Effects of Key Soil Organisms on Nutrient Dynamics in Temperate Agroecosystems

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SUMMARY. Soil organisms are a diverse group that can influence the nutrient dynamics in temperate agroecosystems profoundly. Many organisms interact in a symbiotic or mutualistic way with plants, and these relationships have co-evolved, permitting plants and soil organisms to flourish in the soil environment. Numerous controlled lab or small plot-scale studies have demonstrated that soil organisms can mobilize or transfer substantial quantities of nutrients to crops, in relationship to crop requirements. However, the simple scaling up of such results to explain conditions on a large field scale is very much constrained by a lack of information on the spatio-temporal distribution of soil organisms in temperate agroecosystems. The numbers, diversity and activity of soil organisms in temperate agroecosystems are affected by agricultural management practices such as tillage operations, but our knowledge of the key organisms or groups of organisms that contribute to nutrient cy-

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cling and crop production under different sets of management practices is limited. Better management of nutrients in temperate agroecosystems requires better knowledge of soil biota, their effects on nutrient cycling and their contribution to crop production.

KEYWORDS. Soil fauna, soil biological activity, symbiotic, free-living, nutrient uptake, crop production

INTRODUCTION

Soil organisms are a diverse group that can influence the nutrient dynamics in temperate agroecosystems profoundly. The cycling of nutrients through their biomass is a key process that, along with photosynthesis, maintains life on earth. Even the smallest and least mobile of the soil organisms has evolved mechanisms to derive energy and nutrients from soil organic matter (OM) and minerals. Many also interact in a symbiotic or mutualistic way with plants, and these relationships have co-evolved, permitting plants and soil organisms to flourish in the soil environment. The numbers and diversity of plants and belowground organisms in a particular soil are strongly influenced by soil physical and chemical properties, but these organisms can also modify the physical and chemical characteristics of soil and change the trajectory of soil development.

Although it is well known that soil organisms can mobilize or transfer substantial quantities of nutrients to crops, in relationship to crop requirements, it is difficult to simply scale up these results to the field scale. In temperate agroecosystems, the contribution of soil organisms to nutrient cycling and crop production is largely ignored, and many producers rely on synthetic fertilizers to provide the nutrients required by their crops. Environmental concerns for soil, water and air quality are prompting producers to re-evaluate their agricultural practices and fertilizer use. For agriculture to be sustainable, we must devise better management practices to maintain or increase crop yields without degrading soils and the environment. Nutrient management is central to the development of more sustainable agricultural systems, but better management of nutrients requires better knowledge of soil biota and their role in nutrient cycling. This article presents an overview of the organisms that inhabit soils and how they transform nutrients in OM and

soil minerals into forms that can be used by plants. We will discuss briefly how agricultural practices affect the activity of soil organisms, with an emphasis on tillage practices.

THE BIOLOGY AND ECOLOGY OF SOIL ORGANISMS

Soil Microorganisms

There are five distinct groups of microorganisms found in agricultural soils (in order of increasing size and cellular complexity): archea, bacteria, fungi, eukaryotic algae and cyanobacteria. Archea are unique organisms adapted to extreme conditions, such as elevated temperature or saline environments, and the only group found in agricultural soils are methanogens that use CO_2 as a source of carbon (C) and as an electron acceptor. The diversity and activity of these organisms are not well known, but their impact on nutrient cycling in temperate agricultural soils is likely quite small (Alexander, 1998). Bacteria are among the most numerous soil microorganisms (10^8 to 10^9 bacteria can be found in 1 g of soil), but they generally account for less than half of the soil microbial biomass (Wollum, 1998). Most bacteria are single cell organisms but the actinomycetes and several species of cyanobacteria are filamentous. These sedentary organisms often live in colonies on soil surfaces and within soil aggregates, attached by the exopolysaccharides secreted on their cell walls. The soil bacteria have diverse metabolic capabilities and mediate many of the biochemical transformations that convert nutrients from organic to inorganic forms during OM decomposition.

The soil fungi have a filamentous growth habit. They are a major component of the soil microbial biomass and their biomass can exceed that of crop roots (Olsson et al., 1999). These organisms "move" through soil as their hyphae grow toward soil patches rich in nutrients or organic debris, but long distance displacement of the fungi is generally achieved through spore dispersal by wind, water and animal vectors. Some fungi also produce motile spores that can swim towards a food source (Morton, 1998). The majority of soil fungi are aerobic heterotrophs capable of decomposing the most complex and recalcitrant organic compounds found in soils (Paul and Clark, 1996). Another important group of soil fungi are the arbuscular mycorrhizal (AM) fungi, obligate biotrophs that derive their energy from living plants rather than from de-

composing OM. Both heterotrophic and biotrophic soil fungi make an important contribution to crop nutrition in temperate agroecosystems.

Eukaryotic algae and cyanobacteria possess chlorophyll and derive their energy from photosynthesis; some cyanobacteria can also fix nitrogen (N_2) from the atmosphere. These organisms are best known as pioneer species that rapidly colonize bare soils, such as those disturbed by glaciation or volcanic activity. They contribute to soil development and nutrient cycling by forming crusts that stabilize the soil structure, particularly in desert and arid soils. However, algae and cyanobacteria probably have a negligible effect on the nutrient dynamics of temperate agroecosystems (Paul and Clark, 1996).

The numbers and activity of soil microorganisms are influenced by environmental factors (e.g., temperature, moisture, aeration, soil texture, pH, salinity, concentration of dissolved nutrients) and biological factors (e.g., predation, competition, symbiosis, mutualistic interactions) (Grayston et al., 1998). Perhaps the most important factor governing the size of soil microbial populations is the amount and quality of the organic substrates available to support their growth and reproduction. The availability of organic substrates varies spatially and temporally in all terrestrial ecosystems, leading to fluctuations in microbial activity, and ultimately, the quantities of nutrient available for plant uptake. At the same time, plants exude C through their roots into the soil, which can alter microbial activity and increase nutrient availability in their root zone (rhizosphere).

Soil Microfauna and Mesofauna

The microfauna and mesofauna of soils are a diverse group of organisms that range in size from 0.02 to 2 mm. Soil microfauna include protozoa and nematodes, while the mesofauna may include tardigrada, collembola, acari, protura, diplurans, symphylids, and pauropoda. The focus of this discussion is the role of protozoa, nematodes, collembola and acari on nutrient dynamics in agricultural soil, as the effect on nutrient cycling of most other soil micro- and meso-fauna is not well known. Interested readers are advised to consult Dindal's (1990) 'Soil Biology Guide' for more information on the less-well studied soil mesofauna.

Protozoa are unicellular eukaryotic organisms ranging in size from 2 to 1000 μm long that inhabit the water films around soil particles, OM and roots. The free-living soil protozoa include flagellates, ciliates, naked amoebae and testate amoebae, and generally number more than 10^6 individuals m^{-2}, with the greatest numbers and biomass found in the

top 5 cm of soils (Ekelund, Rønn, and Christensen, 2001). Small flagellates and naked amoebae inhabit the smallest water-filled pore spaces in soil; ciliates, testate amoebae, rotifers and nematodes share larger pore spaces. The distribution of protozoa varies spatially and temporally, and more protozoa tend to be found within aggregates and in earthworm casts, in the rhizosphere, near decomposing plant and animal residues, and in the drilosphere (lining of earthworm burrows) than in other soil habitats (Bamforth, 1997; Griffiths, 1994; Tiunov et al., 2001). These habitats, which are often "hot spots" of protozoan activity, constitute less than 10% of the soil volume but support more than 90% of the biological activity in most soils (Coleman and Crossley, 1996).

Much of the study on nematodes in agricultural soils has focused on those that are parasites of agricultural plants, and numerous texts have been devoted to their study and control (e.g., Evans, Trudgill, and Webster, 1993). However, both parasitic and non-plant parasitic soil nematodes have a role in nutrient cycling in temperate agroecosystems; many plant parasitic nematodes alter plant root morphology and function, which changes nutrient transformations in the rhizosphere, whereas non-plant parasitic nematodes influence nutrient cycling through their interactions with other organisms in soil food webs. Soil nematodes are classified as bacterivorous, fungivorous, predatory, omnivorous or plant parasite nematodes, depending on their feeding habits. They have been used as indicators of ecosystem health due to the number and diversity of nematodes (more than 10^6 individuals m^{-2} from more than 30 taxa) commonly found in soils (Freckman and Ettema, 1993).

Nematodes inhabit water-filled pores and water films, and tend to be most numerous in the rhizosphere, near decomposing residues and in the drilosphere than in other soil habitats (Griffiths and Caul, 1993; Robertson and Freckman, 1995; Tiunov et al., 2001). Ingham et al. (1985) found that up to 70% of the bacterial and fungal feeding nematodes inhabited soil located 1 to 2 mm from root surfaces. Environmental conditions that affect moisture content in pore spaces, soil temperature, and the availability of food sources cause seasonal fluctuations in nematode populations. Nematode numbers in water-filled pore space increase as soil matric potential decreases (e.g., soil becomes drier), which can stimulate microbivorous grazing and perhaps lead to competition in nematode populations (Savin et al., 2001). Nematode taxa have different temperature optima, but most nematodes grow and survive best when soil temperatures are below 25°C (Ferris, Lau, and Venette, 1995). OM composition affects nematode dynamics; for example, Sohlenius and Boström (1984) found that populations of fungal feeding

nematodes increased during the later stages of barley (*Hordeum vulgare* L.) straw decomposition, which coincided with an increase in fungal biomass and proportion of lignin in the residue.

Two major groups of mesofauna that have an important role in OM decomposition and nutrient cycling in agroecosystems are the springtails (Collembola) and soil mites (Acari). They range from 0.1 to 6 mm in length and include herbivores, bacterivores, fungivores, predators and omnivores, although individuals may change their feeding habits when their preferred food source is limited (Beare et al., 1992; Coleman and Crossley, 1996). Springtails are primitive insects whose populations can reach 10^5 or more individuals m^{-2}. The preferred diet of springtails appears to be decaying plant and animal residues and the microorganisms, particularly the fungi, associated with these residues. Soil mites are chelicerate arthropods related to spiders, and between 10^3 and 10^5 m^{-2} can be found in agroecosystems (Coleman and Crossley, 1996). The suborders of mites found in agricultural soils include the Oribata, Prostigmata, Mesostigmata and Astigmata. Soil mites have diverse feeding habits and consume decaying plant and animal residues (Oritbatida and Astigmata), small arthropods and nematodes (Mesostigmata) and microorganisms, particularly fungi (Prostigmata, Astigmata).

Springtails and mites can be classified based on their body size and habitat in the soil: the largest individuals that live on the soil surface are epedaphic or epigeic, whereas medium-sized individuals that live in the upper 5 to 10 cm of soil are hemiedaphic, and those living in the 15 to 20 cm soil layer are euedaphic (Larink, 1997). Many springtails and mites prefer to live in the rhizosphere rather than away from plant roots in row-cropped agroecosystems (Garrett et al., 2001). Springtail and mite numbers and activities are generally highest during the spring and autumn in temperate agroecosystems when temperature and moisture conditions are most favorable and organic residues are abundant (Larink, 1997).

Soil Macrofauna

In contrast to microfauna and mesofauna, whose range is confined to water films and existing air-filled pore spaces, macrofauna have the capability to create their own niches in soil through their burrowing activities, which can alter soil structure and soil nutrient cycling significantly. Numerous insects and burrowing animals spend part of their life, or specific stages of their life cycle, in the soil, but it is beyond the scope of this contribution to discuss how such organisms affect nutrient dynam-

ics in agroeosystems. Dindal's (1990) 'Soil Biology Guide' provides an excellent description of the insects that reside in soils on a part- and full-time basis.

The major groups of soil macrofauna that may influence nutrient dynamics in agricultural soils include isopods, millipedes, centipedes, harvestmen (Opiliones), enchytraeids and earthworms. The distribution and ecology of most of these organisms in agroecosystems is not well known, and the reader should consult reviews by Didden, Fründ, and Graefe (1997); Wolters and Ekschmitt (1997); and Halaj, Cady, and Uetz (2000) for more information on isopods, millipedes, centipedes, harvestmen, and enchytraeids. The discussion here is limited to the effects of earthworms on nutrient dynamics in temperate agroecosystems.

Earthworms are probably the most important soil-inhabiting invertebrates due to their roles in OM decomposition and soil formation. Earthworms influence nutrient cycling in terrestrial ecosystems directly, through the release of nutrient from their tissues via excretion and mortality, and indirectly, by modifying soil physical, chemical, and biological properties (Blair, Parmelee, and Lavelle, 1995; Edwards and Bohlen, 1996). The earthworm family Lumbricidae is the most common taxa found in temperate agroecosystems. Most of the Lumbricidae found in North American agroecosystems were introduced from Europe. They are the dominant earthworms either because of a lack of endemic (native) species or because they out-compete endemic species for available resources (Kalisz and Wood, 1995). Earthworm populations may contain up to 200 individuals m^{-2} (Edwards, 1983). The LOMBRI-ASSESS database of earthworm populations from approximately 350 study sites found cultivated fields contained, on average, about 90 individuals m^{-2} with a biomass of 7.2 g dry weight m^{-2} (Paoletti, 1999). Generally, there are not more than four to six different species in the earthworm communities in temperate row-cropped agroecosystems (Edwards, 1983).

The main factors that affect the size and distribution of earthworms are environmental stresses on their habitat (climate, soil properties, vegetation, and food resources) and biotic interactions within soil faunal communities (competition, predation, parasitism, and disease) (Edwards and Bohlen, 1996; Curry, 1998). Seasonal fluctuations in earthworm populations related to soil temperature and moisture have been well documented (Edwards and Bohlen, 1996). Earthworms are thought to inhabit discrete patches in soil, but the size of patches occupied by earthworms varies among species and may be related to soil properties such as OM, texture and vegetation (Hendrix et al., 1992; Poier and Richter, 1992).

NUTRIENT TRANSFORMATIONS BY SOIL ORGANISMS

Soil organisms are responsible for transforming nutrients into forms that can be used by plants and can be considered to belong to two groups, plant-symbiotic organisms and free-living organisms. The plant-symbiotic organisms are obligate biotrophs that require a plant host for growth and reproduction and directly transfer nutrients from soils to plants. The free-living organisms are heterotrophs that contribute to plant nutrition indirectly by releasing nutrients from soil OM and mineral surfaces that can be absorbed by plant roots. Although free-living microorganisms and microfauna are not intimately associated with plant roots, their numbers and activity tend to be much greater in the rhizosphere than in bulk soil due to the abundance of C released from plant roots. An estimated 10 to 30% of photosynthates are released into soil through passive and active root excretions, the sloughing off of root cap cells and epidermal cell senescence (Bowen and Rovira, 1999). When rhizodeposition stimulates the activity of free-living soil organisms in a way that causes net mineralization or mobilization of nutrients, it may enhance crop production in temperate agroecosystems.

Plant-Symbiotic Soil Organisms: Mycorrhizal Fungi

The majority of crop plants found in temperate agroecosystems are associated with AM fungi (Olsson et al., 1999). The symbiotic relationship between AM fungi and plant roots involves connections between the fungal cell wall and plant cytoplasmic membranes that permit energy transfer from the plant to the fungi and nutrient and water transfer from the fungi to the plant (Smith and Read, 1997). Nutrient and water absorption by the host plant is improved because the fungal symbiont develops an extensive network of microscopic hyphae attached to plant roots (mycorrhizosphere) that permits the exploitation of a larger volume of soil than possible by the plant roots alone (Marschner, 1995; Smith and Read, 1997).

The AM fungi-plant symbiosis forms early in plant development, and up to 80% of the fungal hyphae isolated from soils under corn (*Zea mays* L.) and barley production may be from AM fungi within 5 weeks after seeding the field (Kabir et al., 1997). Since the concentrations of available nutrients in agricultural soils are highest in surface soils and decline with increasing soil depth, most mycorrhizal hyphae are found in the top 25 cm of the soil profile (Kabir et al., 1998a). Development of the AM fungi-plant symbiosis is affected by the level of plant-available

phosphorus (P) in soils, and degree of mycorrhizal infection of plant roots typically declines when soil P concentrations are high enough to support crop production (Koide and Li, 1990). The degree of mycorrhizal colonization of plant roots and hyphal development also varies with crop species and genotypes (Estaun, Calvet, and Hayman, 1987; Liu et al. 2000a; Peterson and Bradbury, 1995).

As much as 40 to 50% of the C derived from photosynthesis is channelled directly to AM fungi (Harris and Paul, 1987). The quantity of C transferred from the host to the fungal symbiont changes during the growing season as plant nutritional requirements change. Kabir et al. (1997) found the number of mycorrhizal hyphae associated with corn increased to a maximum in mid-summer and then declined. A portion of plant photosynthates accumulates in mycorrhizal biomass, but significant quantities may be exuded from fungal hyphae into the soil. In a laboratory study, the growth and reproduction of the plant pathogenic fungi *Fusarium oxysporum* increased significantly in the presence of active mycorrhizal hyphae, probably due to its use of C substrates that were exuded from mycorrhizal hyphae (St-Arnaud et al., 1995). The transfer of C from plants to soils via AM fungi may stimulate the growth of free-living bacteria, fungi and other soil organisms in the mycorrhizosphere (Finlay and Söderström, 1992). There is growing evidence that the free-living microbial communities in the mycorrhizosphere are specific to the type of plant and arbuscular mycorrhizal fungi present (Andrade, Linderman, and Bethlenfalvay, 1998; Westover, Kennedy, and Kelly, 1997). Further work is needed to determine how these free-living microorganisms, in association with mycorrhizal fungi, contribute to plant growth and nutrition.

Mycorrhizal fungi are best known for their ability to increase plant uptake of nutrients that are relatively immobile, such as P, Cu and Zn, and water (Bolan, 1991; Liu et al. 2000b). They increase the volume of soil exploited by plants through their hyphal networks, and may produce phosphatases that convert organically-bound P into inorganic P that can be absorbed by roots and perhaps produce organic acids that solubilize P bound to soil minerals (Marschner, 1995). Bethlenfalvay and Franson (1989) showed that mycorrhizal fungi inhibit Mn uptake in a mycorrhizal soybean (*Glycine max* L. Merr.), and they also inhibit Fe and Mn uptake by corn, which may help to maintain an optimal nutrient balance in crop tissues (Liu et al., 2000b). Mycorrhizal fungi can also enhance plant uptake of mobile nutrients, such as K, Ca, and Mg, when the concentrations of P and these nutrients in soils are low (Liu et al., 2002).

There is growing interest in inoculating soils with specific types of mycorrhizal fungi to improve crop production. However, all soils contain populations of indigenous mycorrhizal fungi that contribute to crop production. Miller, McGonigle, and Addy (1995) demonstrated that more rapid and vigorous mycorrhizal development in corn occurs with the indigenous fungi already present in no-till soils rather than from fungi introduced to soils through inoculation. Newly introduced fungi must find host roots, colonize them, and finally grow into a mycorrhizal hyphae soil network, whereas indigenous fungi may already exist in the vicinity of the host plant.

In addition, many AM fungi are capable of reducing plant susceptibility to plant-parasitic nematodes and hence improve plant growth and performance (Calvet et al., 2001; Little and Maun, 1996). For example, rhizobacterium (*Rhizobium* spp.) has been demonstrated to induce systemic resistance to infection by the potato cyst nematode *Globodera pallida* (Reitz et al., 2000), and reduce root galls and nematode reproduction (Siddiqui and Mahmood, 2001). The mechanisms that facilitate plant protection from attack by parasitic nematodes through the symbiotic AM fungi are not yet well understood.

Plant-Symbiotic Soil Organisms: N_2-Fixing Bacteria

The conversion of atmospheric dinitrogen (N_2) to ammonia (NH_3) by soil microorganisms is the process of biological N_2 fixation. Biological N_2 fixation produces an estimated 44 to 200 million Mg of fixed N per year. The fertilizer industry fixes about 84 million Mg of N per year, using the Bosch-Haber process that reduces N_2 to NH_3 (Bøckman et al., 1990). Biological N_2 fixation is powered by solar energy, but the industrial production of NH_3 fertilizers accounts for about 1.2% of the world's fossil fuel consumption on an annual basis (Kongshaug, 1998). Farming systems that derive more N from biological fixation than industrial processes may require less fossil fuel consumption to support crop production, and could be more sustainable in the long term.

Biological N_2 fixation by free living, associative and symbiotic organisms has been studied extensively. By far, the most important impact of biologically fixed N to agricultural soils under temperate climates comes from symbiotic associations between *Rhizobium* spp. bacteria and legumes (Weaver and Graham, 1994). The quantity of N_2 fixed in temperate agroecosystems each year varies, but is estimated to range from 164 to 300 kg N ha^{-1} for alfalfa (*Medicago sativa* L.), 57 to 190 kg N ha^{-1} for vetch (*Vicia* sp.) and beans (*Phaseolus* sp.), 46 kg N ha^{-1} for

peas (*Pisum sativum* L.), and 17 to 206 kg N ha^{-1} for soybeans (Newton, 1999). Most of the N fixed by the bacteria is transferred to the host plant and used for plant growth, but some of the N fixed is soon released into the soil, probably in root exudates and dead root cells (Hamel, Smith, and Furlan, 1991). Legumes may be more dependent on N_2 fixation to obtain the N needed for growth when they are grown in mixed than pure stands. Grasses, for example, are more competitive for soil N than legumes (Hamel, Furlan, and Smith, 1992). Nitrogenase, the enzyme responsible for converting N_2 to NH_3, is suppressed by NH_4^+ and NO_3^- so legumes will preferentially use N from the soil rather than N_2 fixed from the atmosphere when soil N concentrations are sufficiently high (Paul and Clark, 1996). Therefore, N fertilizer applications will reduce the amount of biological N_2-fixation occurring from the bacterial-legume symbiosis.

Free-Living Soil Organisms: OM Decomposition

Most soil organisms are involved in OM decomposition, the process by which complex organic substrates are physically fragmented and biochemically degraded to produce soluble organic and inorganic molecules that can be assimilated by plants. The end products of this process include CO_2 respired by the soil organisms, NH_4^+, NO_3^-, $H_2PO_4^-$, HPO_4^{2-}, and SO_4^{2-} ions, and stabilized OM (e.g., humus). The rate of decomposition of an organic substrate is affected by the amount, physical size and chemical composition of the organic material, the types of soil organisms present, and the environmental conditions that affect their activity (de Ruiter, Neutal, and Moore, 1994; Lee and Pankhurst, 1992). Soil microorganisms affect decomposition rates by producing the enzymes required to decompose organic substrates and by altering the soil habitat in ways that are beneficial for biological activity. Soil fauna influence decomposition rates by fragmenting organic materials, which increases the surface area available for microbial colonization, grazing on microorganisms, and by altering the soil habitat in ways that are beneficial for soil microorganisms.

The extracellular phosphatase and sulfatase enzymes secreted by plant roots, bacterial and fungal cells hydrolyse ester bonds (C-O-P, C-O-S) to produce $H_2PO_4^-$, HPO_4^{2-}, and SO_4^{2-} ions. Phosphatase and sulfatase enzymes are inhibited by the reaction products, and agricultural soils receiving P and S fertilizers tend to have much lower phosphatase and sulfatase activities than unfertilized soils (Tabatabai, 1994). Enzyme activity within microbial cells generates energy required for mi-

crobial growth and respiration and produces NH_4^+ and SO_4^{2-} through the hydrolysis of C-N and C-S bonds. The conversion of organically-bound N, P and S to inorganic forms is known as mineralization. The oxidation of NH_4^+ to NO_3^- in agricultural soils (nitrification) is a two-step process where NH_4^+ is converted to NO_2^- by chemotrophic bacteria such as *Nitrosolobus* spp. and *Nitrosospora* spp., and then from NO_2^- to NO_3^- by *Nitrobacter* spp. (Paul and Clark, 1996). The N, P, and S produced from these enzymatic processes in excess of microbial requirements are released into the soil solution, where they can be absorbed by plant roots. In addition, the C, N, P, and S incorporated into microbial biomass are released when microorganisms die (biomass turnover). The quantities of N, P, and S in microbial biomass can be considerable. Olsson et al. (1999) estimated the annual standing stock biomass of soil microorganisms in a linseed (*Linum usitatissimum* L.) field contained 60 to 110 kg N ha^{-1}, 12 to 22 kg P ha^{-1}, and 1.6 to 3 kg S ha^{-1}. Soil microbial biomass containing 17 to 290 kg P ha^{-1} is estimated to release 11 to 190 kg P ha^{-1} $year^{-1}$ (Frossard et al., 2000). It is evident that soil microorganisms can turn over large quantities of nutrients, but the proportion of these nutrients absorbed by crops under field conditions is not well known and requires further investigation.

Seasonal fluctuations in the size of the microbial biomass C, N, P, and S pools in agricultural soils have been attributed to environmental conditions, particularly soil moisture, and the availability of organic substrates. The quantities of nutrients in the microbial biomass pool may be greatest in the spring (Murphy, Fillery, and Sparling, 1998), summer (Perrott, Sarathchandra, and Dow, 1992) or in the fall after harvest (Joergensen, Meyer, and Mueller, 1994). In a clay loam soil, He et al. (1997) found that seasonal variation in the microbial biomass C pool was related to the timing of OM inputs, but changes in the microbial biomass P were related to soil moisture deficits. Microbial biomass P was lowest when the soil moisture deficit was greatest, perhaps because the reduction in soil moisture limited P diffusion to microorganisms, or because plants and microorganisms were competing for P in soil solution. However, Patra et al. (1990) did not observe seasonal changes in the microbial biomass C, N, and P pools in soils under continuous wheat (*Triticum aestivum* L.) and grass pasture.

Variation in microbial biomass may coincide with changes in the quantities of mineralizable substrates during the decomposition process and from predator-prey interaction (Lee and Pankhurst, 1992). Microbial colonization of organic substrates leads first to the mineralization of labile organic substrates (e.g., carbohydrates) and then to progres-

sively recalcitrant organic substrates such as cellulose and lignin. Microbial growth and respiration attracts microbial predators (e.g., protozoa and nematodes) that graze on the microbial biomass. Ingham et al. (1986) found that the population dynamics of bacteria, fungi, protozoa, and nematodes were explained by simple predator-prey interactions. In the spring, microbial growth appeared to stimulate protozoa and nematode populations, leading to a decline in microbial biomass and an increase in inorganic N in soil. In the fall, protozoa and nematode populations declined, bacterial populations increased due to a reduction in predation, and inorganic N concentrations declined as N was immobilized in bacterial biomass.

Despite their small physical size, the protozoa comprise about 30% of the soil faunal biomass, and account for about two-thirds of soil faunal respiration (Foissner, 1987). Protozoa have relatively high energy conversion efficiency, compared to other soil fauna, and allocate proportionately more of their energy to growth and reproduction than most other soil organisms; the protozoan biomass turns over rapidly (10-12 times per year) compared to other soil fauna (1-2 times per year) (Coleman and Crossley, 1996). The main food source for most protozoa is bacteria, and protozoa have the ability to access and graze upon bacteria in very small pore spaces. Foster and Dormaar (1991) observed amoebae producing elongated and branched pseudopodia to probe micropores less than 1 μm wide within soil microaggregates. Protozoan grazing on bacteria results in a release of CO_2 and mineralizes N, P, and S from the bacterial biomass, contributing to soil respiration and liberating nutrients in forms available for plant uptake. The selective grazing pressure of protozoa on bacteria can alter the composition of soil microbial communities and also keeps bacterial populations physiologically young, which stimulates decomposition and nutrient cycling in soils (Darbyshire, 1994; Gupta and Germida, 1989). Protozoa are responsible for an estimated 14 to 66% of the C mineralized, and 20 to 40% of the N mineralized in soils, hence removal of protozoa from soil food webs can slow residue decomposition rates significantly (Foissner, 1999). Increased N mineralization due to protozoan activity has been linked to improved plant growth and N uptake by plants (Alphei, Bonkowski, and Scheu, 1996; Bonkowski, Griffiths, and Scrimgeour, 2000).

Nematodes are involved in OM decomposition and nutrient mineralization, mainly through their grazing on microorganisms and interactions with plants. Increases in soil available NH_4-N, plant growth and shoot N concentrations in the presence of bacterivorous nematodes

have been attributed to N excretion by nematodes and stimulation of bacterial activity by grazing that led to increased N mineralization (Alphei, Bonkowski, and Scheu, 1996; Griffiths, 1994; Ingham et al., 1985). Generally, nematodes excrete about 70% of the microbial biomass N consumed (Bonkowski, Griffiths, and Scrimgeour, 2000; Ferris, Venette, and Lau, 1997). Microfaunal grazing of microorganisms is important for plant growth in temperate agroecosystems. As much as 30% of the N mineralization in agroecosystems has been attributed to the combined microfaunal (protozoa and nematode) activity (Andrén et al., 1990).

Springtails and mites have an important role in OM decomposition and nutrient mineralization through their interactions with microorganisms as well as their effects on soil structure (Coleman et al., 1993; Crossley, Coleman, and Hendrix, 1989). Most of the effects of springtails and mites on nutrient uptake by crop plants in agroecosystems are indirect, since the majority of these organisms do not feed on living plants. Model foodwebs have demonstrated that the feeding activities of springtails and mites can stimulate nutrient turnover from microorganisms and microfauna (de Ruiter, Neutal, and Moore, 1994; Hendrix et al., 1986). Grazing on microorganisms and microfauna is one way that springtails and mites stimulate OM decomposition and N mineralization. Selective feeding on certain fungal species by springtails has been shown to alter the fungal community and hence indirectly affects rates of litter decomposition and nutrient cycling (Moore, Ingham, and Coleman, 1987). Springtails and mites also influence nutrient cycling by fragmenting and redistributing OM in soils, creating new "hot spots" of root, microbial and microfaunal activity (Hansen, 2000).

Although most members of the soil microarthropods do not feed on living plants, the fungal-feeding springtails can alter plant growth and nutrient uptake by selectively feeding on mycorrhizal hyphae. In the laboratory, springtails grazing on mycorrhizal fungi can reduce P uptake and plant yield (Finlay, 1985), but this effect may be due to excessively high numbers of springtails in greenhouse experiments since damage to mycorrhizae by microarthropods is density-dependent (Klironomos and Ursic, 1998). Springtails also feed on several pathogenic fungi that cause take-all and brown foot rot in winter cereal crops and reduce disease severity (Sabatini and Innocenti, 2001). Further investigations will be required to determine whether springtail-mycorrhizal interactions can improve or impair crop performance under field conditions.

The flux of N from earthworm populations in agroecosystems is thought to be considerable, and it is estimated that 10 to 106 kg N ha^{-1} $year^{-1}$ is released from earthworm biomass through mortality and excretion (Andersen, 1983; Schmidt and Curry, 2001; Whalen and Parmelee, 2000). Much of the N released from earthworms through mortality and from excretion products may be readily available for uptake by plants. More than 70% of the N from decomposing earthworms labeled with ^{15}N cycled through the microbial biomass and was recovered in the shoots of ryegrass (*Lolium multiflorum* L.) plants within 16 days after dead earthworms were added to soil (Whalen et al., 1999). In addition, up to 40% of the ^{15}N excreted by earthworms in mucus and urine was recovered in soil NH_4-N and NO_3-N pools (Whalen, Parmelee, and Subler, 2000). Although considerable effort has focused on the role of earthworms in N cycling, there is very little information on how much P, S, and other nutrients are released from earthworms via the direct pathway of mortality and excretion.

Earthworms also influence nutrient cycling indirectly, by modifying soil physical and chemical characteristics and hence altering soil microbial activity, and through grazing on microorganisms. The impact of earthworm species on nutrient cycling via the indirect pathway depends on their feeding habits and life histories, since these factors influence earthworm-microbial interactions. Earthworms consume an estimated 2 to 15 Mg ha^{-1} $year^{-1}$ of OM, including soil OM, surface residues, live and dead roots, mycorrhizae, algae, fungi, bacteria, and protozoa (James, 1991; Whalen and Parmelee, 1999). The portion of ingested organic substrates not assimilated into earthworm tissues is defecated in casts, along with the microorganisms that pass through the earthworm gut. In the short term (e.g., weeks), earthworm casts are a source of plant-available N, P, K, and Ca, and are "hot spots" of bacterial and actinomycete activity compared to bulk soil as these microorganisms further decompose the OM contained in casts (Shipitalo and Protz, 1989; Tiunov and Scheu, 2000). Between 10 and 12% of the N in casts and as much as 50% of the P may be readily-available for plant uptake (James, 1991).

Through time, readily-mineralizable substrates in earthworm casts are utilized and fungi may become relatively more important than bacteria, resulting in a shift from mineralization to immobilization of nutrients in casts and stabilization of cast physical and chemical characteristics (Marinissen and Dexter, 1990; Shipitalo and Protz, 1989). Anecic earthworms also form middens at the top of their burrows, on the soil surface, which contain undecomposed OM and earthworm casts. Mid-

dens appear to act as "external rumens," and are "hot spots" of microbial and soil faunal activity compared to bulk soil (Maraun et al., 1999). The drilosphere possesses physical and chemical characteristics that favor the development of bacterial communities, often dominated by gram-negative bacteria; fungal mycelium and the proportion of germinating hyphae are lower in the drilosphere than in bulk soil (Tiunov, Dobrovol'skaya, and Polyanskaya, 1997; Tuinov, Dobrovol'skaya, and Polyanskaya, 2001). Decomposition rates, microbial activity, and the number of protozoa and nematodes are higher in the drilosphere than in bulk soil (Görres, Savin and Amador, 1997; Tuinov et al., 2001).

Free-Living Soil Organisms: Nutrient Solubilization from Soil Minerals

Nutrients can also become available to plants through the dissolution of soil minerals, which releases nutrients into the soil solution. This process contributes to the inherent fertility of a soil, and is generally more important in fine-textured than coarse-textured soils due to the larger proportion of minerals exposed to weathering factors. Plant roots, organic residues and soil microorganisms produce organic acids that react chemically with soil minerals to solubilize nutrients required by plants (Hinsinger, 2001). Soil organic acids include monocarboxylic, dicarboxylic and tricarboxylic acids containing unsaturated C and OH^- groups (Strobel, 2001). Such organic acids have two major functions related to plant nutrition. First, negatively charged organic acids can stimulate the dissolution of soil minerals by chelating metal cations (e.g., Fe, Zn, Cu, and Mn), creating a soluble compound that can be absorbed by plant roots (Jones and Darrah, 1994; Strobel, 2001). For example, citrate dissolves iron phosphate minerals by first forming a ferric hydroxyphosphate complex and then displaces the phosphate ion through chelation reactions (Bolan et al., 1994). Several species of bacteria, yeasts, actinomycetes, ectomycorrhizal and free-living fungi can solubilize P from Ca-P, Fe-P, and Al-P complexes, kaolinite, gibbsite, and goethite minerals (Illmer, Barbato, and Schinner, 1995; Whitelaw, 2000). The ability of organic acids to chelate metal cations is affected by their molecular structure and increases with the number of functional groups, so that tricarboxylic acids are more effective chelation agents than dicarboxylic and monocarboxylic acids (Bolan et al., 1994).

Second, negatively charged organic acids can compete with anions such as HPO_4^{2-}, $H_2PO_4^-$, and SO_4^{2-} for adsorption sites on soil surfaces. Many organic acids are very reactive and will bind strongly to P

fixation sites, making these sites unavailable for phosphate ions and hence increasing the concentration of P in the soil solution (Hu et al., 2001; Jones and Kochian, 1996). In addition, inoculation of soil with AM fungi and P solubilizing microorganisms stimulates P uptake and plant growth more than inoculation with either AM fungi or P solubilizing microorganisms alone. The simultaneous inoculation of tomato (*Lycopersicon esculentum* L.) growing in hydroxyapatite-amended substrate with the P solubilizing bacteria *Enterobacter agglomerans* and the mycorrhizal fungi *Glomus etunicatu* improved both N and P uptake in a greenhouse study (Kim, Jordan, and McDonald, 1998). The concentrations of oxalic, 2-keto-P-gluconic and citric acid in the root zone increased most when both *E. agglomerans* and *G. etunicatu* were present, but it was not clear whether some of the organic acids present were exuded from mycorrhizal fungi and plant roots, or whether conditions in the mycorrhiosphere stimulated the production of organic acids by P solubilizing bacteria. Further research is needed to determine the quantities and types of organic acids secreted by plant roots, symbiotic microorganisms and free-living microorganisms in response to P deficiencies in agricultural soils.

Nutrient solubilization by organic acids is well documented in laboratory and greenhouse studies, but information is lacking on how organic acids may contribute to nutrient uptake by plants grown in temperate agricultural soils. The concentration of monocarboxylic acids in soil solution ranges from 0 to 1 mM, whereas dicarboxylic and tricarboxylic are present in lower concentrations, perhaps between 0 and 50 μM (Strobel, 2001). Despite the fact that organic acids can be used as an energy source by microorganisms, appreciable quantities of organic acids likely chelate metals in soil solution or become adsorbed to anion exchange sites in the soil matrix (Jones and Brassington, 1998). Organic acid production varies spatially, and the quantities of organic acids produced by P-solubilizing microorganisms are much higher in the rhizosphere than the surrounding soil (Hu et al., 2001; Whitelaw, 2000). It has been suggested that localized P solubilization by organic acids near plant roots and decomposing organic residues is an important mechanism for increasing P availability to plants and other soil organisms (Whitelaw, 2000). Further research is needed to quantify the contribution of organic acids to nutrient cycling and plant nutrition under field conditions in temperate agricultural soils.

Nutrient Losses and Soil Organisms

Plant roots absorb nutrients from the soil solution, but these plant-available nutrients can also be immobilized in microbial biomass and OM, adsorbed on soil surfaces, or lost from soils via gaseous emissions and leaching. Nutrient immobilization is affected by the C:N:P:S ratios of microbial biomass and the organic substrates available for decomposition. Generally, net immobilization of N occurs when the C:N ratio is greater than 25, and net immobilization of P and S occur when the C:P ratio is greater than 300 and the C:S ratio is greater than 400 (Havlin et al., 1999). Soil organisms are also involved in macroaggregate formation and stabilization, which affects the physical location of organic substrates within the soil matrix and their susceptibility to decomposition. Macroaggregates (> 200 μm diameter) are formed when organic debris from roots, microorganisms, and other sources binds to clay particles and microaggregates. Fungal hyphae and plant roots contribute to macroaggregate formation through the secretion of glycoproteins and polysaccharides that act as cementing agents to stabilize macroaggregates (Beare et al., 1997; Rillig et al., 2001). Macroaggregates are enriched with recently incorporated, relatively undecomposed organic substrates, which can be protected from decomposition for a period of time before it is eventually decomposed and redistributed in smaller macroaggregates or microaggregates (Miller and Jastrow, 1992; Puget, Chenu, and Balesdent, 2000). The quantities of nutrients that are immobilized and mineralized from aggregate fractions by soil microorganisms and other soil fauna is not well known.

Soil organisms likely do not have a large role in the chemical reactions that result in nutrient adsorption on soil surfaces and precipitation in soil minerals. However, they can contribute to nutrient losses from soils by transforming nutrients into forms that can be readily transported from soils, or by altering soil properties in ways that facilitate nutrient losses. Nitrifying bacteria transform NH_4^+ into NO_3^-, a more mobile form of N that is susceptible to leaching from agricultural soils. In tile drains under corn fields, NO_3-N concentrations as high as 120 mg L^{-1} have been reported (Logan, Randall, and Timmons, 1980), but other reports give NO_3-N concentrations of 10-60 mg L^{-1} in drainage waters under agricultural fields (Owens et al., 2000). The quantities of NO_3-N leached through agricultural soils are affected by the form of N at application, rate and timing of nutrient applications, crop residues, irrigation rate and method, precipitation, and soil characteristics such as texture and soil OM (Havlin et al., 1999).

Soil organisms that enhance water movement through the soil profile, such as the anecic earthworms *Lumbricus terrestris* L. and *Aporrectodea longa* L., can increase nutrient losses through leaching. These species form vertical permanent or semi-permanent burrows that may extend several meters in depth, and come to the surface to feed on residues that they then drag into their burrows (Edwards and Bohlen, 1996). Nitrogen mineralization and nitrification rates are higher in the walls of earthworm burrows than bulk soil, which can lead to greater NO_3^- leaching through earthworm burrows than other soil (Görres, Savin, and Amador, 1997; Parkin and Berry, 1999). Agricultural practices that increase the numbers of anecic earthworms are expected to promote NO_3^- leaching through the soil profile (Subler and Kirsch, 1998).

The denitrifying bacteria are facultative or obligate anaerobes that use NO_3^- as an electron acceptor in metabolic processes and produce N_2O and N_2. Other anaerobic bacteria such as *Desulfovibrio* spp. are responsible for converting SO_4^{2-} into SO_2 gas, but the dissimilatory reduction of sulfate to gaseous sulfur is not common in temperate agricultural soils since the process requires low oxidation-reduction potentials that are more typical of flooded soils. As much as 30% of the fertilizer N applied to agricultural soils may be lost via denitrification. Denitrification rates are influenced strongly by temperature and rainfall, as well as soil pH, soil bulk density, and soil OM content (Burton et al., 1997; MacKenzie, Fan, and Cardin, 1997). Earthworm casts and burrows contain higher levels of NO_3, soluble organic C and moisture than the bulk soil, which appears to stimulate denitrification and contributes to higher gaseous N losses from these structures than from bulk soil (Parkin and Berry, 1994; Subler and Kirsch, 1998).

IMPACT OF TILLAGE ON SOIL ORGANISMS

Farming practices are designed to maximize crop yields, but often these practices influence many other components of agroecosystems not considered explicitly, such as weed and crop pest populations, water table levels, soil structure and the activity of soil organisms, and the microclimate of agricultural fields. Fertilization, incorporation of crop residues in the fall, crop rotation and tillage are agricultural practices that induce seasonal variation in microbial processes and nutrients dynamics. The impact of agricultural practices on soil biota and nutrient cycling depends greatly on the cultivation method chosen. Tillage practices alter the quantity and quality of plant residues entering the soil, the sea-

sonal and spatial distribution of these residues, the ratio between inputs from above and belowground and change the quality of nutrient inputs (Kandeler, Tscherko, and Speigel, 1999). Plowing buries OM deeper in the soil profile and, under well-aerated conditions, tends to favor the development of a large bacterial-dominated microbial community, whereas no-till favors the development of a fungal-based microbial community (Beare et al., 1992). The decomposer community in conventional tillage agroecosystems may be more prone to nutrient losses via leaching, whereas no-till systems may conserve more nutrients, due to the dominance of fungi that tend to immobilize rather than mineralize plant-available nutrients (Hendrix et al., 1986). Tillage affects different members of soil food webs in different ways. The numbers, diversity, and activities of soil microorganisms and fauna may all be affected by tillage. Our discussion will focus on how tillage impacts on the key microorganisms and soil fauna.

Effects of Tillage on Soil Microorganisms

Tillage modifies the soil environment by inverting the top 15 to 20 cm of soil, physically fragmenting residues at the soil surface and incorporating them deeper within the soil profile. These alterations to the soil environment affect the distribution, numbers and activity of soil microorganisms significantly. Kabir et al. (1998a) found more fungal hyphae in the top 5 cm of soils under no-tillage than conventional tillage. The abundance and biomass of bacteria, fungi, protozoa, nematodes, and microarthropods are greater on buried litter in conventional tillage systems than surface litter in no-till systems (Beare et al., 1992). However, the response of soil microbial communities to tillage disturbances may depend on soil characteristics. Lupwayi et al. (2001) found that microbial biomass and diversity were lower in tilled than untilled soils that were acidic and contained low OM, but tillage did not affect microbial biomass and diversity significantly in soils with a pH near neutrality and a higher OM content. They concluded that soil microorganisms in acid C-poor soils had less resilience to tillage effects than microorganisms in neutral C-rich soils. Decomposition in no-till systems tends to be slower and more greatly influenced by fungi than in conventionally tilled soils, which have a microbial community dominated by bacteria and bacterivorous soil fauna (Beare et al., 1992).

Tillage can impact AM fungi negatively when tillage operations detach the fungi from their host plant. Colonization of corn roots by AM fungi during the early development of corn was significantly lower in

conventionally-tilled than no-tilled soils, but differences in mycorrhizal colonization were not significant after corn had reached the 12 to 14 leaf stage (Kabir et al. 1998b). However, early disruption of the mycorrhizal fungi-corn symbiosis can impact nutrient uptake and yield significantly (Miller, McGonigle, and Addy, 1995; Liu et al., 2000b). Physical disruption of fungal hyphae by fall tillage operations can reduce the survival of AM fungi; the number of fungal hyphae were 20 to 25% lower in soils plowed in the fall than unplowed (Kabir, O'Halloran, and Hamel, 1997). Although tillage can cause a decline in the number of fungal spores/hyphae, the effects may be more pronounced in systems that are tilled more intensely (more often, to a deeper depth) than in those tilled less intensively.

Soil bacteria are generally less impacted by tillage than soil fungi, and bacterial populations may be larger in conventionally tilled than no-tilled soils. Tillage implements often fragment organic residues, increasing their surface area and mixing them more intimately with soil, providing substrates for bacterial colonization and growth. Differences in the distribution and composition of bacterial communities under conventional and no-tillage systems have been documented (Hendrix et al., 1986; Roper and Gupta, 1995). In general, conventionally-tilled soils have higher mineralization and nitrification rates than no-till soils (Aulakh, Rennie, and Paul, 1984; Rice and Smith, 1982). No-till soils tend to have higher soil water contents than conventionally-tilled soils due to the retention of organic residues on the soil surface, and these conditions favor the development of anaerobic microsites. Greater fluxes of N_2O and N_2 from denitrifying bacteria have been documented under no-till than conventionally-tilled soils (Burton et al., 1997; MacKenzie, Fan, and Cardin, 1997).

Effects of Tillage on Soil Micro-, Meso-, and Macro-Fauna

Tillage can affect the numbers, populations and diversity of soil fauna in multiple ways. Leaving crop residues on the soil surface can increase soil moisture and provide a source of food for some of the larger soil fauna. Incorporating residues can permit soils to warm more quickly in the spring and favor the growth of fauna that graze primarily on soil microorganisms, particularly bacteria, and detritus. Some populations of soil fauna decline in tilled systems due to mechanical damage from the tillage implements. The impact of tillage on soil fauna will depend on the frequency and degree of disturbance of the soil physical and

chemical properties, as well as the types of organisms present, since some are more susceptible to tillage than others (Kladivko, 2001).

Tillage and other agricultural practices influence protozoan and nematode populations by modifying the soil environment and by altering the quantity of food (bacteria and fungi) available. There have been relatively few studies to assess the effect of tillage practices on protozoa. Bamforth (1997) suggested the number and diversity of protozoa would be greater in no-till than conventional tillage systems because tillage disrupts the continuity of the water-filled pores that are the protozoan habitat. In addition, populations of bacterial-feeding protozoa would be favored in bacterial-dominated conventional tillage than fungal-dominated no-tillage agroecosystems. Roper and Gupta (1995) reported that no-till agroecosystems with retained stubble had 10 to 100 times more fungal-feeding protozoa and 5 to 10 times more bacterial-feeding protozoa than stubble-burnt systems. Beare et al. (1992) assessed protozoan populations in litterbags laid on the soil surface or buried in conventional- and no-tillage agroecosystems eight years after the tillage treatments were established, and found generally no difference in the numbers of amoebae, flagellates and ciliates in litterbags from the two tillage systems.

An increase in tillage intensity can reduce the populations of nematodes susceptible to mechanical damage and alter the vertical distribution of nematodes. Bouwman and Zwart (1994) found greater nematode biomass in integrated management systems with lower agrochemical inputs and reduced tillage than conventional management systems. The dominant microbial-feeding nematodes were bacterivores, and more herbivores and omnivore/predators were found in integrated than conventional management systems. However, burial of crop residues can stimulate microbial activity and provide food for microbiovorous nematodes (Yeates and Bongers, 1999). The effects of tillage on soil microfauna are not entirely clear, and Wardle (1995) contends that there are insufficient data from field studies to fully understand how these soil fauna are affected by tillage. More detailed investigation of protozoan and nematode populations in conventional- and no-tillage agroecosystems under field conditions is warranted.

Springtails and soil mites can be mechanically damaged or disrupted by tillage. The inversion of clods, a common feature in moldboard plowed agroecosystems, can cause individuals to be trapped in soil clods (Wardle, 1995). Springtails and mites of the suborder Mesostigmata that live relatively close to the soil surface tend to decline with increasing tillage intensity (Larink, 1997). However, soil mites vary in their

response to tillage events. Cryptostigmatid, mesostignmatid, and astigmatid populations often decline after tillage events, but astigmatid populations appear to recover from tillage disturbances more rapidly (Behan-Pelletier, 1999). Beare et al. (1992) investigated microarthropod populations in litterbags laid on the soil surface or buried in conventional- and no-tillage agroecosystems. There was no difference in the number of microarthropods in surface litterbags from the two tillage systems, but more fungivorous, predatory and total microarthropods in litterbags buried in conventional tillage than no-tillage systems. Beare et al. (1992) suggested that a larger proportion of the springtails and mites in conventional- than no-tillage agroecosystems were omnivores, and shift their feeding habits depending on the availability and biomass of other organisms in soil foodwebs. Although it is difficult to make generalizations about how tillage affects soil mesofauna, Kladivko (2001) reports that the populations of springtails and soil mites are decreased by tillage more often than they are increased.

Tillage affects earthworm populations by changing the amount, quality and location of their food supply, and altering soil physical properties such as soil moisture and temperature. Earthworm populations are also susceptible to mechanical damage from tillage implements, and it has been estimated that rotary cultivation can reduce the biomass of earthworms in a field by up to 68% (Böström, 1995). Inversion of the top 10 to 20 cm of the soil profile during tillage exposes some endogeic earthworm species to avian predators (Giller et al., 1997). Generally, earthworm numbers are higher in no-tillage than conventional tillage agroecosystems (Kladivko, 2001). Higher earthworm numbers and biomass in no-tillage agroecosystems have been attributed to more beneficial soil conditions, including the presence of surface litter, favorable temperature and moisture conditions, and a lack of disturbance. Yet, in some cases, earthworm numbers and biomass may be no different, or slightly lower in no-tillage than conventional-tillage agroecosystems (Kladivko, Alhouri, and Weesies, 1997). After many years of conventional tillage, there may be insufficient numbers of some larger earthworm species, such as *Lumbricus terrestris*, remaining in the area to re-colonize the agroecosystems (Kladivko, 2001). However, earthworm biodiversity and activity generally increase when producers switch from conventional tillage to no-tillage systems (Clapperton et al., 1997; Emmerling, 2001; Parmelee et al., 1990).

CONCLUSIONS AND FUTURE DIRECTIONS

It can be concluded that soil organisms, whether they are associated with plants in a symbiotic relationship or free-living, have a role in nutrient cycling and nutrient uptake by crops. The relationship is much clearer for the symbiotic organisms that are intimately associated with plant roots than the non-symbiotic soil organisms, but there are still many questions to be answered about the interactions among symbiotic organisms, plant roots and free-living soil organisms. Although symbiotic organisms such as mycorrhizal fungi have an important role in nutrient mineralization and uptake, there is growing recognition that mycorrhizal fungi may reduce plant susceptibility to diseases caused by plant parasitic nematodes. Research is needed to better understand these interactions, and to determine their influence on crop production under field conditions.

Many free-living soil organisms, from the smallest soil microorganisms to the largest soil fauna are involved in OM decomposition and nutrient mineralization. Yet, linking the activities of these organisms to nutrient uptake by crops grown in agricultural fields is very difficult. Part of the reason is that most studies showing a linkage between soil organisms and crop production have been conducted in a laboratory setting, and many have focused on the effects of a single, or perhaps a few, soil organisms. Promising techniques that are being used to better understand the interactions among free-living soil organisms and their collective effects on nutrient dynamics and plant growth under field conditions include the use of radioisotopes and stable isotopes (to trace nutrient transformations in the soil-plant system) and manipulation experiments (where organisms are added or removed from the soil-plant system).

The degree of perturbation that occurs in agroecosystems is typically much greater than other terrestrial ecosystems, particularly in those agroecosystems that are continuously cropped and disturbed through cultivation and other agricultural practices. Certain soil organisms are relatively sensitive to tillage and other management practices, but recover rapidly after soils are disturbed, whereas other soil organisms are relatively insensitive to the human perturbations of agroecosystems. These types of soil organisms may have a larger role in nutrient cycling and crop production than those organisms whose populations decline progressively with each disturbance event. There is a growing body of information about the impacts of agricultural practices on the populations and trophic structure of different soil organisms. Future investigations should help us to identify the key organisms or groups of organisms re-

sponsible for nutrient cycling in temperate soils under different set of agricultural management practices. Better fertilizer recommendations in temperate cropping systems could be devised if the contributions of soil organisms to crop production were considered. Research is needed to assess the economic and environmental benefits of agricultural practices that consider the role of soil organisms explicitly. This would be an improvement on agricultural management schemes that underrate the complex interactions among the diverse organisms present in the soil environment and largely ignore their role in nutrient cycling and crop production.

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