
10 Soil and Crop Management Effects on Soil Microbiology

Ann C. Kennedy, Tami L. Stubbs, and William F. Schillinger

CONTENTS

Introduction	295
Soil Microbial Communities	296
Microbial Diversity	298
Nutritional Strategies	300
Management Effects on Soil Microbial Communities	301
Plant Influences	302
Roots and Rhizosphere	302
Plant Competition	303
Plant Diversity/Crop Rotation	303
Crop Residue	304
Resources	306
Nutrient Status/Cycling	306
Plant Growth-Regulating Compounds	306
Amendments	308
Agromicrobials	308
Arbuscular Mycorrhiza (AM)	308
Biological Control	309
Organic/Low-Input Farming	309
Genetically Modified Organisms (GMOs)	310
Disturbance	310
Tillage	311
Grazing	315
Strategies for Managing Microorganisms	315
Conclusions	316
References	316

INTRODUCTION

Life in soil is responsible for a multitude of processes vital to soil function. Microorganisms can have a profound effect on plant growth, soil organic matter (SOM) accumulation, and soil condition or soil quality. For more than 3.5 billion years, microorganisms have been a life force on earth, establishing communities well before any other life forms. Since the beginning, natural selection has ever increased the microbial diversity in soils. All life is dependent on microbial processes (Price, 1988), and SOM transformations are due to microbial processes (Altieri, 1999). In turn, SOM sustains that life and is crucial to soil function. Strategies that increase SOM tend to enhance soil biological processes and vice versa. Understanding these processes and implementing strategies to enhance SOM, improve soil quality, and maintain biological diversity will help attain sustainable agriculture.

Soil Quality

Soil quality is defined as the capacity of a soil to function within ecosystem boundaries to sustain biological productivity, maintain environmental quality, and promote plant and animal health (Doran and Parkin, 1994). It is easy to visualize a healthy, rich soil and to remember its smell. Descriptive and analytical measurements of the physical, chemical, and biological properties are sometimes used to characterize soil quality. Indicators of soil quality are needed to measure changes in soil function that occur because of alteration in management. Total organic matter can be an indicator; however, changes in total SOM usually respond very slowly to changes in management and thus lack sensitivity. Soil organisms contribute to the maintenance of soil quality because they control many key processes. Soil microorganisms and their communities are continually changing and adapting to changes in their environment. A high-quality soil is biologically active and contains a balanced population of microorganisms. The dynamic nature of soil microorganisms makes them a sensitive indicator to assess changes in soil quality due to management (Kennedy and Papendick, 1995).

This chapter explores microbiological changes occurring with soil and crop management in farming systems. Our discussion of community structure includes microbial survival strategies and delineation of groups of organisms, such as bacteria and fungi, nutritional-based groups or species, and functional determinations. Our goal is to describe changes in the soil biota with management to help identify soil microbial parameters useful in assessing management practices for conserving and enhancing SOM, soil quality, and crop production.

SOIL MICROBIAL COMMUNITIES

The number of microbial species on earth is estimated to exceed 100,000 and may be more than a million (Hawksworth, 1991b; American Society for Microbiology, 1994). Unfortunately, only 3 to 10% of the earth's microbial species have been identified or studied in any detail (Hawksworth, 1991a). The full potential of these groups of organisms has not been explored. The diversity of microorganisms is thought to exceed that of any other life form (Torsvik et al., 1990; Ward et al., 1992). It is estimated that several thousand genomes are present in each gram of soil (Torsvik et al., 1990).

Soil microorganisms are responsible for many soil processes, such as SOM turnover, soil humus formation, cycling of nutrients, and building soil tilth and structure (Table 10.1; Lynch, 1983; Wood,

TABLE 10.1
Beneficial Functions of Soil Microorganisms in Agricultural Systems

- Release plant nutrients from insoluble inorganic forms
 - Decompose organic residues and release nutrients
 - Form beneficial soil humus by decomposing organic residues and through synthesis of new compounds
 - Produce plant growth-promoting compounds
 - Improve plant nutrition through symbiotic relationships
 - Transform atmospheric nitrogen into plant-available N
 - Improve soil aggregation, aeration, and water infiltration
 - Have antagonistic action against insects, plant pathogens, and weeds (biological control)
 - Help in pesticide degradation
-

1991). These functions are performed by many different genera and species. Beneficial soil bacteria enhance plant performance by increasing solubility of minerals (Okon, 1982), N_2 fixation (Albrecht et al., 1981), producing plant hormones (Brown, 1972; Arshad and Frankenberger, 1998), and suppressing harmful pathogens (Chang and Kommendahl, 1968). Beneficial mycorrhizal fungi can enhance plant growth by increasing nutrient (Fitter, 1977; Hall, 1978; Rovira, 1978; Ocampo, 1986) and water (Tinker, 1976) uptake and soil structure by enhancing aggregate formation and stability (Wright and Upahyaya, 1998; Chapter 6). Conversely, plant-suppressive bacteria impair seed germination and delay plant development by producing phytotoxic substances (Woltz, 1978; Suslow and Schroth, 1982; Alstrom, 1987; Schippers et al., 1987). Pathogenic fungi greatly reduce the survival, growth, and reproduction of plants (Shipton, 1977; Bruehl, 1987; Burdon, 1987). Another example of the importance of microorganisms to agriculture is the production of antibiotics by strains of fluorescent *Pseudomonas* bacteria that suppress the root disease take-all (*Gaeumannomyces graminis* var. *tritici*) in continuous winter wheat (*Triticum aestivum* L.) cropping systems (Thomashow and Weller, 1988).

Specific microorganisms can be manipulated to produce beneficial effects for agriculture and the environment (Lynch, 1983), e.g., rhizobia to increase plant available N (Sprent, 1979), mycorrhizal associations to assist nutrient and water uptake (Sylvia, 1998; Mohammad et al., 1995), or biological control of plant pests to reduce chemical inputs (Cook and Baker, 1983; Kennedy et al., 1991). Bacterial or fungal inoculants can be added to soil to aid in the bioremediation of harmful substances such as petroleum hydrocarbons (Rhykerd et al., 1999; Mohn and Stewart, 2000), polycyclic aromatic hydrocarbons (Allen et al., 1999), and a wide range of environmental pollutants (Cameron et al., 2000).

The presence of a large and diverse soil microbial community is crucial to the productivity of any agroecosystem. This diversity is influenced by almost all crop and soil management practices, including the type of crops grown. Plants and their exudates influence soil microorganisms and the soil microbial community found near roots (Duineveld et al., 1998; Ibekwe and Kennedy, 1998; Ohtonen et al., 1999). In turn, the composition of the microbial community influences the rate of residue decomposition and nutrient cycling in agroecosystems (Beare et al., 1993). The basic groups of microorganisms in soil are bacteria (including actinomycetes), fungi, algae, and protozoa. Bacteria and fungi are decomposers involved in nutrient cycling and SOM processes and are critical in the functioning of the soil food web. Ninety-five percent of plant nutrients must pass through these organisms to higher trophic levels (Moore, 1994).

Bacteria are diverse metabolically and perform numerous functions. Bacteria convert SOM into carbon (energy sources) used by others in the soil food web, break down pesticides and pollutants, and immobilize and maintain valuable nutrients such as N in the root zone. Bacteria readily colonize the substrate-rich rhizosphere (Figure 10.1). Actinomycetes are a specialized group of soil bacteria that degrade plant materials such as cellulose. Actinomycetes are important in mineralization of nutrients and some can produce antibiotics. Actinomycetes can tolerate low soil water potential better than other bacteria, but are not tolerant of low soil pH (Alexander, 1998).

Fungi, like bacteria, are vital members of the food web. Fungi are especially important at lower pH, because many bacteria are adversely affected by acid soils. Fungi are able to withstand unfavorable conditions, such as water stress and extreme temperatures, better than other microorganisms (Papendick and Campbell, 1975). They are critical for residue decomposition and accumulation of stable SOM fractions through breakdown of more complex carbon sources such as cellulose, lignin, and other organic materials. These decomposition products are then available for use by other organisms. Fungal mycelia bind soil particles together to form aggregates that increase water-holding capacity and infiltration and reduce erosion. Fungi can be saprophytes on detrital material or in associations with plant roots (Swift and Boddy, 1984). The more recalcitrant material left from decomposition then accumulates as SOM. Hyphae of arbuscular mycorrhizal (AM) fungi produce the protein glomalin, which improves soil structure (Chapter 6).



FIGURE 10.1 Scanning electron micrograph of soil bacteria from a Palouse silt loam.

Algae occur in soil at populations of 10^3 to 10^4 g^{-1} soil, far fewer than bacteria and fungi. The greatest populations of algae are found in moist soil, but their numbers decrease with increasing soil depth. Some algal species are nitrogen fixers and produce mucigel, which can stabilize soil aggregates. Algae are susceptible to soil disturbance and can be good indicators of soil quality. Their populations increase in agricultural systems with reduced disturbance where the surface soil and residue maintain a higher moisture regime for longer periods (Harris et al., 1995), and as a result foster algal growth on the soil surface.

Protozoa are found at populations of 10^3 to $>10^5$ g^{-1} soil. These single-celled organisms prey on bacteria and other microorganisms, and thus regulate bacterial populations (Opperman et al., 1989) and influence SOM decomposition by regulating decomposer populations. Protozoa are crucial to the functioning of soil and other ecosystems because of their role in nutrient cycling and in providing energy for other microorganisms, plants, and animals (Foissner, 1999). Fluctuations in microbial populations with tillage affect protozoan populations because protozoa feed on these organisms. Protozoa can be useful indicators of changes in soils because their populations react rapidly to changes in the environment (Foissner, 1999).

MICROBIAL DIVERSITY

There are two primary ways that diversity can be evaluated: species diversity and functional diversity. Functional diversity can be a better parameter than species diversity to learn about soil processes and stable SOM fraction formation (Mikola and Setälä, 1998). However, it is often difficult to obtain actual measurements of functional diversity, whereas evaluating species diversity, when specific species can be assessed, is easier. The number of organisms in various microbial groups might not be sufficient to illustrate the breadth of diversity found in the soil. Although an increase in microbial products, such as SOM or CO_2 , can be an indicator of increased functioning, it might not necessarily be due to higher functional diversity. One of the earliest studies involving soil diversity and soil respiration (Salonius, 1981) established differences in bacterial and fungal diversity by inoculating soil with varying soil suspensions. Respiration rate was reduced with the lower dilution or the assumed lower microbial diversity. The true extent or dimension of the diversity of soil microorganisms is unknown, although molecular investigations suggest that culturing techniques underestimate population numbers (Holben and Tiedje, 1988; Torsvik et al., 1990). The functioning of a group of organisms is as important as the number of species in regulating ecosystem processes (Grime, 1997; Wardle et al., 1997; Bardgett and Shine, 1999). How much diversity is required to ensure sustainable and efficient SOM turnover, as well as other important functions? Greater use of diversity indices is limited by absence of detailed information on the composition

of microbial species in soil (Torsvik et al., 1990). Diverse systems are thought to have higher agricultural productivity, resilience to stress, and be more sustainable and provide risk protection (Giller et al., 1997; Wolters, 1997). A diverse system has a wider range of function with more interactions among microorganisms that influence each other to varying degrees. A higher number of different types of organisms present in a system means there are more to perform various processes and fill a niche that might not be filled if a particular group is inhibited by stress (Andren et al., 1995).

Substrate-utilization patterns have been used to obtain fingerprints of community structure (Garland, 1996; Bossio and Scow, 1995; Haack et al., 1995; Wunsche et al., 1995; Zak et al., 1994). These measures can also indicate functional diversity, metabolic potential (Degens, 1999; Haack et al., 1995; Wunsche et al., 1995), and nutritional strategies (Zak et al., 1994). Soil microbial communities as indicated by whole-soil fatty acid methyl ester (FAME) analysis can be differentiated by geographic region (Kennedy and Busacca, 1995) and cropping pattern (Cavigelli et al., 1995). The living microbiological component of soil can be estimated by phospholipid fatty acid (PLFA) analyses (Zelles et al., 1994). Another method for measuring microbial diversity is the DNA hybridization technique, which uses similarity indices. This technique illustrated that extracted bacteria and whole-community DNA had 75% similarity (Griffiths et al., 1996). The DNA microarray technology can be used to rapidly analyze microbial communities based on phylogenetic groupings and increases the ease of molecular analyses (Guschin et al., 1997). These analyses can help further understand the changes occurring among soil communities with various management practices.

Microbial diversity can be linked to susceptibility and resiliency of soil to stress, and thus might affect some soil functions such as SOM decomposition. Partial fumigation of grassland soils produces differing degrees of diversity, with longer fumigation times producing soils with less diversity. There is no direct correlation between the progressive fumigation to reduce diversity and measures of soil function, such as soil microbial biomass, soil respiration, and N mineralization. However, soils with lower diversity initially have more ability to decompose added grass residue (Griffiths et al., 2000). There is greater susceptibility to copper toxicity with decreasing diversity. Soils that contained the most diverse populations showed the greatest resilience to copper-induced stress by quickly rebounding, as shown by an increase in grass residue decomposition rates. In a similar study, no differences were seen in decomposition of *Medicago* residues even though the residues were added to both organic and conventionally farmed soils with different SOM levels (Gunapala et al., 1998). Organically farmed soils initially contained a more abundant microbial population as measured by microbial biomass C and N. When organic amendments were added, soil from the conventionally farmed system increased in microbial biomass C to a level that was comparable to the soil in the organic system. The biotic community in the conventionally farmed soil was sufficient and could respond to added substrate as well as the organic soils did. The microbial communities in this study functioned adequately whether from conventional or organic farming systems (Gunapala et al., 1998).

A reduction in functional diversity does not necessarily impede a soil's ability to decompose residue. Degens (1998) used fumigation to alter functional diversity in a grassland and measured *in situ* catabolic potential (Degens and Harris, 1997) to characterize the ability of the soil community to metabolize C substrates, with substrate added to the soil directly. The functional indices were different among fumigated, unfumigated, and fumigated and inoculated with untreated soil. There was no relationship between functional diversity and decomposition of wheat straw added into these systems. Water potential might have been the overriding factor controlling decomposition rate, because soils with reduced functional diversity continued decomposing the wheat straw under optimum moisture conditions.

Diversity of soil microorganisms can impact antagonists of pathogens and pathogen load, thus influencing their impact on plant growth. Decreased diversity of actinomycetes, some of which are antagonists of pathogens, correlated with an increase in pathogens of tomato (Workneh and van

Bruggen, 1995). *Cochliobolus sativus*, a pathogen causing a serious disease in wheat, was found in higher numbers, and individual isolates exhibited greater pathogenicity in a continuous wheat rotation than in wheat in a 3-year rotation. This increased pathogenicity was attributed to a reduction in microbial diversity (El Nashaar and Stack, 1989). Take-all decline of wheat occurs after several years of monoculture and is correlated with the appearance of several different types of organisms and alterations in microbial populations in the rhizosphere (McSpadden-Gardener and Weller, 2001). The impact of the microbial community on pathogen load and pathogenicity is complex and changes with the make-up and diversity of the community.

Assuming all functional groups are present, more microbial diversity might not necessarily be crucial to ecosystem functioning. Soil biodiversity and nutrient cycling were not linked in a study of Nigerian tropical soils (Swift et al., 1998). A study comparing native bush soils with those under cultivation showed greater abundance and diversity of soil fauna in the former, but little difference in decomposition of surface residues. Although variation in species richness might not be discernible in many environments, differences can be important in stressed systems or when conditions are altered (Yachi and Loreau, 1999). Organic matter accumulation and rate of decomposition can be important, although slowly changing indicators of ecosystem functioning in less-stressed systems.

The quality and quantity of substrate can affect community structure. Griffiths et al. (1999) used synthetic root exudates to study community structure. Microbial community changes occurred with continual substrate loading increases, and fungi dominated over bacteria in high-substrate conditions. Different organisms have the ability to be a dominant portion of the community when changes in efficiency occur because of changes in optimal growth factors, substrate quality, or substrate concentration. This knowledge is important when considering additions of organic amendments to agricultural soils.

NUTRITIONAL STRATEGIES

The concept of *r*- and *K*-strategies is an ecological classification system based on the ability of an organism to survive in different environments (MacArthur and Wilson, 1967). To indicate two contrasting methods of selection in animals, *K* refers to the carrying capacity and *r* to the maximum intrinsic rate of natural increase (r_{max}). Although most microorganisms are considered *r*-strategists and plants and animals *K*-strategists, there are differences in growth strategies among microorganisms (Andrews and Harris, 1986; Table 10.2). *K*-strategists favor competition at carrying capacity, whereas *r*-strategists take advantage of easily available substrates with fast growth rates to facilitate colonization of new habitats in response to a flush of nutrients or other fluxes. Organisms can be both *r*- and *K*-strategists, depending on circumstances. An organism can exhibit an *r*-strategy when faced with fresh resources and an unstable environment, i.e., when organic amendments are applied, but become a *K*-strategist after resources are depleted and only more recalcitrant substrate is available. Age of plant roots and plant type can also influence the dominant strategy. *K*-strategists were found in higher numbers on older wheat roots than in younger roots (De Leij, 1993). The root surface of ryegrass had more *K*-strategists than that of white clover (Sarathchandra et al., 1997). Spore formation is a tactic of *r*-strategists to survive during low nutrient availability. Although the initial colonists of a residue might be *r*-strategists, organisms involved in humus degradation or lignin and cellulose degradation are *K*-strategists. Most soil bacteria are generally considered *r*-strategists, whereas fungi and actinomycetes are usually *K*-strategists (Bottomley, 1998).

The type of strategy used and various processes influence soil and plant functioning. For example, when root exudates were added to soils contaminated with heavy metals, certain bacterial populations increased, the dominance of various strategy organisms depending on availability of substrate and soil conditions (Kozdroj and van Elsas, 2000). Exudates added to these polluted soils decreased the overall diversity in favor of *r*-strategists, whereas *K*-strategists dominated soils not amended with exudates. In another study, organisms with the same community structure exhibited

TABLE 10.2
Characteristics of *r*- and *K*-Strategists in Ecological Classification

Characteristic	<i>r</i> -Strategist	<i>K</i> -Strategist
General	Rapid reproductive rate, extreme fluctuation	Adapt to environment, stable and permanent
Growth rate	Rapid	Moderate
Substrate-utilization efficiency	Low efficiency	Higher efficiency
Diversity of substrates utilized	Simple, readily available, not resource limited	Complex, diverse, may be resource limited
Phenotype	Polymorphic to monomorphic	Monomorphic
Morphology	Smaller cells, mycelium not highly differentiated	Larger cells, well-developed mycelium
Reproduction	Simple genetic exchange, rapid rate	Complex genetic exchange, slow rate
Population dynamics	Explosive, density-independent nonequilibrium, below carrying capacity, recolonization, high migration	Stable, density dependent by competition or grazing, equilibrium dynamics at or near carrying capacity, low migration
Tolerance to niche overlap	High tolerance	Low tolerance
Residue colonists	Early	Late
Competitive adaptations	Few	Many
Microbial types	Cyanobacteria, dinoflagellates blooms; <i>Aspergillus</i> , <i>Penicillium</i> , <i>Pseudomonas</i> , <i>Bacillus</i> ; heterotrophs, spore formers	Humus, lignin and cellulose degraders, spirilla, vibrios, <i>Agrobacterium</i> , <i>Corynebacterium</i> and basidiomycetes

Source: Modified from Andrews, J. H. 1984. In M. G. Klug and C. A. Reddy (Eds.), *Current Perspectives in Microbial Ecology*. American Society for Microbiology, Washington, D.C., pp. 1-7.

different catabolic response profiles when grown in different soil environments, illustrating the effect of management on the community's functional diversity (Degens, 1999).

In addition to *r*- and *K*-strategies, oligotrophic response can be used to characterize organisms in an ecosystem. Organisms are grouped based on their nutritional strategies. Oligotrophs are organisms that grow under low nutrient supply and subsist on more resistant SOM, whereas copiotrophs flourish in nutrient-rich environments. Bacteria with enhanced growth under high nutrient concentrations are described as copiotrophs. Oligotrophs are more prevalent than copiotrophs in low-substrate concentrations. The proportion of copiotrophs to oligotrophs varies over time; the ratio of copiotrophs to oligotrophs increased immediately after cover crop residue incorporation but decreased 26 d later when readily available C declined (Hu et al., 1999). High quantities of readily available C early in the experiment might have inhibited oligotroph growth (Hu et al., 1999). Crop selection, region of the root system, and proximity to plant roots influence the number of oligotrophs and copiotrophs as well as their ratio (Maloney et al., 1997). It is important to understand the response of the microbial community to varying levels of C inputs to better manage for residue decomposition, competition with crop pathogens, and to improve the survival of introduced microorganisms (Hu and van Bruggen, 1997). Analysis of microbial community survival and nutritional strategies can aid in investigations of changes with management.

MANAGEMENT EFFECTS ON SOIL MICROBIAL COMMUNITIES

Throughout each season, crop management, resource additions, or soil disturbance influence the microbial community (Figure 10.2). Each crop or soil management practice affects the microbial community and formation or degradation of SOM.

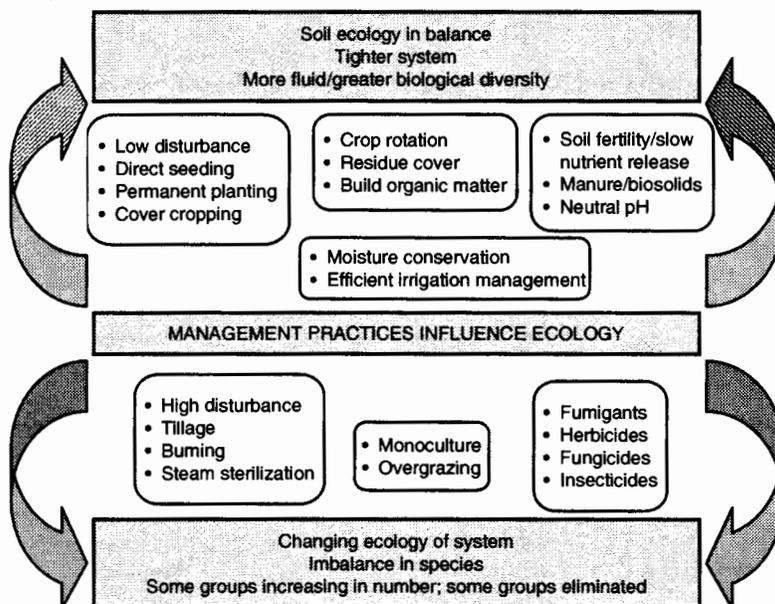


FIGURE 10.2 Management effects on soil biology. Practices that favor build-up of soil organic matter can lead to higher biological diversity, whereas practices that involve high disturbance and reliance on chemical additives can result in limited microbial diversity or elimination of some biological groups.

PLANT INFLUENCES

Roots and Rhizosphere

The rhizosphere is a dynamic zone of soil under the influence of plant roots (Bowen and Rovira, 1999; Pinton et al., 2001) and has high microbial numbers (Grayston et al., 1998), activity, and diversity (Kennedy, 1998). The rhizosphere is a region of intense microbial activity because of its proximity to plant root exudates, making rhizosphere microbial communities distinct from those of bulk soil (Curl and Truelove, 1986; Whipps and Lynch, 1986). Nutrients exuded by the root or germinating seed stimulate microbial activity (Rouatt and Katznelson, 1961). Interactions between plants and rhizosphere microorganisms can play a critical role in plant competition. Competitive interaction among plants can also be important to develop rhizosphere soil communities. Free-living bacteria and fungi from rhizospheres of different pairs of plant species in two fields utilized different substrates and grew differently in the presence of antibiotics, osmotic stresses, and zinc (Westover et al., 1997). Results from these two fields suggest that adjacent plant species influence populations of rhizosphere bacteria and fungi, creating local microscale heterogeneity in rhizosphere soil (Westover et al., 1997). Similar results have been obtained for AM communities associated with certain grass species (McGonigle and Fitter, 1990; Johnson et al., 1992), rhizosphere bacterial populations associated with particular wheat genotypes (Neal et al., 1973), and root bacterial communities following bacterial inoculation (Gilbert et al., 1993).

Composition of plant species can influence the microbial community because of differences in chemical composition of root exudates (Christensen, 1989). Peas and oats exude different amounts of amino acids (Rovira, 1956). Environmental factors regulating plant growth can affect root exudation, including temperature (Rovira, 1959; Vancura, 1967; Martin and Kemp, 1980), light (Rovira, 1956), and soil water (Martin, 1977). Plants significantly influence the make-up of their own rhizosphere microbial communities (Miller et al., 1989). This is the result of different plant species and cultivars transporting varying amounts of C to the rhizosphere (Liljeroth et al., 1990) as well as different compositions of exudates. Ibekwe and Kennedy (1999) showed that wheat

(*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), pea (*Pisum sativum* L.), jointed goatgrass (*Aegilops cylindrica* L.), and downy brome (*Bromus tectorum* L.) grown in two soil types had different rhizosphere microbial communities. Barley cultivars differed in the abundance of fungi and bacteria present in their rhizoplanes and rhizospheres, and these differences were sustained over different stages of plant growth (Liljeroth and Bååth, 1988). Two corn (*Zea mays*) cultivars (*Fusarium* susceptible and resistant) and grass (*Poa pratense*) lines (disease susceptible and resistant) differed in the numbers of rhizosphere bacteria, with susceptible lines having the highest numbers (Miller et al., 1989). These results were obtained even with no known presence of the pathogen. The rhizosphere microbial communities as determined by Biolog (Biolog® GN microtiter plates, Hayward, CA) differed with plant species of wheat, ryegrass (*Lolium perenne*), bentgrass (*Agrostis capillaris*), and clover (*Trifolium repens*). Plant species affected C-utilization profiles of the rhizosphere microbial communities of wheat, ryegrass, clover, and bentgrass. Microorganisms in the rhizospheres of wheat, ryegrass, and clover had higher utilization of C sources than in the bentgrass rhizosphere. Soil type, however, did not affect the nonrhizosphere soil microbial community profiles (Grayston et al., 1998). In natural plant communities, different plant combinations exhibited unique rhizosphere populations of free-living bacteria and fungi with differing abilities to utilize C substrates and withstand stresses (Westover et al., 1997). Unique C-source utilization patterns among rhizosphere communities of hydroponically grown wheat, white potato (*Solanum tuberosum*), soybean (*Glycine max*), and sweet potato (*Ipomoea batatas*) were found by using Biolog plates (Garland, 1996). C-source utilization patterns could distinguish among soils from six plant communities (Zak et al., 1994).

Substrate-utilization patterns have been used successfully to differentiate bacteria associated with different cropping and management practices (Garland, 1996; Zak et al., 1994). Crop effects can be associated with plant exudates as a result of the enhanced utilization or inhibition of substrates, similar to the organic content of root hairs, mucilage, or root cell lysates of the particular crop (Garland, 1996). Bossio and Scow (1995) found pattern differences associated with rice straw treatments and flooding. These systems are highly reactive to changes in their environment and can thus serve as easily attained, reliable fingerprints of community shifts as a function of substrate use.

Plant Competition

Competitive interactions of the plant can influence plant productivity and are affected by soil microorganisms, such as mycorrhizal fungi (Crowell and Boerner, 1988; Hetrick and Wilson, 1989; Allen and Allen, 1990) and *Rhizobium* (Turkington et al., 1988; Turkington and Klein, 1991; Chanway and Holl, 1993). Evidence suggests that soilborne pathogens affect plant competitiveness and plant succession (Van der Putten and Peters, 1997). A pathogen-resistant species, sand fescue (*Festuca rubra* ssp. *arenaria*), outcompeted the susceptible species, marram grass (*Ammophila arenaria*), when both coastal grasses were exposed to pathogens (Van der Putten and Peters, 1997).

Plant Diversity/Crop Rotation

Plant species and numbers can drive the make-up of the microbial community and the diversity of rhizosphere microbial populations. The above- and belowground plant community can influence microbial spatial heterogeneity in soil. Aboveground shoot material contributes organic material to the surface layers of soil. Decaying root systems also function as a source of nutrients for the surrounding microorganisms (Swinnen et al., 1995). Compared with monocropping, crop rotation can improve conditions for diversity in soil organisms because of variability in type and amount of organic inputs, and allow for time periods, or breaks, when there is no host available for a particular pest (Altieri, 1999). Diversity in crop rotation can allow for higher C inputs and diversity of plant material added to soils, depending on the residue level and carbon quality of the crops in

rotation. Crop rotation enhances beneficial microorganisms, increases microbial diversity, interrupts the cycle of pathogens, and reduces weed and insect populations. Legumes in a crop rotation supply symbiotically fixed nitrogen to the system, use less water than many other crops, and reduce pathogen load. Studies have long shown the positive effects of crop rotation on crop growth, attributing these to changes in composition of microbial community (Shipton, 1977; Cook, 1981; Johnson et al., 1992).

Crop rotation and plant cover affected soil microbial biomass C and N of long-term field experiments in Iowa, with the highest values found in the longer rotations (4 years vs. 2 years) and multicropping systems, and the lowest in the continuous corn–soybean system. The varied diversity and quality of crop residues, amount of readily decomposable organic material, and root density led to increased soil microbial biomass under crop rotation. N fertilization did not affect microbial biomass in these studies (Moore et al., 2000).

Allelopathic interactions can occur between crops and weeds, between two crops, from decomposing crop and weed residues, and from crop and weed exudates (Anaya, 1999). Nonpathogenic allelopathic bacteria can produce plant-inhibiting compounds (Barazani and Friedman, 1999). Crop rotation can be used to alleviate the allelopathic or autopathic effects a crop plant might have on itself. Monocropping encourages proliferation of allelopathic bacteria (Barazini and Friedman, 1999).

By rotating crops, it is possible to lessen the negative effects a crop might have on itself and on subsequent crops (Rice, 1995). The populations and aggressiveness of pathogens can be altered with crop rotation, illustrating changes in microbial diversity and function due to management (El Nashaar and Stack, 1989). In a long-term study, *Cochliobolus sativus*, a pathogen of spring wheat, was found in higher numbers and individual isolates exhibited greater aggressiveness or ability to cause severe disease in continuous wheat, when compared with wheat in a 3-year rotation. Continuous monocropping led to changes in the soil community, which increased pathogen load and reduced barley growth compared with that by grains in multiple-crop rotation (Olsson and Gerhardson, 1992). Continuous monocropping of wheat, however, can lead to suppression of the take-all pathogen or take-all decline. This natural defense occurs in soils in the presence of fluorescent pseudomonad bacteria that produce the antibiotics phenazine and phloroglucinol (Mazzola et al., 1995). Barley plants produce compounds that can help protect it from fungus (*Drechslera teres*) and armyworm (*Mythimna convecta*) larvae (Lovett and Hoults, 1995).

Crop rotation can influence root colonization by mycorrhizae. In years following spinach (*Spinacea oleraceae*) and bell pepper (*Capsicum annum*), spore populations of most species of AM were depressed and had lower infectivity compared with that in years following wheat, rice, or corn (Douds et al., 1997). Cover crops, such as autumn-sown cereals or vetches, increase the AM inoculum potential for subsequent crops (Boswell et al., 1998; Galvez et al., 1995). Cover crops aid in maintaining a viable mycelial network. A cover crop of winter wheat inoculated with AM increased AM infection rate, and in turn increased the growth and yield of a subsequent corn crop (Boswell et al., 1998). Soil from no-till, low-input fields with a hairy vetch cover crop maintained higher levels of colonization by indigenous AM than soils that had been tilled or received high-input management (Galvez et al., 1995). Use of cover crops can maintain AM when inoculum levels might otherwise be low and enhance infection of the subsequent crop.

Crop Residue

Additions of crop residue are critical to maintain or increase SOM levels in agricultural soils (Figure 10.3). Cropping systems vary in residue quality and quantity, the microbial community supported, contributions to SOM, and ability to withstand the effects of disturbance. The residue decomposition process depends on the organisms present, type of SOM, and environmental conditions (Martin, 1933). Residue decomposition can also be affected by availability of carbon for microbial growth, physical separation because of landscape position, soil horizonation, or encapsulation of SOM in

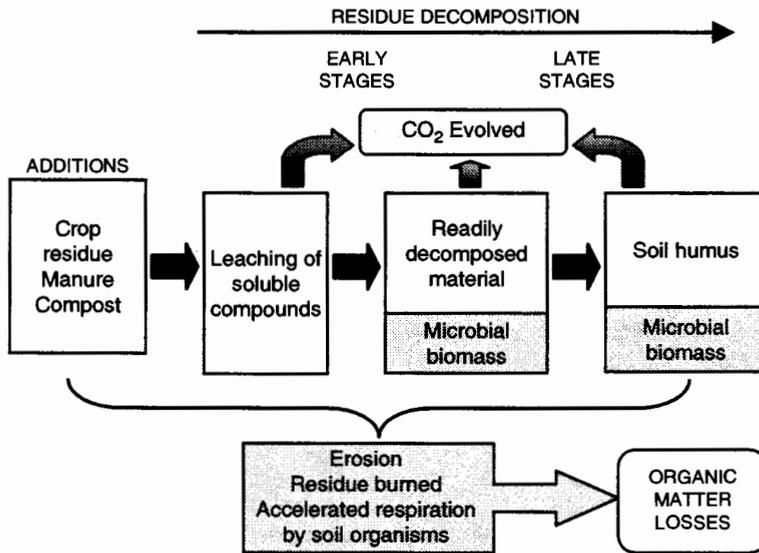


FIGURE 10.3 Fate of organic amendments added to croplands. As residue decomposes, a portion is lost to the atmosphere through CO₂ evolution. The remainder can be utilized by soil microorganisms, eventually increasing soil organic matter content. Rapid removal of organic residues through processes such as erosion, burning, and intensive tillage can slow the formation of, or over time deplete, soil organic matter.

soil aggregates and clay peds, and low N availability (Paul, 1984). Water, temperature, soil pH, aeration and oxygen supply, nutrient availability, crop residue composition, C:N ratio of crop residue, and microflora are critical factors in residue degradation (Parr and Papendick, 1978).

Residue quality and management influence the composition of the microbial community. Higher numbers of culturable bacteria, including actinomycetes, were observed from decomposing soybean residues in buried bags than from wheat or corn. Fungal populations were highest on corn and lowest on wheat (Broder and Wagner, 1988). Sorghum (*Sorghum bicolor* (L.) Moench) residues buried by conventional tillage contained greater fungal hyphal length but fewer actual fungal propagules than with no-till, whereas no-till mineral soil had greater fungal hyphal length but no difference in propagule counts compared with conventionally tilled soils (Beare et al., 1993). In their study of sorghum residues, Beare et al. (1993) identified genera of fungi that were specialized for surface residue, whereas buried residues contained no specialized fungal community.

Crop species (Cookson et al., 1998) and cultivar residues (Chaloux et al., 1995) vary in their decomposition rate as well as the microbial populations they support. The amount of C mineralized from crop residues depends on the type of residue and residue composition (Henriksen and Breland, 1999). Amino acids and simple sugars, which are metabolized most rapidly in the residue-decomposition process, support populations of *r*-strategists. More complex compounds such as cellulose and lignin are broken down by *K*-strategists or oligotrophs. Lupine (*Lupinus albus*) residue decomposes more rapidly and supports higher populations of bacteria and fungi than does wheat or barley residue (Cookson et al., 1998).

Surface management (undisturbed on surface, incorporation, burning, or mechanical removal) of wheat or barley stubble also affects decomposition and microbial populations. However, wheat straw incorporated into soil had a higher decomposition rate, mass lost, and substrate-induced respiration than where stubble was burned or removed (Cookson et al., 1998). Residue management did not affect residue decomposition or microbial activity of barley or lupine (Cookson, et al., 1998). The authors hypothesized that the higher lignin:N ratio of wheat caused the response to incorporation.

Decomposition of residue by microorganisms is dependent on the presence of mineral N supply or high N residues (low C:N ratios; Wagner and Wolf, 1998). Decay rate is better correlated with initial N content of residue than with lignin content or low soil N. To adequately meet the needs of the microorganisms involved in decomposition without requiring either added fertilizer or mineral N sources from the soil, residues must contain at least 1.5 to 1.7% N, corresponding to a C:N ratio of ca. 25 or 30 (Parr and Papendick, 1978). The effects of adding inorganic N fertilizer to hasten decomposition of low N residue occur quickly, and after several months the effects of added N on decay cannot be detected (Parr and Papendick, 1978). Knowledge of changes in C and N availability is required to manage crop fertility needs throughout the growing season. Active C and N pools in SOM in agricultural fields vary seasonally, and are dependent on crop rotation, tillage depth, and N fertilization (Franzleubbers et al., 1994). Each of these factors affects the type and amount of substrate available for microbial utilization.

RESOURCES

Nutrient Status/Cycling

Nutrient availability and the role of microorganisms in nutrient immobilization are important concerns in agriculture. Manipulations of food webs to maintain plant nutrition while minimizing N losses are worthwhile goals of sustainable agricultural systems (Altieri, 1999).

Bacterial and fungal abundance in the rhizosphere is influenced by the nutrient status of both plant and soil. The percent mycorrhizal cover on roots of *Plantago lanceolata* was positively correlated with leaf N and P, whereas root colonization by bacteria and other fungi was negatively correlated with plant P (Newman et al., 1981). It might be difficult to separate the effects of soil nutrients on rhizosphere populations from effects involved with increased or altered root exudation of organic compounds. Grasses grown in monoculture can modify N availability (Wedin and Tilman, 1990), and it has been hypothesized that changes in soil N availability influenced by plant species affect composition of AM fungal communities (Johnson et al., 1992). Microbial population changes occur with added fertilizer and tillage. Nitrogen fertilization increased numbers of fungi and Gram-negative bacteria in rhizosphere of rice (Emmimath and Rangaswami, 1971). Kirchner et al. (1993) found that in no-till treatments receiving N fertilizer, fungal populations were higher than under no-till conditions with no fertilizer added. Higher fungal populations in the fertilized treatment were due to increased corn crop growth and higher amounts of residue to serve as substrate for microbial populations, as well as increased root growth and higher amounts of root exudates, which, in turn, increase microbial biomass. Soils that were conventionally tilled, planted with a crimson clover cover crop, and rotated with corn had more actinomycetes, *Bacillus* spp., and total culturable bacteria than corn grown under conventional tillage with fertilizer added, whereas fungi and Gram-negative bacteria were not different.

Plant Growth-Regulating Compounds

Plant growth-regulating compounds are substances produced by plants and microorganisms in the rhizosphere that enhance seed germination and plant growth (Arshad and Frankenberger, 1998). Soil microorganisms synthesize plant growth regulators, such as auxins, abscissic acid, cytokinins, ethylene, and gibberellins (Frankenberger and Arshad, 1995). These compounds and the organisms that produce them can protect against plant pathogens and stimulate biofertilization (fixation of atmospheric N₂ or solubilization of nutrients) and plant growth (Figure 10.4). The mechanisms of action are often not readily apparent. Initially, it was thought that N₂ fixation by *Azotobacter* and *Azospirillum* was the major reason for plant growth promotion; however, other substances, such as auxins, cytokinins and gibberellins, can stimulate growth (Hussain and Vancura, 1970; Barbieri et al., 1993; Janzen et al., 1992). *Bacillus* and *Rhizobium* also produce plant growth-stimulating compounds (Frankenberger and Arshad, 1995). Plant growth promotion can also be an indirect

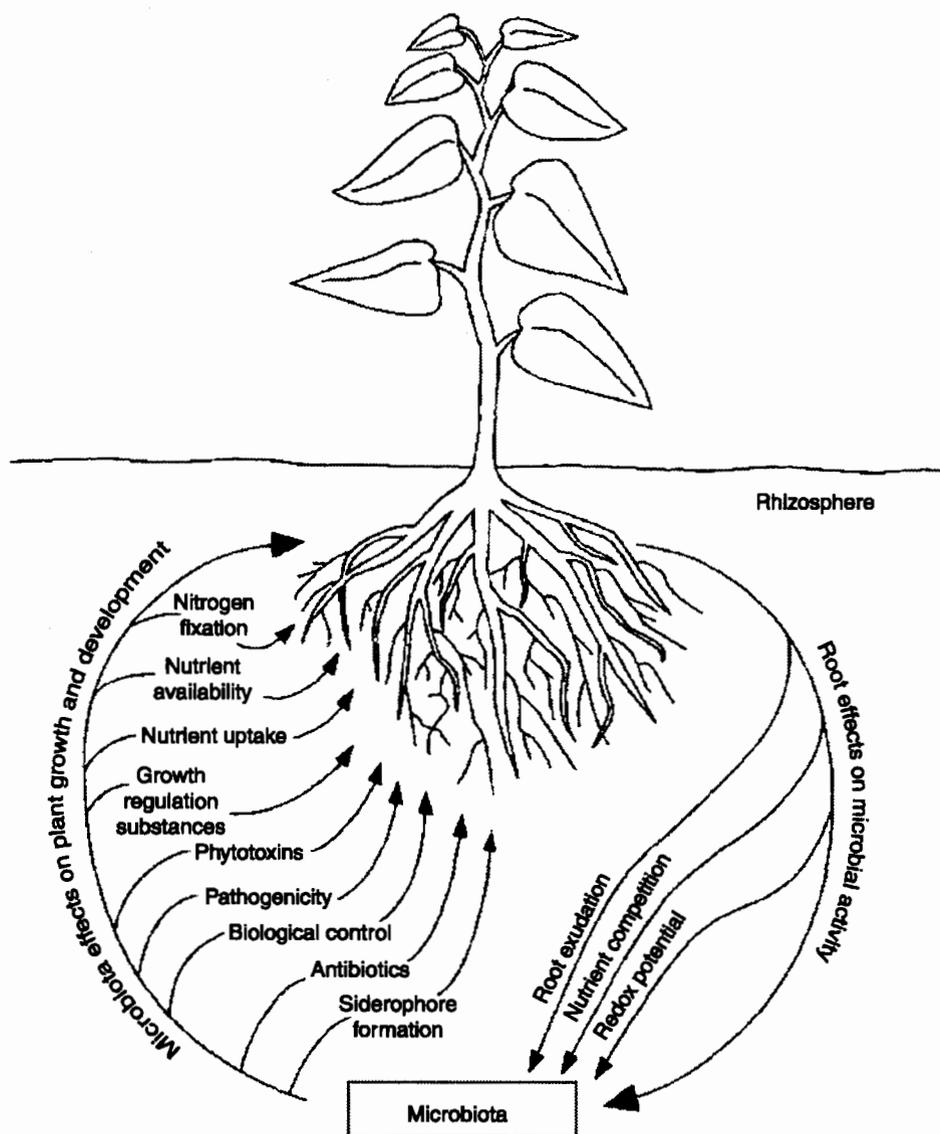


FIGURE 10.4 Plant–microbe interactions affecting plant growth. (From Frankenberger, W.T., Jr., and M. Arshad. 1995. *Phytohormones in Soils: Microbial Production and Function*. Marcel Dekker, New York, 503 pp. With permission.)

effect of siderophore or antibiotic production, which leads to the reduction in pathogen colonization and infection of the seed and root (Kloepper et al., 1989; Glick 1995).

Microbially derived auxins, ethylene, and other compounds have also been implicated in plant growth inhibition. Plant growth inhibition can be correlated with elevated indole acetic acid levels produced by rhizobacteria in sugarbeet (*Beta vulgaris*; Loper and Schroth, 1986), sour cherry (*Prunus corasus* L.; Dubeikovskiy et al., 1993), maize (Sarwar and Frankenberger, 1994), lettuce (*Lactuca sativa*; Barazani and Friedman, 1999), and several weed species (Sarwar and Kremer, 1995). Ethylene, produced by plants, soil fungi, yeasts, and bacteria, can affect plant development from seed germination to senescence (Beyer et al., 1984). Microbial synthesis of ethylene can be affected by the availability of organic substrates and crop residues (Goodlass and Smith, 1978; Lynch and Harper, 1980; Arshad and Frankenberger, 1990).

Amendments

Throughout the history of agriculture, farmers have added amendments to soil to increase crop yield. These additions have the potential to increase SOM accumulation and plant productivity. Soil amendments can also cause alterations to the soil microbial community. These changes can be quantified by microbial population structure and soil enzyme techniques. Soil microbial populations and activity increase, in general, with manure additions (Altieri, 1999). Manure also increases populations of Collembola and earthworms (Altieri, 1999).

Biosolids (sewage sludge) is a material that is sometimes applied for agricultural benefit. Long-term application of biosolids with low and high metal contents added (Cd, Cu, Ni, Zn) showed few differences in the effects on culturable bacteria, but had a dramatic effect on the whole bacterial community, where numbers of the α subdivision of Proteobacteria increased with high metal concentration (Sandaa et al., 2001). Caution must be exercised before applying large amounts of biosolids to agricultural lands, and biosolids should be tested for their heavy-metal content before application. Heavy-metal accumulations from biosolids application can negatively affect microbial communities. Zinc-contaminated agricultural soils (from biosolids) were tested for microbial diversity and catabolic versatility (Wenderoth and Reber, 1999). Microbial diversity was reduced, and the microbial community experienced a shift to less Gram-positive bacteria and more Gram-negative bacteria compared with the nonstressed system. The diversity of the Gram-negative bacteria declined under high zinc stress. Stress or heavy-metal contamination can affect overall populations, specific groups, and also the diversity within various groups, as the individual species have different ways to adapt to stress.

Agromicrobials

Numerous agromicrobial products have been touted to increase soil fertility, microbial diversity, and crop yields. Microbial inoculants such as effective microorganisms (EM) containing yeasts, fungi, bacteria and actinomycetes increase yields of onion (*Allium cepa* L.) and pea, and increase cob weights of sweet corn (Daly and Stewart, 1999). The consistency of plant response to these types of products has not yet been demonstrated, and further critical study is needed.

Arbuscular Mycorrhiza (AM)

Mycorrhiza are nonpathogenic fungi that form symbiotic associations with plant roots (Chapter 6). Mycorrhiza are involved in the nutrient cycling process, especially in stressed environments (e.g., P-deficient soils) and can play an active role in SOM accumulation by increasing plant growth by solubilization of nutrients and by producing recalcitrant compounds (glomalin). Fungal hyphal threads allow roots to expand the volume of soil that can be explored for nutrients and water that otherwise might be inaccessible to the plant. Mycorrhizal associations enhance nutrient uptake in the rhizosphere and expand the volume of soil the root can explore (Sylvia, 1998). This relationship is especially beneficial under moisture-limiting conditions. Wheat plants inoculated with AM and subjected to water stress at three different times had higher grain yield and biomass than plants that were not inoculated with AM (Ellis et al., 1985). In the Palouse region of eastern Washington, mycorrhizal fungi lessened the severity of water stress in winter wheat (Mohammed et al., 1995). AM species, abundance, and spore distribution are affected by tillage and crop inputs (Douds et al., 1995). *Glomus occultum* numbers were higher under no-till, whereas other *Glomus* species were more abundant under conventional tillage in a corn-soybean rotation (Douds et al., 1995).

The interactions of AM and other microorganisms often benefit plants, although the relationships are not always readily evident (Edwards et al., 1998). Presence of AM can enhance relationships with introduced organisms in the rhizosphere of crops. Edwards et al. (1998) found that

biological control agents for *P. fluorescens* did not affect AM function in the rhizospheres of tomato (*Lycopersicon esculentum*) and leek (*Allium porrum*). AM plants had higher shoot weights than non-AM plants, and *P. fluorescens* populations were higher in the presence of AM.

Biological Control

Biological control is the use of pathogens, parasites, or other predators to reduce the population or activity of pest organisms (DeBach, 1964). Another broader definition includes all forms of intervention, such as genes and gene products, to reduce the impact of pests on crops and beneficial organisms (Cook, 1987). The three major strategies for biological control are classical, inundative, and integrated management (DeBach, 1964; TeBeest, 1991). The classical approach involves the importation of exotics or the use of natural enemies for release, dissemination, and self-perpetuation on target pests. The addition of a virulent strain to suppress pests is the inundative approach. The biocontrol agent is not self-sustaining and must be applied to the target host every season. Integrated management is a broad approach that involves management practices to conserve or enhance native enemies of pests. Biological control is an alternative to pesticides and is part of sustainable agriculture management.

Biological control agents have been investigated for their control of diseases, such as take-all root disease in wheat. The phenomenon known as take-all decline (the reduction in severity of take-all disease) is attributed to naturally occurring strains of fluorescent pseudomonads that produce the antibiotics phenazine and phloroglucinol in annually monocropped wheat (Thomashow and Weller, 1988). Deleterious rhizobacteria have been shown to inhibit such weeds as downy brome (*Bromus tectorum* L.; Kennedy et al., 1991), jointed goatgrass (*Aegilops cylindrica* Host.; Kennedy et al., 1992), and velvetleaf (*Abutilon theophrasti* Medik.; Kremer, 1987). Several fungal isolates have been investigated for use in weed biological control, such as *Fusarium* spp. against leafy spurge (*Euphorbia* spp.) in the rangelands of the U.S. and Canada (Caesar et al., 1999), *Exserohilum monoceras* for grass weeds (*Echinochloa* spp.) in rice production (Zhang and Watson, 1997), and *Colletotrichum gloeosporioides* f. sp. *aeschynomene* to control northern jointvetch (*Aeschynomene virginica*; Luo and TeBeest, 1999). Several conditions must be met before a biological control agent can be widely used in a crop or rangeland situation. The agent must have adequate shelf life (Cross and Polonenko, 1996), the ability to be mass-produced (Oleskevich et al., 1998), the ability to survive and compete in a field situation, and a simple method of application of the organism and subsequent delivery of the plant-inhibitory compound (Kremer and Kennedy, 1996).

Organic/Low-Input Farming

Organic farming does not allow use of synthetic pesticides or fertilizers and is intended to reduce the detrimental effects of agriculture on soils, animals, food, and the environment. Organic matter and microbial biomass are higher in organic farming systems than in conventional systems (Fließbach and Mäder, 1997; Reganold et al., 1993; Murata and Goh, 1997; Wander et al., 1994). AM fungi were 30 to 60% higher in roots of plants from low-input practices in a long-term field trial that compared organic and conventional systems (Mader et al., 2000). In this study, AM was highest in the control soils, lowest in the conventional system, and intermediate in the organic system. The control soils were not fertilized, whereas the pesticide use, disturbance, and high fertility in the conventional systems reduced AM infection. Soils under animal-based organic management had higher levels of the light fraction of particulate SOM than crop-based organic systems or conventional systems (Wander et al., 1994). This might be the result of a more biologically active substrate pool due to a lower C:N ratio and higher respiration rate, higher amounts of organic residue added, and less soil disturbance in the animal-based system. Microbial biomass C and dissolved organic C increased as organic inputs increased, and microbial communities as determined by PLFA were

different in organic farms and conventional farms (Lundquist et al., 1999). Organic management systems that employed animal manure and legumes for N supply were equally profitable as higher-input conventional systems after 15 years in a study in Pennsylvania (Drinkwater et al., 1998). The organic management systems had lower leaching losses of N and higher levels of soil organic C and N.

Biodynamic agriculture is an organic farming system that uses specific fermented preparations as either field sprays or compost inoculants (Koeppel et al., 1976). Soil quality parameters were not different among biodynamic, organic, and conventional management systems, but differed with fertilization level (Penfold et al., 1995). Field-applied biodynamic sprays and compost did not alter soil microbial characteristics compared with conventional practices in a cereal-legume cropping system in the state of Washington (Carpenter-Boggs et al., 2000a). In other studies in the state of Washington, however, biodynamic management resulted in higher microbial biomass, respiration, and SOM than organically managed or conventionally managed systems (Goldstein, 1986). Biodynamic preparations for compost development altered compost microbial community and increased compost temperature (Carpenter-Boggs et al., 2000b).

Genetically Modified Organisms (GMOs)

The impact of the addition of genetically modified organisms (GMOs) on soil populations and plant productivity is of interest as more GMOs are introduced into agricultural systems. In a microcosm study of soils from Canada and the U.S., assessment of nontarget effects of two GMOs indicated that there were functional and community differences as long as GMOs persisted in soil; however, effects differed with the GMOs used (Gagliardi et al., 2001). Inoculation of transgenic potatoes with two bacterial biological control agents did not reduce survival of bacterial biological control agents compared with nontransgenic potatoes, nor was the indigenous bacterial community impacted by the introduced bacteria (Lottman et al., 2000). When a GMO and wild-type *Pseudomonas fluorescens* were inoculated into the rhizosphere of wheat, both bacterial strains caused shifts in the native microbial populations in the rhizosphere and phylloplane of wheat; however, there were no changes in nonrhizosphere soil and no negative effects on plant health (De Leij et al., 1995). Addition of a genetically modified *P. fluorescens* in the rhizosphere of pea affected soil enzymes activities and microbial communities (Naseby and Lynch, 1998). Differences are evident with the introduction of some GMOs, but the impact of these differences on soil microbial community, plant productivity, soil quality, and SOM accumulation is case specific, and long-term impacts are not clear.

DISTURBANCE

Agroecosystem function and SOM dynamics are greatly influenced by anthropogenic activities. Soil erosion caused by excessive tillage is the most visual example of humankind's influence on soil function. Microorganisms are highly sensitive to physical soil disturbance (Elliott and Lynch, 1994), and their population dynamics can serve as early warning indicators of changes in soil quality. Fluxes in microbial diversity and functional diversity can contribute greatly to the understanding of soil quality and the development of sustainable agroecosystems (Thomas and Kevan, 1993; di Castri and Younes, 1990; Hawksworth, 1991a). Soil organisms are useful in classifying disturbed or contaminated systems, because diversity can be affected by minute changes in the ecosystem. Severe disturbances, such as those caused by heavy tillage with a moldboard plow (which completely inverts the surface soil), overgrazing, and pollutants, can reduce aboveground plant diversity and growth. This reduction in plant biomass and lack of a varied carbon source decreased microbial growth and functioning (Christensen, 1989; Zak, 1992).

100 Years of Dryland Farming in the Inland Pacific Northwest, U.S.A.

Winter wheat–fallow, in which only one crop is grown every 2 years, is the dominant cropping system in the low-precipitation dryland cropping region of the inland Pacific Northwest. Early settlers grew a wheat crop every year after they first broke the land out of native bunch grass and sagebrush in the 1880s. Grain yields were frequently low; however, it soon became apparent that farmers could better stabilize yields by having a fallow year to store soil moisture between wheat crops. During the fallow year, essential nutrients, mainly N, were released through mineralization of SOM. The native grass prairie provided a reserve of readily decomposable SOM that supplied nitrogen for crop use for many years. A rapid reduction in SOM content occurred when prairie soils were brought under cultivation, especially when alternated with fallow. In some soils, more than 25% of the organic matter was lost in the first 20 years of farming. In undisturbed native soil, SOM in the top 10 cm of soil is 4% at Pullman, WA (530 mm precipitation), 3% at Pendleton, OR (410 mm precipitation), and 1.5% at Lind, WA (240 mm precipitation). Distinct decreases in SOM have been observed on farmland compared to undisturbed native soil in all three areas. Organic matter content in the top 10 cm of cropland soil at Lind, for example, is at present less than 1%. Data are available on the long-term fate of SOM in a continuous winter wheat–fallow rotation from an ongoing 70-year-old study at Pendleton, OR (Rasmussen et al., 1989; Figure 10.5). Since 1931, SOM has continually declined under all residue management methods except when 22 mt (fresh weight) ha⁻¹ of cattle manure was applied every other year. SOM decline has been highest when stubble was burned in the fall and when no nitrogen was applied. Maintaining an adequate nitrogen supply and returning all residue to the soil has reduced, but not arrested, SOM decline (Figure 10.5).

Tillage

Up to 50% of the SOM in some soils has been lost after years of intensive tillage, clearing vegetation, and draining wetlands for farming (Cambardella and Elliott, 1993). Carbon is sequestered in soils through “humification of organic residues, building of organomineral complexes to form aggregates, positioning of SOM beneath the tillage layer, use of deep rooting crops, and calcification” (Bruce et al., 1999). Emissions of CO₂ from agricultural soils can be reduced by minimizing or eliminating tillage and by growing perennial crops (Lal et al., 1999). In the U.S., many farmers have 10-year contracts under the Conservation Reserve Program (CRP) to grow perennial grasses and shrubs for environmental and soil-conserving benefits (USDA-FSA, 2000). Improved farming techniques, higher productivity from farmland, and government programs that pay landowners to plant permanent vegetation on highly erodible lands have combined to increase levels of SOM in many soils (Lal et al., 1999). No-till farming results in less CO₂ released to the atmosphere than do intensive tillage (moldboard plowing) and minimum tillage (disk harrowing; Reicosky and Lindstrom, 1993). Incorporated straw emits more CO₂ than does surface straw or soil with no straw applied (Curtin et al., 1998). Gale and Cambardella (2000) compared contributions of root and surface residues to soil organic C in no-till soils, and found that the greatest increases were due to maintenance of root-derived C, illustrating the importance of leaving root biomass intact (no disturbance) for maximum SOM accumulation.

Conservation-tillage systems maintain at least 30% of the crop residue on the soil surface (Stroo et al., 1989) and help prevent soil erosion by wind and water (Figure 10.6; Papendick, 1996). Positive attributes of retaining crop residue on the soil surface are improved soil quality (Karlen et al., 1994; Dalal et al., 1991; Doran et al., 1996) through increased biological activity, leading to improved soil aggregation and more SOM content (Elliott and Papendick, 1986).

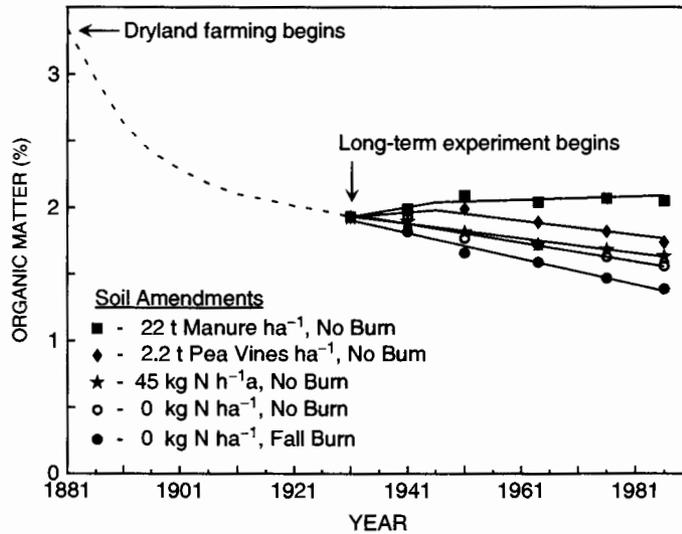


FIGURE 10.5 Soil organic matter decline in a winter wheat–summer fallow rotation at Pendleton, OR. Rapid decline in SOM occurred after the onset of dryland farming in the early 1880s. A long-term experiment was initiated in 1931 to test effects of soil amendments (cattle manure and pea vines), N fertility (0 and 45 kg ha⁻¹), and burning of residue. SOM steadily declined in all treatments except on addition of 22 mt manure ha⁻¹ every other year with no burning of residue. (Modified from Rasmussen, P. E., H.P. Collins, and R.W. Smiley. 1989. Long-term Management Effects on Soil Productivity and Crop Yields in Semi-arid Regions of Eastern Oregon. Oregon State University Bulletin 675, Corvallis, OR.)



FIGURE 10.6 No-till planting in the dryland wheat production region of the inland Pacific Northwest. No-till preserves plant residue on the soil surface for erosion control, promotes microbial populations, and provides other environmental benefits.

Conservation tillage, increased cropping intensity (e.g., reduction in fallow), crop rotation, and use of cover crops improve soil quality (Karlen et al., 1992). Crop residues on the soil surface, however, can negatively affect crop yield by impairing seedling emergence, serving as hosts for pathogens, or nutrient immobilization (Elliott and Papendick, 1986). Even distribution of crop residue at harvest and selection of a no-till planter for specific soil and residue conditions reduce the possibility of yield loss.

No-till increases microbial biomass in surface soils (0 to 15 cm; Drijber et al., 2000), increases the ratio of fungi to bacteria, and provides for a more diverse population of residue decomposers and a slower release of nutrients than does conventional tillage (Altieri, 1999). The changes in the physical and chemical properties of soil resulting from tillage greatly alter the matrix supporting growth of the microbial population. Within a given soil, there is considerable variation in the composition of the microbial community and diversity with depth in the profile. In agricultural systems, microbial activities differ drastically with depth, with the highest microbial activity occurring near the surface in no till, and more evenly distributed activity throughout the plow layer of tilled soil (Doran, 1980).

Composition of the microbial community influences the rate of residue decomposition and nutrient cycling in both no-till and tillage-based systems (Beare et al., 1993). Fungi dominate decomposition in a no-till system, whereas the bacterial component is responsible for a greater portion of the decomposition of residue with tillage. In a study of the diversity of native prairie and cultivated soils, diversity indices were higher with tillage than with grassland (Kennedy and Smith, 1995). With the substrate exposed by tillage, more surface area was available for colonization and more activity occurred. Increase in diversity seen early on with disturbance indicates a change in the microbial community to one that exhibits a greater range of substrate utilization and stress resistance. When comparing microbial numbers among burned, tilled, or no-tilled fields of double-cropped wheat and soybean in Georgia, there were no changes in total bacteria or nitrifiers with burning or tillage. Plots that were not burned or tilled initially had higher numbers of algae, actinomycetes, and fungi; however, there were no treatment differences later in the growing season (Harris et al., 1995). Preemergent herbicides had no effect on microbial numbers in that study. Buried sorghum residue under conventional tillage contained more fungal hyphae and CFU than surface residue in no-till soil did; however, in bulk soil there were no differences in fungal CFU between treatments, and higher numbers of fungal hyphae were found in no-till soil (Beare et al., 1993). These studies illustrate the alteration of the make-up of microbial communities and possibly the diversity of basic microbial groups with disturbance.

Studies have shown varying results with regards to N immobilization in reduced-tillage systems. When farmers first convert to minimum- or no-till cropping, they often encounter lower N availability for the first several years because of reduced mineralizable N. SOM (and N) accumulates under no-till, however, and a new equilibrium is established in which mineralized N and microbial biomass C are higher than under intensive tillage (Simard et al., 1994). Higher tillage intensity under conventional tillage decreased the amount of N mineralized per unit of biomass C, which could lead to a decline in SOM quality. In a long-term (11-year) study in Canada, soil C and mineralizable N were highest with no till compared with conventional tillage, regardless of cropping sequence or cropping frequency (Campbell et al., 1996). Conversely, decomposing surface residues in some no-till systems can immobilize enough N to cause N deficiency in succeeding crops (Knowles et al., 1993), and increased tillage intensity reduces the potential for N immobilization (Follett and Schimel, 1989). In these instances, cropping intensity and rotation (Kolberg et al., 1999; Knowles et al., 1993) and fertilizer placement (Knowles et al., 1993) must be managed to ensure success of no-till farming systems. Carbon gains in the soil are a function of both residue input and clay content of the soil. After 20 years of wheat and barley residue maintenance by using no-till and high N fertilization in Australia, organic C, total N, and microbial biomass were higher and pH was lower at the soil surface than under conventional tillage in which residue was burned and lower levels of N were applied (Dalal et al., 1991).

SOM increases when crop residue is retained on the soil surface (as in no-till systems), when erosion is reduced, and crops are adequately fertilized (Campbell and Zentner, 1993). In the Canadian prairies, potential exists for C sequestration under a long-term (12- to 15-year) no-till continuous wheat farming system compared with a system using conventional tillage wheat-fallow

because of lower CO₂ flux from the soil and more organic matter accumulation with reduced residue disturbance and continuous cropping (Curtin et al. 2000). Four years of no till increased SOM in the top 2.5 cm of soil compared with conventional tillage in a Mississippi study with grain sorghum–corn, cotton and soybean–wheat rotations (Rhoton, 2000). No-till in the sorghum–corn rotation showed the maximum accumulations of soil organic content, especially in the top 2 cm of soil, compared with conventional tillage and rotations that included soybean in the Great Plains (McCallister and Chien, 2000).

Although numerous studies indicate higher SOM under no till vs. conventional tillage, some studies show little or no difference in SOM between the two systems, especially in low-precipitation regions where residue production from crops is minimal (A.C. Kennedy, unpublished data). Macroorganic matter (>50 µm) and microbial biomass-C can be good indicators of changes in residue management; however, effects of tillage might be limited to vertical distribution without influencing SOM turnover (Angers et al. 1995). Needelman et al. (1999) found that no-till fields in a corn–soybean rotation in Illinois had higher SOM in the top 0 to 5 cm of soil than that in conventionally tilled fields, but SOM was not different between the two tillage treatments when the entire sampling depth (0 to 30 cm) was considered. SOM levels did not differ from conventional tillage levels in the top 15 cm of soil after 30 years of a no-till wheat–sorghum–fallow rotation in Kansas (Thompson and Whitney, 2000). Maintaining or increasing SOM is critical to crop production to improve soil water-holding capacity and aeration, provide nutrients for plants and microbes, and maintain soil physical properties such as friability and low bulk density. The amounts of SOM that accumulate in different systems vary greatly with geographic location (soil type, precipitation, and climate), length of time for which a particular management scheme is used, tillage intensity, and crop residue inputs.

Population and diversity of genomic patterns of the N₂-fixing bacteria *Bradyrhizobium* increased with no-till compared to conventional tillage in southern Brazil (Ferreira et al. 2000), even though the field was last inoculated 15 years before the study. Along with no-till, crop rotations containing soybean increased populations of *Bradyrhizobium*. Treatments that did not include soybean in rotation for 17 years and were in conventional tillage contained the least amount of *Bradyrhizobium*.

Wardle et al. (1999) studied three methods of controlling weeds (mulching, herbicides, tillage) and found that mulching (adding residue) increased soil C, microbial biomass, and activity in surface soils (1 to 10 cm) over the course of a 7-year study in New Zealand; however, some immobilization of N might have occurred late in the study. Herbicide application did not adversely affect microbial biomass and activity. Where less weed biomass was present, microbial respiration was reduced, probably because of more decomposition of weeds than crop plants. Tillage for weed control was not detrimental to substrate-induced respiration, CO₂-C released from chloroform fumigation, or soil organic C in the study. The authors emphasized the need for long-term studies, as many of their results were not apparent until after 6 years.

Although most of the effects of reduced tillage are positive, there are some instances wherein more physical soil disturbance is advantageous. Direct seeding wheat into cereal or grass residue increases the risk of infection by pathogens causing the diseases take-all, Rhizoctonia (*Rhizoctonia solani*) root rot, Cephalosporium (*Cephalosporium gramineum*) stripe, and *Pythium* root rot (*Pythium* spp.; Cook and Haglund, 1991). Crop residue can serve as a host for the pathogens (Cook, 1986). Crop rotation and tillage are suggested to alleviate disease pressure in wheat (Cook and Haglund, 1991). Abawi and Widmer (2000) cite numerous examples in which yield of bean was increased because of less disease with intensive tillage compared with reduced tillage or no-till. The increase in yield with tillage was attributed to reduced compaction, improved drainage, and higher soil temperature, which led to improved bean root competition against pathogens.

Grazing

Careful management of grazing lands is needed to protect soils from the negative effects of overgrazing and to maintain benefits of permanent plant cover. Livestock grazing is thought to be less damaging to soil quality than is conventional crop management; however, soil quality can be impacted by compaction and continual removal of plant cover (Southon and Cattle, 2000). Cattle grazing can also affect the biomass and biodiversity of plants by causing patches that differ in size and plant species (Cid and Brizuela, 1998). Also, because of overgrazing, species composition in grazing lands can shift from perennial species to annual grasses (DiTomaso, 2000). This land then becomes more susceptible to invasion by broadleaf weed species, which degrades soil productivity (DiTomaso, 2000). Although many weed species have deep taproots, they produce less aboveground biomass than do most crop plants, often leaving surface soil vulnerable to erosion. A high infestation of spotted knapweed (*Centaurea maculose*) reduced water infiltration rates (DiTomaso, 2000). Additionally, overgrazing and recolonization with weed species led to less soil moisture available to grass species and less contribution to SOM than did fibrous root systems of grass species (DiTomaso, 2000). Abril and Bucher (1999) showed the negative effects of overgrazing of rangelands in Argentina, where the overgrazed site had the lowest SOM and microbial activity. In a comparison of restored, partially restored, and overgrazed rangelands, they found that soil water, SOM, N content, and microbial activity were highest at the restored site. In another study on the soil quality of grasslands in New Mexico, Liu et al. (2000) found no negative effects on microbial diversity (substrate utilization) or microbial activity (enzyme analysis) from intense grazing; however, burning reduced microbial diversity.

Integrated systems combining crop production and livestock production with perennials are suggested as a means to improve soil quality and combat the decline in organic C of soil from the Great Plains of the U.S. after decades of cultivation (Krall and Schuman, 1996). Well-managed grasslands used for livestock grazing adjacent to streams can protect or enhance soil quality by stabilizing stream banks and reducing erosion (Lyons et al. 2000). These managed riparian areas can reduce the impact of livestock grazing and help restore degraded stream banks.

STRATEGIES FOR MANAGING MICROORGANISMS

Although the technology for managing microorganisms for sustainable agricultural production systems has not yet been developed, several strategies have been used for centuries to optimize soil life (see Chapter 2 for a discussion on SOM management). First, management practices that increase SOM should be used, especially in SOM-depleted systems. Organic matter is responsible for providing substrate for microorganisms, but also improves microbial habitat. Organic matter, in various forms of decay, improves soil physical properties, increases water-holding capacity and nutrient availability, and acts as a cementing agent for holding soil particles together. SOM can be maintained or increased by incorporating crop residues, crop rotation, cover crops, permanent plantings, maintaining soil fertility, and adding animal manures or biosolids. Addition of plentiful amounts of organic residues helps ensure a productive soil and stimulates plant growth by providing food for microorganisms. The movement toward sustainable farming systems, with diverse, healthy soil microbial communities that closely imitate the processes of native, undisturbed systems, can be realized by using these practices or adopting a combination of several practices.

A second strategy is to ensure a diverse plant community through crop rotation or grazing management. Minimizing fallow or increasing root growth in soil will provide substrate additions and adequate nutrition for a healthy soil and large, diverse populations of microorganisms. Tillage and burning of crop residues often negatively and dramatically affect the chemical and physical properties of soil, which alter growth of microorganisms and processes for which they are responsible. Minimum tillage or no till helps prevent erosion of valuable topsoil.

Options for Farmers

The following management principles will help maximize soil quality in low-precipitation areas, such as in the inland Pacific Northwest:

- Minimize tillage to the degree feasible to leave as much residue as possible on or near the soil surface.
- Maintain adequate nitrogen inputs. Because of the linkage between soil N and organic matter, adequate (but not excessive) nitrogen inputs are a requisite for optimum crop growth and residue return.
- Minimize the use of summer fallow, if possible. Consider recropping to spring wheat or barley after wet winters. Use a no-till drill, if feasible, to plant seed and fertilize in one pass through the standing residue of the previous crop.
- Emphasize wind and water erosion control, because any loss of topsoil increases loss of SOM.

Applying large quantities of organic materials, such as cattle manure, can increase SOM. This, however, is not a realistic option for most farmers because of the large quantities of manure required, as the size of the average farm exceeds 1000 ha.

CONCLUSIONS

Microorganisms are responsible for a multitude of soil processes, such as SOM dynamics, nutrient cycling, and changes in soil structure. In agroecosystems, microorganisms can affect all levels within the ecosystem through functions such as N and C cycling, plant growth promotion and inhibition, and natural biological control. Microorganisms have more diversity than does any other group of organisms on earth, but our knowledge of these organisms is still limited. We need to increase our understanding of microbial communities and their functioning in agroecosystems. Several strategies have been suggested to optimize soil life. The most critical to sustainability is to use management practices that increase SOM, reduce disturbance, and maintain a diverse plant community. There is a wealth of genetic potential in the soil, but we do not presently have the means or understanding to use the full potential of the earth's oldest inhabitants. With a better understanding of soil ecology and changes in soil biota with management, best management practices can be developed to conserve and enhance SOM, soil quality, and crop production for sustainable agricultural systems.

References

- Abawi, G. S., and T. L. Widmer. 2000. Impact of soil health management practices on soil borne pathogens, nematodes, and root diseases of vegetable crops. *Appl. Soil Ecol.* 15:37–47.
- Abril, A., and E. H. Bucher. 1999. The effects of overgrazing on soil microbial community and fertility in the Chaco dry savannas of Argentina. *Appl. Soil Ecol.* 12:159–167.
- Albrecht, S. L., Y. Okon, J. Lonquist, and R. H. Burris. 1981. Nitrogen fixation by corn-*Azospirillum* associations in a temperate climate. *Crop Sci.* 21:301–306.
- Alexander, D. B. 1998. Bacteria and archaea. In Sylvia, D. M., J. J. Fuhrmann, P. G. Hartel, and D. A. Zuberer (Eds.), *Principles and Applications of Soil Microbiology*. Prentice-Hall, New York, pp. 44–71.
- Allen, C. C. R., D. R. Boyd, F. Hemenstall, M. J. Larkin, and N. D. Sharma. 1999. Contrasting effects of a nonionic surfactant on the biotransformation of polycyclic aromatic hydrocarbons to *cis*-dihydrodiols by soil bacteria. *Appl. Environ. Microbiol.* 65:1335–1339.

- Allen, E. B., and M. F. Allen. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. In Grace, J. B. and D.A. Tilman (Eds.), *Perspectives on Plant Competition*. Academic Press, San Diego, CA, pp. 367–389.
- Alstrom, S. 1987. Factors associated with detrimental effects of rhizobacteria on plant growth. *Plant Soil* 102: 3–9.
- Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. *Agric. Ecosyst. Environ.* 74:19–31.
- American Society for Microbiology. 1994. *Microbial Diversity Research Priorities*. American Society for Microbiology, Washington, D.C., 7 pp.
- Anaya, A. L. 1999. Allelopathy as a tool in the management of biotic resources in agroecosystems. *Crit. Rev. Plant Sci.* 18:697–739.
- Andren, O., J. Bengtsson, and M. Clarholm. 1995. Biodiversity and species redundancy among litter decomposers. In Collins, H.P., G.P. Robertson, and M. J. Klug (Eds.), *The Significance and Regulation of Soil Biodiversity*. Kluwer, Dordrecht, pp. 141–151.
- Andrews, J. H. 1984. Relevance of r- and K-theory to the ecology of plant pathogens. In Klug, M. G. and C. A. Reddy (Eds.), *Current Perspectives in Microbial Ecology*. American Society for Microbiology, Washington, D.C., pp. 1–7.
- Andrews, J., and H. R. F. Harris. 1986. r- And K-selection in microbial ecology. *Adv. Microb. Ecol.* 9:99–147.
- Angers, D. A., R. P. Voroney, and D. Cote. 1995. Dynamics of soil organic matter and corn residues affected by tillage practices. *Soil Sci. Soc. Am. J.* 59:1311–1315.
- Arshad, M., and W. T. Frankenberger, Jr. 1990. Ethylene accumulation in soil in response to organic amendments. *Soil Sci. Soc. Am. J.* 54:1026–1031.
- Arshad, M., and W. T. Frankenberger. 1998. Plant growth-regulating substances in the rhizosphere: Microbial production and functions. *Adv. Agron.* 62:45–151.
- Barazani, O., and J. Friedman. 1999. Allelopathic bacteria and their impact on higher plants. *Crit. Rev. Plant Sci.* 18:741–755.
- Barbieri, P., and E. Galli. 1993. Effect on wheat root development of inoculation with an *Azospirillum brasilense* mutant with altered indole-3-acetic acid production. *Res. Microbiol.* 144:69–75.
- Bardgett, R. D., and A. Shine. 1999. Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. *Soil Biol. Biochem.* 31:317–321.
- Beare, M. H., B. R. Pohl, D. H. Wright, and D. C. Coleman. 1993. Residue placement and fungicide effects of fungal communities in conventional and no-tillage soils. *Soil Sci. Soc. Am. J.* 57:392–399.
- Beyer, E. M., Jr., P. W. Morgan, and S. F. Yang. 1984. Ethylene. In Wilkins, M. B. (Ed.), *Advanced Plant Physiology*. Pitman Publishing, London, pp. 111–126.
- Bossio D. A., and K. M. Scow. 1995. Impacts of carbon and flooding on the metabolic diversity of microbial communities in soils. *Appl. Environ. Microbiol.* 61: 4043–4050.
- Boswell, E. P., R. T. Koide, D. L. Shumway, and H. D. Addy. 1998. Winter wheat cover cropping, VA mycorrhizal fungi and maize growth and yield. *Agric. Ecosyst. Environ.* 67:55–65.
- Bottomley, P. J. 1998. Microbial ecology. In Sylvia, D. M., J. J. Fuhrmann, P. G. Hartel, and D. A. Zuberer (Eds.), *Principles and Applications of Soil Microbiology*. Prentice-Hall, New York, pp. 149–167.
- Bowen, G. D., and A. D. Rovira. 1999. The rhizosphere and its management to improve plant growth. *Adv. Agron.* 66: 1–102.
- Broder, M. W., and G. H. Wagner. 1988. Microbial colonization and decomposition of corn, wheat, and soybean residue. *Soil Sci. Soc. Am. J.* 52:112–117.
- Brown, M. E. 1972. Plant growth substances produced by microorganisms of soil and rhizosphere. *J. Appl. Bacteriol.* 35: 443–451.
- Bruce, J. P., M. Frome, E. Haites, H. Janzen, R. Lal, and K. Paustian. 1999. Carbon sequestration in soils. *J. Soil Water Conserv.* 54:382–389.
- Bruhl, G. W. 1987. *Soilborne Plant Pathogens*. MacMillan, New York.
- Burdon, J. J. 1987. *Diseases and Plant Population Biology*. Cambridge University Press, New York.
- Caesar, A. J., G. Campobasso, and G. Terragitti. 1999. Effects of European and U.S. strains of *Fusarium* spp. pathogenic to leafy spurge on North American grasses and cultivated species. *Biol. Control* 15:130–136.
- Cambardella, C. A., and E. T. Elliott. 1993. Carbon and nitrogen distribution in aggregates from cultivated and native grassland soils. *Soil Sci. Soc. Am. J.* 57:1071–1076.

- Cameron, M. D., S. Timofeevski, and S. D. Aust. 2000. Enzymology of *Phanerochaete chrysosporium* with respect to the degradation of recalcitrant compounds and xenobiotics. *Appl. Microbiol. Biotechnol.* 54:751–758.
- Campbell, C. A., B. G. McConkey, R. P. Zentner, F. Selles, and D. Curtin. 1996. Long-term effects of tillage and crop rotations on soil organic C and total N in a clay soil in southwestern Saskatchewan. *Can. J. Soil Sci.* 76:395–401.
- Campbell, C. A., and R. P. Zentner. 1993. Soil organic matter as influenced by crop rotations and fertilization. *Soil Sci. Soc. Am. J.* 57:1034–1040.
- Carpenter-Boggs, L., A. C. Kennedy, and J. P. Reganold. 2000a. Organic and biodynamic management: Effects on soil biology. *Soil Sci. Soc. Am. J.* 64:1651–1659.
- Carpenter-Boggs, L., J. P. Reganold, and A. C. Kennedy. 2000b. Effects of biodynamic preparations on compost development. *Biol. Agric. Hortic.* 17: 313–328.
- Cavigelli, M. A., G. P. Robertson, and M. J. Klug. 1995. Fatty acid methyl ester (FAME) profiles as measures of soil microbial community structure. In Collins, H. P., G. P. Robertson, and M. J. Klug (Eds.), *The Significance and Regulation of Soil Biodiversity*. Kluwer, Dordrecht, pp. 99–113.
- Chaloux, N., S. Libmond, and J.-M. Savoie. 1995. A practical enzymatic method to estimate wheat straw quality as raw material for mushroom cultivation. *Bioresour. Technol.* 53:277–281.
- Chang, I. P., and T. Kommendahl. 1968. Biological control of seedling blight of corn by coating kernels with antagonistic microorganisms. *Phytopathology* 58: 1395–1401.
- Chanway, C. P., and F. B. Holl. 1993. First year field performance of spruce seedlings inoculated with plant growth promoting rhizobacteria. *Can. J. Microbiol.* 39:1084–1088.
- Christensen, M. 1989. A view of fungal ecology. *Mycologia* 81:1–19.
- Cid, M. S., and M. A. Brizuela. 1998. Heterogeneity in tall fescue pastures created and sustained by cattle grazing. *J. Range Manage.* 51:644–649.
- Cook, R. J. 1981. The influence of rotation crops on take-all decline phenomena. *Phytopathology* 71:189–192.
- Cook, R. J. 1986. Plant health and the sustainability of agriculture, with special reference to disease control by beneficial microorganisms. *Biol. Agric. Hortic.* 3:211–232.
- Cook, R. J. 1987. Research Briefing Panel on Biological Control in Managed Ecosystems. Committee on Science, Engineering, and Public Policy, National Academy of Sciences, National Academy of Engineering and Institute of Medicine. National Academy Press, Washington, D.C., 12 pp.
- Cook, R. J., and K. F. Baker. 1983. *The Nature and Practice of Biological Control of Plant Pathogens*. American Phytopathological Society, St. Paul, MN, 539 pp.
- Cook, R. J., and W. A. Haglund. 1991. Wheat yield depression associated with conservation tillage caused by root pathogens in the soil not phytotoxins from the straw. *Soil Biol. Biochem.* 23:1125–1132.
- Cookson, W. R., M. H. Beare, and P. E. Wilson. 1998. Effects of prior crop residue management on microbial properties and crop residue decomposition. *Appl. Soil Ecol.* 7:179–188.
- Cross, J. V., and D. R. Polonenko. 1996. An industry perspective on registration and commercialization of biocontrol agents in Canada. *Can. J. Plant Pathol.* 18:446–454.
- Crowell, H. F., and R. E. Boerner. 1988. Influences of mycorrhizae and phosphorus on belowground competition between two old-field annuals. *Environ. Exp. Bot.* 28:381–392.
- Curl, E., and B. Truelove. 1986. *The Rhizosphere*. Springer-Verlag, Berlin, 288 pp.
- Curtin, D., F. Selles, H. Wang, C. A. Campbell, and V. O. Biederbeck. 1998. Carbon dioxide emissions and transformation of soil carbon and nitrogen during wheat straw decomposition. *Soil Sci. Soc. Am. J.* 62:1035–1041.
- Curtin, D., H. Wang, F. Selles, B. G. McConkey, and C. A. Campbell. 2000. Tillage effects on carbon fluxes in continuous wheat and fallow-wheat rotations. *Soil Sci. Soc. Am. J.* 64:2080–2086.
- Dalal, R. C., P. A. Henderson, and J. M. Glasby. 1991. Organic matter and microbial biomass in a Vertisol after 20 yr. of zero-tillage. *Soil Biol. Biochem.* 23:435–451.
- Daly, M. J., and D. P. C. Stewart. 1999. Influence of “effective microorganisms” (EM) on vegetable production and carbon mineralization: A preliminary investigation. *Am. J. Sust. Agric.* 14:15–25.
- De Leij, F. A. A. M., E. J. Sutton, J. M. Whipps, J. S. Fenlon, and J. M. Lynch. 1995. Impact of field release of genetically modified *Pseudomonas fluorescens* on indigenous microbial populations of wheat. *Appl. Environ. Microbiol.* 61:3443–3453.
- De Leij, F. A. A. M., J. M. Whipps, and J. M. Lynch. 1993. The use of colony development for the characterization of bacterial communities in soil and roots. *Microb. Ecol.* 27:81–97.

- DeBach, P. 1964. *Biological Control of Insects, Pests and Weeds*. Reinhold, New York, 844 pp.
- Degens, B. P. 1998. Decreases in microbial functional diversity do not result in corresponding changes in decomposition under different moisture conditions. *Soil Biol. Biochem.* 30:1989–2000.
- Degens, B. P. 1999. Catabolic response profiles differ between microorganisms grown in soils. *Soil Biol. Biochem.* 31: 475–477.
- Degens, B. P., and J. A. Harris. 1997. Development of physiological approach to measuring the catabolic diversity of soil microbial communities. *Soil Biol. Biochem.* 29:1309–1320.
- di Castri, F., and T. Younes. 1990. Ecosystem function of biological diversity. *Biol. Int.* 22 (Special Issue):1–20.
- DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts and management. *Weed Sci.* 48:255–265.
- Doran, J. W. 1980. Soil microbial and biochemical changes associated with reduced tillage. *Soil Sci. Soc. Am. J.* 44: 765–771.
- Doran, J. W., and T. B. Parkin. 1994. In Doran, J. W., D. C. Coleman, D. F. Bezdicek, and B. A. Stewart (Eds.), *Defining Soil Quality for a Sustainable Environment*. Special Publication No. 35, American Society of Agronomy, Madison, WI, pp. 1–45.
- Doran, J. W., M. Sarrantonio, and M. A. Liebig. 1996. Soil health and sustainability. In D.L. Sparks (Ed.), *Advances in Agronomy*. Academic Press, New York, pp. 1–54.
- Douds, D. D., Jr., L. Galvez, M. Franke-Snyder, C. Reider, and L. E. Drinkwater. 1997. Effect of compost addition and crop rotation point upon VAM fungi. *Agric. Ecosyst. Environ.* 65:257–266.
- Douds, D. D., Jr., L. Galvez, R. R. Janke, and P. Wagoner. 1995. Effect of tillage and farming system upon populations and distribution of vesicular-arbuscular mycorrhizal fungi. *Agric. Ecosyst. Environ.* 52:111–118.
- Drijber, R. A., J. W. Doran, A. M. Parkhurst, and D. J. Lyon. 2000. Changes in soil microbial community structure with tillage under long-term wheat-fallow management. *Soil Biol. Biochem.* 32:1419–1430.
- Drinkwater, L. E., P. Wagoner, and M. Sarrantonio. 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. *Nature* 396:262–265.
- Dubeikovskiy, A. N., E. A. Mordukhova, V. V. Kochetkov, F. Y. Polikarpova, and A. M. Boronin. 1993. Growth promotion of blackcurrant softwood cuttings by recombinant strain *Pseudomonas fluorescens* BSP53a synthesizing an increased amount of indole-3-acetic-acid. *Soil Biol. Biochem.* 25:1277–1281.
- Duineveld, B. M., A. S. Rosado, J. D. vanElsas, and J. A. vanVeen. 1998. Analysis of the dynamics of bacterial communities in the rhizosphere of the chrysanthemum via denaturing gradient gel electrophoresis and substrate utilization patterns. *Appl. Environ. Microbiol.* 64:4950–4957.
- Edwards, S. G., J. Peter, W. Young, and A. H. Fitter. 1998. Interactions between *Pseudomonas fluorescens* biocontrol agents and *Glomus mosseae*, an arbuscular mycorrhizal fungus, within the rhizosphere. *FEMS Microbiol. Lett.* 166:297–303.
- El Nashaar, H. M., and R. W. Stack. 1989. Effect of long-term continuous cropping of spring wheat on aggressiveness of *Cochliobolus sativus*. *Can. J. Plant Sci.* 69:395–400.
- Elliott, L. F., and J. M. Lynch. 1994. Biodiversity and soil resilience. In Greenland, D. J. and I. Szabolcs (Eds.), *Soil Resilience and Sustainable Land Use*. CAB International, Wallingford, U.K., pp. 353–364.
- Elliott, L. F., and R. I. Papendick. 1986. Crop residue management for improved soil productivity. *Biol. Agric. Hortic.* 3:131–142.
- Ellis, J. R., H. J. Larsen, and M. G. Boosalis. 1985. Drought resistance of wheat plants inoculated with vesicular-arbuscular mycorrhizae. *Plant Soil* 86:369–378.
- Emmimath, V. S., and G. Rangaswami. 1971. Studies of the effect of heavy doses of nitrogenous fertilizer on the soil and rhizosphere microflora of rice. *Mysore J. Agric. Sci.* 5:39–58.
- Ferreira, M. C., D. D. Andrade, L.M.D. Chueire, S. M. Takemura, and M. Hungria. 2000. Tillage method and crop rotation effects on the population sizes and diversity of *Bradyrhizobia* nodulating soybean. *Soil Biol. Biochem.* 32:627–637.
- Fitter, A. H. 1977. Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. *New Phytol.* 79:119–125.
- FlieBach, A., and Mäder, P. 1997. Carbon source utilization by microbial communities in soils under organic and conventional farming practice. In Insam, H. and A. Rangger (Eds.), *Microbial Communities — Functional versus Structural Approaches*. Springer-Verlag, Berlin, pp. 109–120.
- Foissner, W. 1999. Soil protozoa as bioindicators: Pros and cons, methods, diversity, representative examples. *Agric. Ecosyst. Environ.* 74:95–112.

- Follett, R. F., and D. S. Schimel. 1989. Effect of tillage practices on microbial dynamics. *Soil Sci. Soc. Am. J.* 53:1091–1096.
- Frankenberger, W. T., Jr., and M. Arshad. 1995. *Phytohormones in Soils: Microbial Production and Function*. Marcel Dekker, New York, 503 pp.
- Franzluebbers, A. J., F. M. Hons, and D. A. Zuberer. 1994. Seasonal changes in soil microbial biomass and mineralizable C and N in wheat management systems. *Soil Biol. Biochem.* 26:1467–1475.
- Gagliardi, J. V., J. S. Buyer, J. S. Angle, and E. Russek-Cohen. 2001. Structural and functional analysis of whole-soil microbial communities for risk and efficacy testing following microbial inoculation of wheat roots in diverse soils. *Soil Biol. Biochem.* 33:25–40.
- Gale, W. J., and C. A. Cambardella. 2000. Carbon dynamics of surface residue- and root-derived organic matter under simulated no-till. *Soil Sci. Soc. Am. J.* 64:190–195.
- Galvez, L., D. D. Douds, Jr., P. Wagoner, L. R. Longnecker, L. E. Drinkwater, and R. R. Janke. 1995. An overwintering cover crop increases inoculum of VAM fungi in agricultural soil. *Am. J. Altern. Agric.* 10:152–156.
- Garland, J. L. 1996. Patterns of potential C source utilization by rhizosphere communities. *Soil Biol. Biochem.* 28:223–230.
- Gilbert, G. S., J. L. Parke, M. K. Clayton, and J. Handelsman. 1993. Effects of an introduced bacterium on bacterial communities on roots. *Ecology* 74:840–854.
- Giller, K. E., M. H. Beare, P. Lavelle, A. N. Izac, and M. J. Swift. 1997. Agricultural intensification, soil biodiversity and agroecosystem function. *Appl. Soil Ecol.* 6:3–16.
- Glick, B. R. 1995. The enhancement of plant growth by free-living bacteria. *Can. J. Microbiol.* 41:109–117.
- Goldstein, W. Q. 1986. Alternative crops, rotations and management systems for the Palouse. Ph.D. Dissertation, Washington State University, Pullman, WA (Dissertation Abstract 87–11988).
- Goodlass, G., and K. A. Smith. 1978. Effects of organic amendments on evolution of ethylene and other hydrocarbons from soil. *Soil Biol. Biochem.* 10:201–205.
- Grayston, S. J., S. Wang, C. D. Campbell, and A. C. Edwards. 1998. Selective influence of plant species on microbial diversity in the rhizosphere. *Soil Biol. Biochem.* 30:369–378.
- Griffiths, B. S., K. Ritz, R. D. Bardgett, R. Cook, S. Christensen, F. Ekelund, S. Sorensen, E. Bååth, J. Bloem, P. C. de Ruiter, J. Dolfing, and B. Nicolardot. 2000. Ecosystem response of pasture soil communities to fumigation-induced microbial diversity reductions: An examination of the biodiversity-ecosystem function relationship. *Oikos* 90:279–294.
- Griffiths, B. S., K. Ritz, N. Ebbelwhite, and G. Dobson. 1999. Soil microbial community structure: Effects of substrate loading rates. *Soil Biol. Biochem.* 31:145–153.
- Griffiths, B. S., K. Ritz, and L. A. Glover. 1996. Broad-scale approaches to the determination of soil microbial community structure: Application of the community DNA hybridization technique. *Microb. Ecol.* 31:269–280.
- Grime, J. P. 1997. Biodiversity and ecosystem function: The debate deepens. *Science* 277:1260–1261.
- Gunapala, N., R. C. Venette, H. Ferris, and K. M. Scow. 1998. Effects of soil management history on the rate of organic matter decomposition. *Soil Biol. Biochem.* 30:1917–1927.
- Guschin, D. Y., B. K. Mobarry, D. Proudnikov, D. A. Stahl, B. Rittman, and A. D. Mirzabekov. 1997. Oligonucleotide microchips as genosensors for determinative and environmental studies in microbiology. *Appl. Environ. Microb.* 63:2397–2402.
- Haack, S. K., H. Garchow, M. J. Klug, and L. J. Forney. 1995. Analysis of factors affecting the accuracy, reproducibility, and interpretation of microbial community carbon source utilization patterns. *Appl. Environ. Microbiol.* 61:1458–1468.
- Hall, J. R. 1978. Effects of endomycorrhizas on the competitive ability of white clover. *N.Z. J. Agric. Res.* 21:509–515.
- Harris, P. A., H. H. Schomberg, P. A. Banks, and J. Giddens. 1995. Burning, tillage and herbicide effects on the soil microflora in a wheat-soybean double-crop system. *Soil Biol. Biochem.* 27:153–156.
- Hawksworth, D. L. 1991a. *The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture*. CAB International, Redwood Press, Melksham, U.K., 302 pp.
- Hawksworth, D. L. 1991b. The fungal dimension of biodiversity: Magnitude, significance, and conservation. *Mycol. Res.* 95:641–655.
- Henriksen, T. M., and T. A. Breland. 1999. Evaluation of criteria for describing crop residue degradability in a model of carbon and nitrogen turnover in soil. *Soil Biol. Biochem.* 31:1135–1149.

- Hetrick, B. A. D., and G. W. T. Wilson. 1989. Suppression of mycorrhizal fungus spore germination in non-sterile soil: Relationship to mycorrhizal growth response in big bluestem. *Mycologia* 81:382–390.
- Holben, W. E., and J. M. Tiedje. 1988. Applications of nucleic acid hybridization in microbial ecology. *Ecology* 69:561–568.
- Hussain, A., and A. Vancura. 1970. Formation of biologically active substances by rhizosphere bacteria and their effect on plant growth. *Folia Microbiologia* 19:468–478.
- Hu, S. J., A. H. C. van Bruggen, and N. J. Grünwald. 1999. Dynamics of bacterial populations in relation to carbon availability in a residue-amended soil. *Appl. Soil Ecol.* 13:21–30.
- Hu, S., and A. H. C. van Bruggen. 1997. Microbial dynamics associated with multiphasic decomposition of ¹⁴C labeled cellulose in soil. *Microb. Ecol.* 33:134–143.
- Janzen, R. A., S. B. Rood, J. F. Dormaar, and W. B. McGill. 1992. *Azospirillum brasilense* produces gibberellin in pure culture and on chemically defined medium in co-culture on straw. *Soil Biol. Biochem.* 24:1061–1064.
- Ibekwe, A. M., and A. C. Kennedy. 1998. Phospholipid fatty acid profiles and carbon utilization patterns for analysis of microbial community structure under field and greenhouse conditions. *FEMS Microbiol. Ecol.* 26:151–163.
- Ibekwe, A. M., and A. C. Kennedy. 1999. Fatty acid methyl ester (FAME) profiles as a tool to investigate community structure of two agricultural soils. *Plant Soil* 209:151–161.
- Johnson, N. C., P. J. Copeland, B. K. Crookston, and F. L. Pflieger. 1992. Mycorrhizae: Possible explanation for yield decline with continuous corn and soybean. *Agron. J.* 84:387–390.
- Karlen, D. L., N. S. Eash, and P. W. Unger. 1992. Soil and crop management effects on soil quality indicators. *Am. J. Altern. Agric.* 7:48–55.
- Karlen, D. L., N. C. Wollenhaupt, D. C. Erbach, E. C. Berry, J. B. Swan, N. S. Eash, and J. L. Jordahl. 1994. Crop residue effects on soil quality following 10 years of no-till corn. *Soil Tillage Res.* 31:149–167.
- Kennedy, A. C. 1998. The rhizosphere and spermosphere. In Sylvia, D. M., J. J. Fuhrman, R. G. Hartel, and D. A. Zuberer (Eds.), *Principles and Applications of Soil Microbiology*. Prentice-Hall, New York, pp. 389–407.
- Kennedy, A. C., and A. J. Busacca. 1995. Microbial analysis to identify source of PM-10 material. In *Proceedings of the Air and Waste Management Association Specialty Conference on Particulate Matter: Health and Regulatory Issues*. April 4–6, 1995, Pittsburgh, PA, pp. 670–675.
- Kennedy, A. C., L. F. Elliott, F. L. Young, and C. L. Douglas. 1991. Rhizobacteria suppressive to the weed downy brome. *Soil Sci. Soc. Am. J.* 55:722–727.
- Kennedy, A. C., A. G. Ogg, Jr., and F. L. Young. 1992. Biocontrol of jointed goatgrass. United States Patent 5,163,991, November 17, 1992.
- Kennedy, A. C., and R. I. Papendick. 1995. Microbial characteristics of soil quality. *J. Soil Water Conserv.* 50:243–248.
- Kennedy, A. C., and K. L. Smith. 1995. Soil microbial diversity and the sustainability of agricultural soils. *Plant Soil* 170:75–86.
- Kirchner, M. J., A. G. Wollum II, and L. D. King. 1993. Soil microbial populations and activities in reduced chemical input agroecosystems. *Soil Sci. Soc. Am. J.* 57:1289–1295.
- Kloepper, J. W., F. M. Scher, M. Laliberte, and B. Tipping. 1989. Free-living bacterial inocula for enhancing crop productivity. *Trends Biotechnol.* 7:39–43.
- Knowles, T. C., B. W. Hipp, P. S. Graff, and D. S. Marshall. 1993. Nitrogen nutrition of rainfed winter wheat in tilled and no-till sorghum and wheat residues. *Agron. J.* 85:886–893.
- Koepf, H. H., B. D. Petersson, and W. Schaumann. 1976. *Bio-Dynamic Agriculture: An Introduction*. Anthroposophic Press, Spring Valley, NY.
- Kolberg, R. L., D. G. Westfall, and G. A. Peterson. 1999. Influence of cropping intensity and nitrogen fertilizer rates on *in situ* nitrogen mineralization. *Soil Sci. Soc. Am. J.* 63:129–134.
- Kozdroj, J., and J. D. van Elsas. 2000. Response of the bacterial community to root exudates in soil polluted with heavy metals assessed by molecular and cultural approaches. *Soil Biol. Biochem.* 32:1405–1417.
- Krall, J. M., and G. E. Schuman. 2000. Integrated dryland crop and livestock production systems on the Great Plains: Extent and outlook. *J. Crop Prod.* 9:187–191.
- Kremer, R. J. 1987. Identity and properties of bacteria inhabiting seeds of selected broadleaf weed species. *Microb. Ecol.* 14:29–37.

- Miller, H. J., G. Henken, and J. A. VanVeen. 1989. Variation and composition of bacterial populations in the rhizospheres of maize, wheat, and grass cultivars. *Can. J. Microbiol.* 35:656–660.
- Mohammed, M. J., W. L. Pan, and A. C. Kennedy. 1995. Wheat responses to vesicular-arbuscular mycorrhizal fungal inoculation of soils from eroded toposequence. *Soil Sci. Soc. Am. J.* 59:1086–1090.
- Mohn, W. W., and G. R. Stewart. 2000. Limiting factors for hydrocarbon biodegradation at low temperature in Arctic soils. *Soil Biol. Biochem.* 32:1161–1172.
- Moore, J. C. 1994. Impact of agricultural practices on soil food web structure: Theory and application. *Agric. Ecosyst. Environ.* 51:239–247.
- Moore, J. M., S. Klose, and M. A. Tabatabai. 2000. Soil microbial biomass carbon and nitrogen as affected by cropping systems. *Biol. Fertil. Soils* 31:200–210.
- Murata, T., and K. M. Goh. 1997. Effects of cropping systems on soil organic matter in a pair of conventional and biodynamic mixed cropping farms in Canterbury, New Zealand. *Biol. Fertil. Soils* 25:372–381.
- Naseby, D. C., and J. M. Lynch. 1998. Establishment and impact of *Pseudomonas fluorescens* genetically modified for lactose utilization and kanamycin resistance in the rhizosphere of pea. *J. Appl. Microbiol.* 84:169–175.
- Neal, J. L., R. I. Larson, and T. G. Atkinson. 1973. Changes in rhizosphere populations of selected physiological groups of bacteria related to substitution of specific pairs of chromosomes in spring wheat. *Plant Soil* 39:209–212.
- Needelman, B. A., M. M. Wander, G. A. Bollero, C. W. Boast, G. K. Sims, and D. G. Bullock. 1999. Interaction of tillage and soil texture: biologically active soil organic matter in Illinois. *Soil Sci. Soc. Am. J.* 63:1326–1334.
- Newman, E. I., A. J. Heap, and R. A. Lawley. 1981. Abundance of mycorrhizas and root-surface microorganisms of *Plantago lanceolata* in relation to soil and vegetation: A multi-variate approach. *New Phytol.* 89:95–108.
- Ocampo, J. A. 1986. Vesicular-arbuscular mycorrhizal infection of “host” and “non-host” plants: Effect on the growth responses of the plants and the competition between them. *Soil Biol. Biochem.* 18: 607–610.
- Ohtonen, R., H. Fritze, T. Pennanen, A. Jumpponen, and J. Trappe. 1999. Ecosystem properties and microbial community changes in primary succession on a glacier forefront. *Oecologia* 119:239–246.
- Okon, Y. 1982. Azospirillum: Physiological properties, modes of association with roots and its application for the benefit of cereal and forage grass crops. *Isr. J. Bot.* 31:214–220.
- Oleskevich, C., S. F. Shamoun, R. F. Vesonder, and Z. K. Punja. 1998. Evaluation of *Fusarium avenaceum* and other fungi for potential as biological control agents of invasive *Rubus* species in British Columbia. *Can. J. Plant Pathol.* 20:12–18.
- Olsson, S., and B. Gerhardson. 1992. Effects of long-term barley monoculture on plant-affecting soil microbiota. *Plant Soil* 143:99–108.
- Opperman, M. H., M. Wood, and P. J. Harris. 1989. Changes in microbial populations following the application of cattle slurry to soil at two temperatures. *Soil Biol. Biochem.* 21:263–268.
- Papendick, R. I. 1996. Farming systems and conservation needs in the Northwest wheat region. *Am. J. Altern. Agric.* 11:52–57.
- Papendick, R. I., and G. S. Campbell. 1975. Water potential in the rhizosphere and plant and methods of measurement and experimental control. In Bruehl, G. W. (Ed.), *Biology and Control of Soil-Borne Pathogens*. American Phytopathological Society, St. Paul, MN, pp. 39–49.
- Parr, J. F., and R. I. Papendick. 1978. Factors affecting the decomposition of crop residues by microorganisms. In W. R. Oschwald (Ed.), *Crop Residue Management Systems*. Madison, WI. ASA Special Publication Number 31, American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America, pp. 101–129.
- Paul, E. A. 1984. Dynamics of organic matter in soils. *Plant Soil* 76:275–285.
- Penfold, C. M., M. S. Miyan, T. G. Reeves, and I. T. Grierson. 1995. Biological farming for sustainable agricultural production. *Aust. J. Exp. Agric.* 35:849–856.
- Pinton, R., Z. Varanini, and P. Nannipieri. 2001. *The Rhizosphere*. Marcel Dekker, New York, p. 424.
- Price, W. P. 1988. An overview of organismal interactions in ecosystems in evolutionary and ecological time. *Agric. Ecosyst. Environ.* 2:369–377.
- Rasmussen, P., H. P. Collins, and R. W. Smiley. 1989. Long-term management effects on soil productivity and crop yields in semi-arid regions of eastern Oregon. Oregon State University Bulletin 675, Corvallis, OR.

- Kremer, R. J., and A. C. Kennedy. 1996. Rhizobacteria as biocontrol agents of weeds. *Weed Technol.* 10:601–609.
- Lal, R., R. F. Follett, J. Kimble, and C. V. Cole. 1999. Managing U.S. cropland to sequester carbon in soil. *J. Soil Water Conserv.* 54:374–381.
- Liljeroth, E., and E. Bååth. 1988. Bacteria and fungi on roots of different barley varieties (*Hordeum vulgare* L.). *Biol. Fertil. Soils* 7:53–57.
- Liljeroth, E., J. A. VanVeen, and H. J. Miller. 1990. Assimilate translocation to the rhizosphere of two wheat lines and subsequent utilization by rhizosphere microorganisms at two soil nitrogen concentrations. *Soil Biol. Biochem.* 22:1015–1021.
- Liu, X., W. C. Lindemann, W. G. Whitford, and R. L. Steiner. 2000. Microbial diversity and activity of disturbed soil in the northern Chihuahuan Desert. *Biol. Fertil. Soils* 32:243–249.
- Loper, J. E., and M. N. Schroth. 1986. Influence of bacterial sources of indole-3-acetic acid on root elongation of sugar beet. *Phytopathology* 76:386–389.
- Lottmann, J., H. Heuer, J. de Vries, A. Mahn, K. Doring, W. Wackernagel, K. Smalla, and G. Berg. 2000. Establishment of introduced antagonistic bacteria in the rhizosphere of transgenic potatoes and their effect on the bacterial community. *FEMS Microbiol. Ecol.* 33:41–49.
- Lovett, J. V., and A. H. C. Hoult. 1995. Allelopathy and self-defense in barley. In Inderjit, K. M., M. Dakshini, and F. A. Einhellig (Eds.), *Allelopathy: Organisms, Processes, and Applications*. American Chemical Society, Washington, D.C., pp. 170–183.
- Lundquist, E. J., K. M. Scow, L. E. Jackson, S. L. Uesugi, and C. R. Johnson. 1999. Rapid response of soil microbial communities from conventional, low input and organic farming systems to a wet/dry cycle. *Soil Biol. Biochem.* 31:1661–1675.
- Luo, Y., and D. O. TeBeest. 1999. Effect of temperature and dew period on infection of northern jointvetch by wild-type and mutant strains of *Colletotrichum gloeosporioides* f. sp. *aeschynomene*. *Biol. Control* 14:1–6.
- Lynch, J. M. 1983. *Soil Biotechnology: Microbiological Factors in Crop Productivity*. Blackwell Scientific Publications, Oxford, 191 pp.
- Lynch, J. M., and S. H. T. Harper. 1980. Role of substrates and anoxia in the accumulation of soil ethylene. *Soil. Biol. Biochem.* 12:363–368.
- Lyons, J., S. W. Trimble, and L. K. Paine. 2000. Grass versus trees: Managing riparian areas to benefit streams of central North America. *J. Am. Water Resour. Assoc.* 36:919–930.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, 203 pp.
- Mader, P., S. Edenhoffer, T. Boller, A. Wiemken, and U. Niggli. 2000. Arbuscular mycorrhizae in a long-term field trial comparing low-input (organic, biological) and high-input (conventional) farming systems in a crop rotation. *Biol. Fertil. Soils* 31:150–156.
- Maloney, P. E., A. H. C. van Bruggen, and S. Hu. 1997. Bacterial community structure in relation to the carbon environments in lettuce and tomato rhizospheres and in bulk soil. *Microb. Ecol.* 34:109–117.
- Martin, J. K. 1977. Effect of soil moisture on the release of organic carbon from wheat roots. *Soil Biol. Biochem.* 9:303–304.
- Martin, J. K., and J. R. Kemp. 1980. Carbon loss from roots of wheat cultivars. *Soil Biol. Biochem.* 12:551–554.
- Martin, T. L. 1933. Influence of chemical composition of organic matter on rate of decomposition. *J. Am. Soc. Agron.* 25:341–346.
- Mazzola, M., D. K. Fujimoto, L. S. Thomashow, and R. J. Cook. 1995. Variation in sensitivity of *Gaeumannomyces graminis* to antibiotics produced by fluorescent *Pseudomonas* spp., and effect on biological control of take-all of wheat. *Appl. Environ. Microbiol.* 61:2554–2559.
- McCallister, D. L., and W. L. Chien. 2000. Organic carbon quantity and forms as influenced by tillage and cropping sequence. *Commun. Soil Sci. Plant Anal.* 31:465–479.
- McSpadden-Gardener, B. B., and D. M. Weller. 2001. Changes in populations of rhizosphere bacteria associated with take-all disease of wheat. *Appl. Environ. Microbiol.* 67: 4414–4425.
- McGonigle, T. P., and A. H. Fitter. 1990. Ecological specificity of vesicular-arbuscular mycorrhizal associations. *Mycol. Res.* 94:120–122.
- Mikola, J., and H. Setälä. 1998. Relating species diversity to ecosystem functioning: Mechanistic backgrounds and experimental approach with a decomposer food web. *Oikos* 83:180–194.

- Reganold, J. P., A. S. Palmer, J. C. Lockhart, and A. N. Macgregor. 1993. Soil quality and financial performance of biodynamic and conventional farms in New Zealand. *Science* 260:344–349.
- Reicosky, D. C., and M. J. Lindstrom. 1993. Fall tillage method: Effect on short-term carbon dioxide flux from soil. *Agron. J.* 85:1237–1243.
- Rhoton, F. E. 2000. Influence of time on soil response to no-till practices. *Soil Sci. Soc. Am. J.* 64:700–709.
- Rhykerd, R. L., B. Crews, K. J. McInnes, and R. W. Weaver. 1999. Impact of bulking agents, forced aeration, and tillage on remediation of oil-contaminated soil. *Bioresour. Technol.* 67:279–285.
- Rice, E. L. 1995. *Biological Control of Weeds and Plant Diseases: Advances in Applied Allelopathy*. University of Oklahoma Press, Norman, OK, 439 pp.
- Rouatt, J. W., and H. Katznelson. 1961. A study of the bacteria on the root surface and in the rhizosphere soil of crop plants. *J. Appl. Bacteriol.* 24:164–171.
- Rovira, A. D. 1956. Plant root excretions in relation to the rhizosphere effect: I. The nature of root exudates from oats and peas. *Plant Soil* 7: 178–194.
- Rovira, A. D. 1959. Root excretions in relation to the rhizosphere effect. IV. Influence of plant species, age of plant, light, temperature, and calcium nutrition on exudation. *Plant Soil* 11:53–64.
- Rovira, A. D. 1978. Microbiology of pasture soils and some effects of microorganisms on pasture plants. In Wilson, J. R. (Ed.), *Plant Relations in Pastures*. CSIRO, East Melbourne, Australia, pp. 95–110.
- Salonius, P. O. 1981. Metabolic capabilities of forest soil microbial populations with reduced species diversity. *Soil Biol. Biochem.* 13:1–10.
- Sandaa, R.-A., V. Torsvik, and O. Enger. 2001. Influence of long-term heavy-metal contamination on microbial communities in soil. *Soil Biol. Biochem.* 33:287–295.
- Sarathchandra, S.U., G. Burch, and N. R. Cox. 1997. Growth patterns of bacterial communities in the rhizoplane and rhizosphere in white clover (*Trifolium repens* L.) and perennial ryegrass (*Lolium perenne* L.) in long-term pasture. *Appl. Soil Ecol.* 6:293–299.
- Sarwar, M., and W. T. Frankenberger, Jr. 1994. Influence of L-tryptophan and auxins applied to the rhizosphere on the vegetative growth of *Zea mays* L. *Plant Soil* 160:97–104.
- Sarwar, M., and R. J. Kremer. 1995. Enhanced suppression of plant growth through the production of L-tryptophan derived compounds by deleterious rhizobacteria. *Plant Soil* 172:261–269.
- Schippers, B., A. W. Bakker, and P. A. Bakker. 1987. Interactions of deleterious and beneficial rhizosphere microorganisms and the effect of cropping practices. *Annu. Rev. Phytopathol.* 25:339–358.
- Shipton, P.J. 1977. Monoculture and soilborne plant pathogens. *Annu. Rev. Phytopathol.* 15:387–407.
- Simard, R. R., D. A. Angers, and C. Lapierre. 1994. Soil organic matter quality as influenced by tillage, lime, and phosphorus. *Biol. Fertil. Soils* 18:13–18.
- Southern, N., and S. Cattle. 2000. Monitoring soil quality for central tablelands grazing systems. *Commun. Soil Sci. Plant Anal.* 31:2211–2229.
- Sprent, J. L. 1979. *The Biology of Nitrogen-Fixing Organisms*. McGraw-Hill, London.
- Stroo, H. F., K. L. Bristow, L. F. Elliott, R. I. Papendick, and G. S. Campbell. 1989. Predicting rates of wheat residue decomposition. *Soil Sci. Soc. Am. J.* 53:91–99.
- Suslow T. V., and M. N. Schroth. 1982. Role of deleterious rhizosphere bacteria as minor pathogens in reducing crop growth. *Phytopathology* 72:111–115.
- Swift, M. J., and L. Boddy. 1984. Animal-microbial interactions in wood decomposition. In Anderson, J. M., A. D. M. Rayner, and W. H. Walton (Eds.), *Invertebrate-Microbial Interactions*. Cambridge University Press, Cambridge, U.K. pp. 89–131.
- Swift, M. J., O. Andren, L. Brussaard, M. Briones, M. M. Couteaux, K. Ekschmitt, A. Kjoller, P. Loiseau, and P. Smith. 1998. Global change, soil biodiversity, and nitrogen cycling in terrestrial ecosystems: three case studies. *Glob. Change Biol.* 4:729–743.
- Swinnen, J., J. A. Van Veen, and R. Merckx. 1995. Root decay and turnover of rhizodeposits in field-grown winter wheat and spring barley estimated by ¹⁴C pulse-labelling. *Soil Biol. Biochem.* 27:211–217.
- Sylvia, D. M. 1998. Mycorrhizal symbioses. In Sylvia, D. M., J. J. Fuhrman, R. G. Hartel, and D. A. Zuberer (Eds.), *Principles and Applications of Soil Microbiology*. Prentice-Hall, New York, pp. 408–426.
- TeBeest, D. O., 1991. *Microbial Control of Weeds*. Chapman and Hall, New York, 284 pp.
- Thomas, V. G., and P. G. Kevan. 1993. Basic principles of agroecology and sustainable agriculture. *J. Agric. Environ. Ethics* 5:1–18.
- Thomashow, L. S., and D. M. Weller. 1988. Role of a phenazine antibiotic from *Pseudomonas fluorescens* in biological control of *Gaeumannomyces graminis* var. *tritici*. *J. Bacteriol.* 170:3499–3508.

- Thompson, C. A., and D. A. Whitney. 2000. Effects of 30 years of cropping and tillage systems on surface soil test changes. *Commun. Soil Sci. Plant Anal.* 31:241–257.
- Tinker, P. B. 1976. Roots and water. Transport of water to plant roots in soil. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 273:445–461.
- Torsvik, V., J. Goksoyr, and F. L. Daae. 1990. High diversity in DNA of soil bacteria. *Appl. Environ. Microbiol.* 56:782–787.
- Turkington, R., F. B. Holl, C. P. Chanway, and J. D. Thompson. 1988. The influence of microorganisms, particularly *Rhizobium*, on plant competition in grass-legume communities. *Symp. Brit. Ecol. Soc.* 28:343–366.
- Turkington, R., and E. Klein. 1991. Competitive outcome among four pasture species in sterilized and unsterilized soils. *Soil Biol. Biochem.* 23:837–843.
- USDA-FSA. 2000. The conservation reserve program 20th signup. U.S. Department of Agriculture, Farm Service Agency, Washington, D.C.
- Van der Putten, W. H., and B. A. M. Peters. 1997. How soil-borne pathogens may affect plant competition. *Ecology* 78:1785–1795.
- Vancura, V. 1967. Root exudates of plants: III. Effects of temperature and “cold shock” on the exudation of various compounds from seeds and seedlings of maize and cucumber. *Plant Soil* 27:319–328.
- Wagner, G. H., and D. C. Wolf. 1998. Carbon transformations and soil organic matter formation. pp. 218–258. In Sylvia, D. M., J. J. Fuhrman, R. G. Hartel, and D. A. Zuberer (Eds.), *Principles and Applications of Soil Microbiology*. Prentice-Hall, New York.
- Wander, M. M., S. J. Traina, B. R. Stinner, and S. E. Peters. 1994. Organic and conventional management effects on biologically active soil organic matter pools. *Soil Sci. Soc. Am. J.* 58:1130–1139.
- Ward, D., M. Bateson, R. Weller, and A. Ruff-Roberts. 1992. Ribosomal RNA analysis of microorganisms as they occur in nature. *Adv. Microb. Ecol.* 12:219–286.
- Wardle, D. A., G. W. Yeates, K. S. Nicholson, K. I. Bonner, and R. N. Watson. 1999. Response of soil microbial biomass dynamics, activity and plant litter decomposition to agricultural intensification over a seven-year period. *Soil Biol. Biochem.* 31:1707–1720.
- Wardle, D. A., O. Zachrisson, G. Hornberg, and C. Gallet. 1997. The influence of island area on ecosystem properties. *Science* 277:1296–1299.
- Wedin, D. A., and D. Tilman. 1990. Special effects of nitrogen cycling: A test with perennial grasses. *Oecologia* 84:433–441.
- Wenderoth, D. F., and H. H. Reber. 1999. Correlation between structural diversity and catabolic versatility of metal-affected prototrophic bacteria in soil. *Soil Biol. Biochem.* 31:345–352.
- Westover, K. M., A. C. Kennedy, and S. E. Kelley. 1997. Patterns of rhizosphere microbial community structure associated with co-occurring plant species. *J. Ecol.* 85:863–873.
- Whipps, J. M., and J. M. Lynch. 1986. The influence of rhizosphere on crop productivity. *Adv. Microb. Ecol.* 9:187–244.
- Wolters, V. 1997. *Functional Implications of Biodiversity in Soil*. Office for Official Publications of the European Communities, Luxembourg.
- Woltz, S. S. 1978. Nonparasitic plant pathogens. *Annu. Rev. Phytopathol.* 16:403–430.
- Workneh, F., and A. H. C. van Bruggen. 1995. Bacterial density, composition and diversity in organically and conventionally managed rhizosphere soil in relation to suppression of corky root of tomatoes. *Appl. Soil Ecol.* 1:219–230.
- Wood, M. 1991. Biological aspects of soil protection. *Soil Use Manage.* 7:130–136.
- Wright, S. F., and A. Upadhyaya. 1998. A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. *Plant Soil* 198:97–107.
- Wunsche, L., L. Bruggemann, and W. Babel. 1995. Determination of substrate utilization patterns of soil microbial communities: An approach to assess population changes after hydrocarbon pollution. *FEMS Microbiol. Ecol.* 17:295–306.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment. The insurance hypothesis. *Proc. Natl. Acad. Sci. USA* 96:1463–1468.
- Zak, J. C. 1992. Response of soil fungal communities to disturbance. In G. C. Carroll and D. T. Wicklow (Eds.), *The Fungal Community: Its Organization and Role in the Ecosystem*. Marcel Dekker, New York, pp. 403–426.

- Zak, J. C., M. R. Willig, D. L. Moorhead, and H. G. Wildman. 1994. Functional diversity of microbial communities: A quantitative approach. *Soil Biol. Biochem.* 26:1101–1108.
- Zelles, L., Q. Y. Gai, R. X. Ma, R. Rackwitz, K. Winter, and F. Beese. 1994. Microbial biomass, metabolic activity and nutritional status determined from fatty acid patterns and poly-hydroxybutyrate in agriculturally managed soils. *Soil Biol. Biochem.* 26:439–446.
- Zhang, W., and A. K. Watson. 1997. Efficacy of *Exserohilum monoceras* for the control of *Echinochloa* species in rice (*Oryza sativa*). *Weed Sci.* 45:144–150.

SOIL ORGANIC MATTER
IN
SUSTAINABLE AGRICULTURE

Edited by
Fred Magdoff
Ray R. Weil



CRC PRESS

Boca Raton London New York Washington, D.C.

Library of Congress Cataloging-in-Publication Data

Soil organic matter in sustainable agriculture / edited by Fred Magdoff and
Ray R. Weil.

p. cm. -- (Advances in agroecology)

Includes bibliographical references and index.

ISBN 0-8493-1294-9 (alk. paper)

1. Humus. 2. Soil ecology. 3. Sustainable agriculture. I. Magdoff, Fred, 1942- II. Weil,
Ray R. III. Series

S592.8.S674 2004

631.4'17--dc22

2004043574

This book contains information obtained from authentic and highly regarded sources. Reprinted material is quoted with permission, and sources are indicated. A wide variety of references are listed. Reasonable efforts have been made to publish reliable data and information, but the authors and the publisher cannot assume responsibility for the validity of all materials or for the consequences of their use.

Neither this book nor any part may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, microfilming, and recording, or by any information storage or retrieval system, without prior permission in writing from the publisher.

All rights reserved. Authorization to photocopy items for internal or personal use, or the personal or internal use of specific clients, may be granted by CRC Press LLC, provided that \$1.50 per page photocopied is paid directly to Copyright Clearance Center, 222 Rosewood Drive, Danvers, MA 01923 U.S.A. The fee code for users of the Transactional Reporting Service is ISBN 0-8493-1294-9/04/\$0.00+\$1.50. The fee is subject to change without notice. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

The consent of CRC Press LLC does not extend to copying for general distribution, for promotion, for creating new works, or for resale. Specific permission must be obtained in writing from CRC Press LLC for such copying.

Direct all inquiries to CRC Press LLC, 2000 N.W. Corporate Blvd., Boca Raton, Florida 33431.

Trademark Notice: Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation, without intent to infringe.

Visit the CRC Press Web site at www.crcpress.com

© 2004 by CRC Press LLC

No claim to original U.S. Government works

International Standard Book Number 0-8493-1294-9

Library of Congress Card Number 2004043574

Printed in the United States of America 1 2 3 4 5 6 7 8 9 0

Printed on acid-free paper