bush (Larrea tridentata), food webs with additionnal 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 insecticide chlordane) than with mites (no insecticide). Without mites, nematode grazing may have decreased the decomposition rates. 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*

**31-** Soils act as an environemental buffer physically, chemically and biologically. Physically, soils may filter materials such as pesticides and fertilisers 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 polymerized and incorporated into humus by 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 allellopathic chemicals. Carbon coumpounds are stored in plant. microbre 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 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 chapparal with *Adenostoma fasiculatum* (Wicklow 1981). Fire eliminates the allelopathic effect temporally. However, it returns after re-establishment of the microbial community. Agronomists have utilised fire to manage soil fungal pathogens of wheat, barley and rice.

**32-** The presence of particular groups of organisms has ben associated with the suppression of plant disease. First, springails *Proisotoma minuata* 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 Vampyrellidae perforate conidia of *Cochliobolus sativus* on barley (Old,1967). Protozoa have been reported to play an active role in disease suppression by

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consuming pathogenic nematodes, bacteria and fungi (Zwart et al. 1994). Generally, plant pathogens have faster growth rate 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 graminis* under conditions of no-till, continuous wheat productions (Ryder et al. 1990).

## 4. *Designing and maintaining soil communities for optimum fuctions*

**33-** Modern agricultural methods have repalaced or substituted natural and seasonal patterns of ecological processes with inorganic materials. These subtitutions 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 scientits 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).

**34-** 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 availability to plants and other organisms. We cannot conclude that soil biodiversity causes ecosystem function because there is insufficient evidence to support claim.

**35-** To better mimic nature, soil ecosystems must be designed and managed to foster food webs containing mutiple functionnal groups or taxa (i.e. complex community) and ber relatively mature successionally. This can be achieved by incorporating four types of activities:
- reduction or elimination of cultivation, heavy machinery and general
   biocides;
- incorporating perennial crops and organic material;

- synchronising nutrient release and water availability with plant demand;

- monitoring biological activity.

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

**36**- Decomposition rates are sensitive to physical disturbances such as cultivation. For example, decomposition rates are 1.4 to1.9 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).

**37-** Soil managed by conventional, reduced, or no tillage practices have distinct biological and functional properties (Doran 1980; Hendrix et al. 1986). Plant residue is disturbed 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 (Steven 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 a secondary colonisers after decay is initiated (Beare 1997). Relative abundace 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 Coleman1987; Walter 1987, Neher and Campbell 1994; Beare 1997).

**38-** 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 affected negatively, and others positively, by cultivation (Wardle 1995). The lack of response of 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.

**39-** Soil fumigation with general biocides has short and/or long-term impacts on soil community composition and abundance. Biocides may either impact the microbes of 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; Ettma and Bongers 1993; Edwards and Bohlen 1996). Phenoxy acetic acid and 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 æstivus)* 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 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 (Kowhler 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.

**40-** Benefits of eliminating general biocides are illustrated by two case studies (Ingham 1998) involving strawberry *(Fragaria X 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 certains 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 number of bacterial species.  A remediation program was implemented to reverse the apparent enviromental problems. Spent mushroom compost (high fungal content) was applied to soil at a rate of 60 tons 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 soils 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*

**41-** 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; Wasileska 1979: Freckman and Ettma 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.

**42-** 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 Dutch polder soil (van de Bund 1970).

**43-** 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.

**44-** Caution is adviced 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).

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**45-** 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*

**46-** Fertiliser addition affects soil microflora and indirectly impacts soil mesofauna by changing their food resources (Weil and Kroonje 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 greater or lesser nitrogen content.

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

**48-** Appropriate timing of water is important for disease management. For example, frequent irrigation episodes may increase potential of root rot diseases caused by *Phytophtora spp.* The reproductive biology of *Phytophtora 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 (Fig. 3). Phytophtora root rots have been well documented world-wide, including those of jarrah *(Eucalyptus marginata)* and *Banksia* in Australia and on many vegetable and tree crops in the US (Erwin et al. 1983).

### 4.4 *Monitoring biological activity*

**49-** The successional status of a soil community may reflect the history of disturbance. Succession in cropped agricultural fields begins with depauperated soil after cultivation and clearing of native vegetation which atcs 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).

**50-** Succession can be interrupted at various stages by agricultural practices, such as cultivation and applications of fertilisers 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 Ettma 1983; 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

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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) Sucessional 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 crop (i.e. disturbed) than permanent pasture (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 functionnal 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

**51-** Our challenge is to understand concepts and mechanisms that mimic nature, qualitatively and quantitatively, at appropriate spatial (centimeters 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*

**52-** 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 undrestood at the individual and population level. At the community level, potential competitive exclusion, predation and/or antgonism 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 nutirent cycling, energy flow and disease management must be evaluated.

### 5.2 *Timing of management implementation*

**53-** 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 intensive competition  for nutrients between microbes and plants.

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

**54-** 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

**55-** 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 requirement. 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 agricutural 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.

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# 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». Œcologia **106**: 111-126.

**Anderson, R.V., Gould, W.D., Woods, L.E., Cambardella, C. Ingham, R.E. and Coleman, D.C. (1983)** «Organic and inorganic nitrogenous losses by microbivorous nematodes in soil». Oikos **40**: 75-80.

**Andre, H.M., Noti, M.I. and Lebrun, P. (1994)** «The soils fauna: the other last biotic frontier». Biodiversity and Conservation **3**:45-56

**Andrén, O., Bengtsson, J.and Clarholm M. (1995)** «Biodiversity and species redundancy among litter decomposers» In: Collins, H.P., Robertson, G.P. and Klug, M.J. (eds) The Significance and Regulation of Soil Biodiversity, pp 141-151. Kluwer Academic Publisherd, Dortrecht, The Nederlands.

**Andrén, O. and Lagerlöf, J. (1983)** «Soil fauna (microarthropods. enchytraeids, nematodes) in Swedish agricultural cropping systems». Acta Agriculturae Scandinaviae **33**: 33-52.

**Andrén, O. Paustian, K. and Rosswall, T. (1988)** «Soil biotic interactions in the functionning of agroecosystems». Agriculture, Ecosystems and Environment **24**: 57-67.

**Barker, K.R. and Campbell, C.L. (1981)** «Sampling nematode populations». In: Zuckerman, B.M. Rhode, R.A. (eds) Plant parasitic nematodes. vol. III pp.451-474. Academic Press NY.

**Beare, M.H. (1997)** «Fungal and bacterial pathways of organic matter decomposition and nitrogen mineralization in arable  soil». In: Brussard,L. and Ferrera-Cerrato, R. (eds) Soil Ecology in Sustainable Agriculture Systems pp.37-70 Lewis Publishers Boca Raton La.

**Beare, M.H., Coleman, D.C. Crossley, D.A., Hendrix, P.F. and Odum, E.P.(1995)** «A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling». In: Collins, H.P., Robertson, G.P. and Klug M.J. (eds) "The significance and Regulations of soil biodiversity", pp 5-22 Kluwer Academic Publishers. Dortrecht, The Netherlands.

**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». Ecological Monographs **62**: 569-591.

**Bengtsson, J., Zheng, D.W., Agren, G.I. 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, N.W. and Pawluk, S. (1984)** «Soil mesofaunal studies under different vegetative regimes in North Central Alberta». Can Jour, Soil. Sci. **64**: 209-223.

**Blevins. R.L., Smith, M.S., Thomas, G.W. and Fry, W.W. (1984)** «Influence of conservation tillage on soil properties». Journal of Soil and Water Conservation **38**: 301-304

**Bolag, J.M., Myers, C.J. and Minard, R.D. (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». Œcologia **83**: 14-19.

**Booth, R.G. and Anderson, J.M. (1979)** «The influence of fungal food quality on the growth and fecundity of *Folsomia candida*  (Collembola: Isotomidae).Œcologia **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, Y.R., Hoitink, H.A.H. and Lipps, P.E. (1988)** «Interactions between organic matter decomposition level and soilborne disease severity» Agriculture, Ecosystems and Environement **24**: 183-193.

**Connell, J.H. (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, D.A. Jr, Mueller, B.R. and Purdue J.C. (1992)** "Biodiversity of microarthropods in agricultural soils: relations to processes».Agriculture, Ecosystems and Environment **40**: 37-46.

**Curl, E.A. and Truelove, B. (1986)** «The Rhizosphere», Springer-Verlag, New York NY 288 pages

**Curl, E.A., Lartey, R. and Perterson, C.C. (1988)** «Interactions between root pathogens and soil microarthropods». Agriculture, Ecosystems and Environment **24**: 249-261.

**Darbyshire, J.F., Davidson, M.S., Chapman, S.J. 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, D.L. (1990)** «Soil Biology Guide» John Wiley, New York 1349 pages.

**Doran, J.W. (1980)** «Soil microbial and biochemical changes associated with reduced tillage». Soil Science Society of America Journal **44**: 765-771.

**Duniway, J.M. (1983)** «Role of physical factors in the development of Phytophtora diseases". In: Erwin, D.C. Bartnicki-Garcia, S. and Tsao, P.H. (eds) Phytophtora: Its Biology, Taxonomy, Ecology and Pathology, pp.175-187. Amercan Phytopathological Society, St-Pauil MN.

**Eash, N.S., Karlen, D.L. and Parkin, T.B. (1994)** "Fungal contributions to soil aggregation and soil quality". In: Doran, J.W., Coleman, D.C., Bezdicek, D.F. and Stewart, B.A. (eds) Defining soil quality for a Sustainable Environment. pp 221-228, SSSA Special publication n° 35, Madison, Wisconsin.

**Edwards, C.A. and Bohlen P.J. (1996)** «Biology and Ecology of Earthworms» 3rd edition Chapman and Hall, London.

**Elliott, E.T., Hunt, H.W. and Walter, C.E. (1988)** «Detrital food web interactions in North America grassland ecosystems» Agriculture, Ecosystems and Environement **24**: 41-56.

**Erwin, D.C., Bartnicki-Garcia, S. and Tsao, P.H. (1983)** «Phytophtora: Its Biology, Taxonomy, Ecology and Pathology». American Phytopathological Society. St-Paul MN 392p.

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**Ettema, C.H. (1998)** «Soil nematode diversity: species coexistance and ecosystem function. Journ. of Nematology **30**: 159-169.

**Ettema, C.H. 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, V.R. and Ferris J.C. (1974) "Inter-relationships between nematode and plant communities in agricultural ecosystems". Agro-ecosystems **1**: 275-299.

**Filser, J. Fromm, H., Nagel, R.F. and Winter, K. (1995)** «Effects of previous intensisve agricultural management on microganisms and the biodiversity of soil fauna». Plant and Soil **170**: 123-129.

**Foissner, W. (1992)** «Comparative studies on the soil life in ecoframed and conventionaly 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, R.C. and Dormaar, J.F. (1991)** «Bacteria-grazing amoebae in situ in the rhizosphere». Biology and Fertility of Soils **11**: 83-87.

**Freckman D.W. and Ettema, C.H. (1993)** «Assessing nematode communities in agroecosystems of varying human intervention». Agriculture, Ecosystems and Environment **45**: 239-261.

**Giller, K.E., Beare, M.H., Lavelle, P., Izac, A-MN. and Swift, M.J. (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 Nematodology **12**: 136-141.

**Griffin, D.M. (1981)** «Water potential as a selective factor in the microbial ecology of soils». In: Parr, J.F., Gardner, W.R. and Elliott. L.F. (eds) Water Potential Relations in Soil Microbiology, pp 141-151. Soil Science Society of America Special Publication n° 9 Madison, Wisconsin.

**Griffiths, B.S. (1994)** «Soil nutrient flow». In: Darbyshire, J. (ed) Soil Protozoa pp.65-91 CAB International. Wallingford, Oxon, UK.

**Gupta, V.V.S,R. and Germida, J.J. (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, D.J.L. and Studdart, R.A. (1974)** «Microarthropods». In: Dickson, D.H. and Pugh, G.J.F. (eds) Biology of Plant Litter Decomposition pp. 489-532. Academic Press New York, NY.

**Hassink, J., Bouwman, L.A., Zwart, K.B. and Brussard L. (1993)** «Relationships between habitable pore space soil biota and mineralization rates in grassland soils». Soil Biology and Biochemistry, **25**: 47-55

**Hawksworth, D.L. and Mound, L.A. (1991)** «Biodiversity database: the crucial significance of collections». In: Hawksworth, D.L. (ed) The biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture pp. 17-29, CAB International, Wallingford, UK.

**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.

**Hobbs, R.J. and Huenneke, L.F. (1992)** «Disturbance, diversity, and invasion: implications for conservation». Conservation Biology **6**: 324-337.

**Holland, E.A. and Coleman, D.C. (1987)** «Litter placement effects on microbial and organic matter dynamics in an agroecosystem». Ecology **68**: 425-433.

**Hunt, H.W., Coleman, D.C., Ingham, E.R., 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". Biology and Fertility of Soils. **3**: 57-68.

**Ingham, E.R. (1998)** «Managing the soil foodweb to benefit plant growth: care and feeding of soil microherbs". Journal of Nematology **29**: 585.

**Ingham, R.E., Trofymow, J.A., Ingham, E.R. and Coleman D.C. (1983)** «Interaction of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth». Ecological Monographs **55**: 119-140.

**Ingham, R.E., Coleman, D.C. and Moore, J.C. (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

**Jackson, W. (1985)** «New Roots for Agriculture» Universisty 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, D.H. (ed) Biology of Mutualism. Ecology and Evolution. pp.40-99, Oxord Press, New York, NY

**Jentschke, G., Bonkowski, M., Godbold, D.L. 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, K.L. and Hutchinson, K.J. (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 n° 4, Productivity of Forest Ecosystems, pp. 485-498.

**Koeehler, H.H. (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, D.L. (ed) The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture, pp 89-104 CAB International, London UK.

**Larson, W.E. and Pierce, F.J. (1991)** «Conservation and enhancement of soil quality». In: IBSRAM Proceeddings 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, D.C. and Doran J.W. (1984)** «Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils». Soils Science Society of America Journal **48**: 1267-1272.

**Moore, J.C. and Ruiter, P.C. (1991)** «Temporal and Spacial heterogeneity of trophic interactions within below-ground food webs" Agriculture, Ecosystems and Environement **34**: 371-397.

**Moore, J.C., Walter, D.E. and Hunt, H.W. (1988)** «Arthropod regulation of micro- and mesobiota in below-ground detrital food webs». Annual Review of Entomology **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.

**Neher, D. and Duniway, J.M. (1992)** «Dispersal of *Phytophtora parasitica* in tomato fields by furrow irrigation». Plant Disease **76**: 582-586.

**Neher, D.A. and Campbell C.L. (1994)** «Nematode communities and microbial biomass in soils with annual and perennial crops» Applied Soil Ecology **1**: 17-28.

**Neher, D.A. and Campbell C.L. (1996)** «Sampling for regional monitoring of nematode communities in agricultural soils». Journal of Nematology **28**: 196-208.

**Neher, D.A. and Barbercheck, M.E. (1998)** «Diversity and role of soil mesaufauna». In: Collins, W. (ed) Importance of Biodiversity in agroecosystem. Lewis Publishers, Chelsea (in press).

**Neher, D.A., Peck, S.L., Rawlings, J.O. and Campbell, C.L. (1995)** «Measures of nematode community structure for an agroecosystems monitoring program and sources of variability among and within agricultural fields». Plant and Soil **170**: 167-181.

**Noe, J.P. and Campbell, C.L. (1985)** «Spatial pattern analysis of plant parasitic nematodes». Journal of Nematology **17**: 86-93.

**Old K.M. (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, P.S., Latham, R.E. and Niesenbaum, R.A. (1989)** «The maintenance of species diversity by disturbance». Quarterlty Review of Biology **64**: 393-418.

**Potter, D.A. (1993)** «Pesticide and fertilizer effects on beneficial invertebrates and consequences for thatch degradation and pest outbreacks in turfgrass». In: Racke, K.D. and Leslie A.R. (eds) Pesticides in Urban Environements: Fate and Significance. pp. 331-343, ACS Symposium Serie n° 522. American Chemical Sopciety, Washington DC.

**Richards, B.N. (1987)** «The microbiology of Terrestrial Ecosystems». Longman Scientific and Technical, New-York, NY 399 pp.

**Ryder, M.H., Brisbane, P.G. and Rovira A.D. (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, U.K.

**Samways, M.H. (1992)** «Some comparative insect conservation issues of north temperate, tropical and south hemisphere lanscapes». Agriculture, Ecosystems and Environment **40**: 137-154.

**Seastedt, T.R. (1984)** «The role of microarthropods in decomposition and mineralization processes". Annual Review of Entomology **29**: 25-46

**Seastedt, T.R., James, S.W. and Todd, T.C. (1988)** «Interactions among soil invertebrates, microbes and plant growth in the tallgrass prairie». Agriculture, Ecosystems and 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 Fertilioty of Soils **6**: 1-8.

**Sommers, L.E., Gilmour, C.M., Wildung, R.E. and Beck, S.M. (1981)** "In: Parr, J.F., Gardner, W.R. and Elliott, L.F. (eds) Water Potential Relations in Soil Microbiology". pp.97-117. Soil Science Society of America, Special Publication n° 9 Madison, Wisconsin.

**Steen, E. (1983)** «Soil animals in relation to agriculture 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: Bornkmann, R., Lee, J.A. and Seaward, C.R,D. (eds) Urban Ecology, pp.89-98. Blackwell Scientific, Oxford, UK.

**Swift, C.J., Heal, O.W. and Anderson, J.C. (1979)** «Decomposition in Terrestrial Ecosystems». University of California, Berkeley, California, 372 pp.

**Teuben, A. and Verhoef, H.A. (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, J.A. and Coleman, D.W. (1982)** «The role of bacterivorous and fungivorus nematodes in cellulose and chitin decomposition in the context of a root/rhizosphere/soil conceptual model». In: Freckman, D.W. (ed) Nematodes in Soil Ecosystems pp.117-138. University of Texas, Austin.

**Van de Bund, C.F. (1970)** «Influence of crop and tillage on mites and springtails in arable soil». Netherlands Journal of Agricultural Science **18**: 308-314.

**Van Vliet, P.C.J., Beare, M.H. and Coleman, D.C. (1995)** «Population dynamics and functional roles of Enchytraeidae (Oligochaeta) in hardwood forest and agricultural ecosystems». Plant and Soil **170**: 199-207.

**Verhoef, H.A. and Brusaard, L. (1990)** «Decomposition and nitrogen mineralization in naural and agro-ecosystems: The contribution of soil animals». Biogeochemistry **11**: 175-211.

**Walter, D.E. (1987)** «Trophic behaviour of (mycophagous) microarthropods» Ecology, **68**: 226-229.

**Walter. D.E. and Ikonen, E.K. (1989)** «Species, guilds, and functional groups: taxonomy and behaviour in nematophagous arthropods». Journal of Nematology **21**: 315-327.

**Walter, D.E., Hudgens, R.A. and Freckamn, D.W. (1986)** «Consumption of nematodes by fungivorous mites, *Tyrophagus spp.* (Acarina: Astigmata: Acaridae)». Œcologia **70**: 357-361.

**Walter, D.E., Hunt, H.W. and Elliott, E.T. (1988)** «Guilds of functional groups? An analysis of predatory arthropods from a shortgrass steppe soil». Pedobiologia **31**: 247-260.

**Wardle, D.A. (1995)** «Impact of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices». Advances in Ecological Research **26**: 105-185.

**Wardle, D.A. and Yeates, G.W. (1993)** «The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: evidence from decomposer food-webs". Œcologia **93**: 303-306.

**Wardle, D.A., Yeates, G.W., Watson, R.N. and Nicholson K.S. (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: Clarholm, C, and Bergstrom, L. (eds) Ecology of Arable Land pp. 123-132 Kluwer Academic, Dortrecht, The Netherlands.

**Wasilewska, L., Jakubczyj, H. and Paplinska, E. (1975)** «Production of *Aphelenchus avenae* Bastian (Nematoda) and reduction of mycelium of saprohpytic fungi by them". Polish Ecological Studies **1**: 61-73.

**Weil, R.R. 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, W.G., Freckman, D.W., Santos, P.F., Elkins, N.Z. and Parker L.W. (1982)** «The role of nematodes in decompostion in desert ecosystems». In: Freckman, D.W. (ed) Nematodes in Soil Ecosystems, pp. 98-115, University of Texas, Austin.

**Wicklow, D.T. (1981)** «Interference competition and the organization of fungal communities». In: Wicklow, D.T. and Carroll, G.C. (eds) The fungal community: Its organization and role in the Ecosystem. pp. 351-375, Marcel Dekker, New York NY.

**Whitaker, R.H. (1975)** «Communities and Ecosystms». 2nd ed. Macmillan, NwpYork, 385 pp.

**Yeates, G.W. (1984)** «Variation in soil nematode diversity under pasture with soil and year». Soil Biology and Biochemistry **16**: 95-102.

**Yeates, G.W.(1994)** «Modification and qualification of the nematode maturity index». Pedobiologia **38**: 97-101.

**Yeates, G.W. and Wardle, D.A. (1996)** «Nematodes as predators and prey: relatioships to biological control and soil processes». Pedobiologia **40**-43-50.

**Yeates, G.W. and Coleman, D.C. (1982)** «Nematodes in decomposition». In: Freckman, D.W. (ed) Nematodes in Soil Ecosystems pp 55-80 University of Texas. Austin.

**Yeates, G.W., Bamforth, S.S., Ross, D.J., Take, K.R. and Sparkling, G.P.(1991)** «Recolonization of methyl bromide sterelized soils under four different field conditions». Biology and Fertility of Soils, **11**: 181-189.

**Zwart, K.B. Kuikman, P.J. and Van Veen, J.A. (1994)** «Rhizosphere protozoa: their significance in nutrient dynamics». In: Darbyshire, J. (ed) Soil Protozoa. pp 93-121 CAB International Wallingford, Oxon UK.

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