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# **Biological Approaches to Sustainable Soil Systems**

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## *The Soil Habitat and Soil Ecology*

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### CONTENTS

5.1	The Soil as Habitat for Microorganisms .....	60
5.1.1	Differences Among Soil Horizons .....	60
5.1.2	Factors in Soil Genesis .....	61
5.1.3	Physical Components of Soil Systems .....	61
5.1.4	Physical Properties and Their Implications for Soil Biology .....	62
5.1.5	Influence of Soil Chemical Properties .....	63
5.1.6	Adaptations to Stress .....	64
5.1.7	Build It and They Will Come.....	65
5.2	Classifying Organisms Within the Soil Food Web .....	65
5.2.1	The Soil Food Web as a System.....	65
5.2.2	Energy and Carbon as Key Limiting Factors.....	67
5.3	Primary Producers.....	68
5.3.1	Energy Capture in Plants Drives the Soil Community .....	68
5.3.2	Roots .....	69
5.3.3	The Rhizosphere .....	70
5.4	Consumers .....	72
5.4.1	Decomposers, Herbivores, Parasites, and Pathogens.....	72
5.4.2	Organic Matter Decomposition.....	73
5.4.3	Grazers, Shredders, and Predators.....	74
5.4.4	They All Interact Together .....	75
5.5	Biological Diversity and Soil Fertility .....	76
5.6	Discussion .....	76
	References .....	77

This chapter reviews the key functions of soil biota and their roles in maintaining soil fertility. We consider the soil as a habitat for organisms, identifying important sources of energy and nutrients for the soil biota and describing the flow of energy and cycling of materials from above to below ground. A more detailed discussion of energy flows follows in the next chapter. The trophic structure of the soil community, i.e., the organized flow of nutrients within it, and the various interactions among organisms comprising the soil food web are considered here. Linkages between above- and below ground processes are highlighted to illustrate their interconnectedness and to show

that soil is not an inert medium, but rather hosts a wide variety of organisms that collectively perform essential ecosystem services.

The functioning of soil systems involves many interactions among plant roots and plant residues, various animals and their residues, a vast diversity of microorganisms, and the physical structure and chemical composition of the soil. To manage soil systems productively, we need to know what practices will help to improve the survival and functioning of beneficial soil organisms while deterring the activity of pathogenic organisms. This volume offers varied examples of how the biological functioning of soil systems can be enhanced to improve their fertility and sustainability.

Here, we present an integrated view of the soil as a fundamental component of terrestrial ecosystems, having a distinct though varying structure and an intricate set of biological relationships. This illustrates how soil organisms contribute to maintaining soil fertility and also how the fertility of soil systems can be improved by managing and enhancing biological interactions. The basic factors and dynamics of soil systems discussed here provide a foundation for understanding the chapters that follow. It is written so that readers not trained in soil science can gain ready access to the subject matter. Persons already familiar with soil science should appreciate the change in perspective that it offers on soil systems, putting living organisms and the organic matter they produce center-stage.

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## 5.1 The Soil as Habitat for Microorganisms

Soil is one of the more complex and highly variable habitats on earth. Any organisms that make their home in soil have had to devise multiple mechanisms to cope with variability in moisture, temperature, and chemical changes so as to survive, function, and replicate. Within a distance of <1 mm, conditions can vary from acid to base, from wet to dry, from aerobic to anaerobic, from reduced to oxidized, and from nutrient-rich to nutrient-poor. Along with spatial variability there is variability over time, so organisms living in soil must be able to adapt rapidly to different and changing conditions. Variations in the physical and chemical properties of the soil are thus important determinants of the presence and persistence of soil biota.

### 5.1.1 Differences Among Soil Horizons

A typical soil profile has both horizontal and vertical structure. At the base of any soil profile is underlying *bedrock*, or **parent material**, which is the type of geological formation upon which and with which the soil above has been formed. Overlying the bedrock is a *C horizon* that has developed directly from modifications of the underlying parent material. This *C horizon* remains the least weathered (changed) of the identifiable horizons, accumulating calcium (Ca) and magnesium (Mg) carbonates released from horizons above. Microbial activity in this *C horizon* is typically very low, in part because of limitations in oxygen (O<sub>2</sub>) and organic matter.

Overlying the *C horizon* is the **subsoil**, or *B horizon*. This is composed of minerals derived from the parent material and of materials that have leached down from the horizons above, including humic materials formed above from the decomposition of organic (plant and animal) matter. Yet, because the *B horizon* is typically still rather low in organic matter, it supports relatively small microbial populations and has little biological activity. The *B horizon* is the zone of maximum illuviation, i.e., deposition or accumulation of silicate clays and of iron (Fe) and aluminum (Al) oxides.

The *A horizon*, denoting the upper layers of soil, is usually fairly high in organic matter and often darker in color. This, along with the *O (organic) horizon*, is the horizon in which plant roots and soil organisms are most active. Within the A horizon there are differing extents of leaching and movement of materials from the horizon above to the horizons below. The interface between the A and B horizons is the zone of maximum eluviation, i.e., removal through downward leaching of silicate clays and Fe and Al oxides. The interface between the A horizon and the O horizon above it is where incoming organic residues become incorporated with the mineral soil. Together with incorporated soil organic matter (SOM), the A horizon is often referred to as the **topsoil**.

The O horizon on the surface is the topmost layer, often referred to as the **litter layer**. The largest component of this layer is undecomposed organic matter (OM), and the origins of these organic materials are easy to distinguish — plant litter, manure, or other organic inputs.

### 5.1.2 Factors in Soil Genesis

In 1941, Hans Jenny (1941) proposed the following soil-forming factors that are still used today:

1. The parent material or underlying geological formation of the region;
2. The climate, referring largely to the temperature and precipitation in the region and to their interaction, which affects soil formation through freezing and thawing cycles;
3. The topography, denoting where soil is located within the landscape, at the top, middle, or bottom of a slope, which has dramatic effects on the outcome of soil formation;
4. Organisms, such as the dominant plant community and associated soil organisms that influence soil formation strongly by depositing OM and aggregating soil minerals; and
5. Time that has passed since the bedrock was laid down in relation to all of the other factors.

These factors combined explain the complex mix of characteristics that differentiate soil types. That soil types can vary considerably over short ranges illustrates the important role of the biota in soil formation because the other factors vary at larger scales both spatially and temporally.

### 5.1.3 Physical Components of Soil Systems

A typical soil is composed of both a mineral fraction and an organic fraction. These two fractions make up the soil solids, with the remaining soil volume composed of pore space, which at any given time is filled with some combination of air and/or water. When soil is saturated with water, all of the air in its pore spaces will have been displaced; conversely, desiccated soil has only air in the spaces between its soil solids.

The SOM content, the nature of the mineral fraction, and the relative proportions of air and water are critical factors affecting microbial activity and function. Soils with their pore space dominated by water are anaerobic. This condition will limit microbial activity to that of anaerobes and facultative anaerobes, i.e., organisms capable of metabolism in the absence of oxygen ( $O_2$ ). The anaerobic process of fermentation is energetically less efficient than aerobic metabolism (Fuhrmann, 2005), and its end-products are generally organic

acids and alcohols, which can be toxic to plants and many microbes. Hence, a soil with much of its pore space occupied by water much of the time will be a less productive soil, even though water is one of plants' critical needs.

A balance, where about half of the soil's pore space is occupied by air and half by water, is more supportive of both plant growth and microbial metabolism. Roots require O<sub>2</sub> in order to respire, and aerobes (microorganisms capable of aerobic respiration) can derive vastly more energy from this process than can be derived through fermentation or anaerobic respiration.

The nature of the mineral fraction determines the soil texture, content, and concentration of mineral elements as well as the presence of heavy metals, which can have some undesirable effects on plant and/or animal life. Phosphorus (P), potassium (K), and magnesium (Mg) are essential plant macronutrients derived from the soil mineral fraction. Hence, the productive capacity of any soil is very dependent on the composition of its mineral fraction (Brady and Weil, 2002).

#### **5.1.4 Physical Properties and Their Implications for Soil Biology**

Other important soil physical properties include texture, bulk density, temperature, aggregation, and structure. Each has important effects on the composition and activity of soil biota.

Texture, which refers to the proportions of sand, silt, and clay in any given soil, will strongly affect the soil's water-holding capacity and its cation- and anion-exchange capacities. The ability of soil to retain water is important because microbes depend on soil water as a solvent for cell constituents and as a medium through which dissolved nutrients can move to their cell surface. Also, water is needed to facilitate the movement of flagellated bacteria, ciliated and flagellated protozoa, and nematodes. Texture thus directly influences biological activity in soil.

Bulk density refers to the weight of soil solids per unit volume of soil. Soils with a bulk density  $< 1 \text{ g cm}^{-3}$  are lighter or loose soils, likely to have good aeration and easy for roots to penetrate and for microbes to navigate. Soils with a bulk density  $> 1 \text{ g cm}^{-3}$  are considered as increasingly heavier or compacted soils. As bulk density increases, soil porosity decreases, and air and water flows become restricted. This impedes soil drainage and root penetration. Such soils are often prone to waterlogging, creating anaerobic conditions.

Temperature will have varying effects on microbial activity depending on the respective organisms' range of tolerance. Psychrophilic organisms thrive in cold soil, at temperatures  $< 10^\circ\text{C}$ ; mesophiles have their greatest rates of activity at temperatures between  $10\text{--}30^\circ\text{C}$ ; while thermophiles are more active at temperatures in excess of  $40^\circ\text{C}$ . Soils in temperate regions experience prolonged periods annually at each of these temperature optima. This leads to marked seasonal shifts in microbial community composition throughout the year and to concomitant changes in the rates of SOM turnover and in the amounts of microbial biomass. Microbial communities in tropical soils also vary seasonally, but this is less determined by temperature.

Soil aggregation is the result of many interacting factors. In their model of soil aggregation, Tisdall and Oades (1982) described the process of aggregation as beginning with the interaction of clay platelets with one another at a scale of  $0.2 \mu\text{m}$ . Microbial colonization of soil particles comes into play at a scale of  $2 \mu\text{m}$ , an order of magnitude greater where bacterial and fungal metabolites serve to glue clay particles together. At a scale of  $20 \mu\text{m}$ , fungal hyphal filaments and various polysaccharides produced by bacteria become the dominant aggregating factors. Then at a  $200\text{-}\mu\text{m}$  scale, roots, and fungal hyphae bind these particles together. The resulting soil is a matrix of mineral particles

bound together by biological materials at various nested scales to form macroaggregates at the 2-mm scale.

Soil structure describes the extent of micro- and macroaggregation of a soil. A well-aggregated soil is more resistant to erosion from rain and wind. Also, it is generally well drained and more conducive for the growth of aerobic populations. It thus tends to be a more productive soil for plants and the soil biota. The process of aggregation as seen in the preceding discussion is the result of activities of plant roots and soil biota, creating intrinsic bonds between physical and biological characteristics of soil systems.

### 5.1.5 Influence of Soil Chemical Properties

Soil chemical properties strongly influence the activity of soil organisms, being at the same time themselves affected by such activity. The more important soil chemical properties affecting on biological activity are:

- pH, i.e., the acidity or alkalinity of a soil
- Cation- and anion-exchange capacity
- Mineral content and solubility
- Buffering capacity
- The concentration of nutrient elements in the soil
- The concentration of O<sub>2</sub>, carbon dioxide (CO<sub>2</sub>), nitrogen (N<sub>2</sub>), and other gases in the soil atmosphere
- Soil water content, and
- Salinity or sodicity.

Both plants and soil organisms have varying tolerances to extremes in soil pH. Most organisms prefer near-neutral pH values between 6 and 7.5. Many soil nutrients are most available for uptake by plant roots within this pH range. When soil is more acidic, the metal elements Fe, manganese (Mn), zinc (Zn), and copper (Cu) increase in solubility, while the solubility of most major nutrient elements — nitrogen (N), P, K, Ca, Mg, and sulfur (S) — decreases. The availability of N, K, S, and molybdenum (Mo) is unaffected at high pH; however, that of P, Ca, Mg, and boron (B) decreases above pH 8.0. In general, fungi and actinomycetes (bacteria that resemble fungi in their morphology and growth habits) appear to be relatively tolerant of both high and low pH, whereas many autotrophic and other heterotrophic bacteria are inhibited at low pH. Hence, in acidic soils, fungi and actinomycetes will tend to predominate. Organisms with greater limits of tolerance to changing abiotic conditions will have a competitive edge, which can affect the activity of others through substrate competition and thus inhibit their growth further.

Living organisms require a range of nutrient elements for their survival. Plants obtain their C (from CO<sub>2</sub>), hydrogen (H<sub>2</sub>) and oxygen (O<sub>2</sub>) from the atmosphere, while the remaining elements must be derived from the soil solution. For most soil microbes, the situation is somewhat different as they derive their energy and cell biomass C mainly from decomposing plant and animal residues and from SOM. Notable exceptions include the cyanobacteria and other photosynthetic bacteria that fix CO<sub>2</sub> directly into cell biomass C using light energy, and the chemolithotrophic bacteria that use the bond energy in reduced compounds, such as NH<sub>4</sub>, to generate reducing potential to fix CO<sub>2</sub> into cell biomass C chemosynthetically.

There are many pathways by which soil organisms obtain their energy, cell biomass C, and nutrients. Soil microbes obtain many of their other needed elements from the soil

solution or soil minerals, which they solubilize to acquire the necessary nutrients, or from the soil atmosphere. Nitrogen is a special case. Almost 80% of the atmosphere is made up of nitrogen ( $N_2$ ) gas. However, atmospheric  $N_2$  is not available to plants until it has been reduced, either industrially, atmospherically, or through the process of biological nitrogen fixation (BNF). Many bacteria and cyanobacteria have the ability to fix  $N_2$ , but the most well-known are the rhizobia that fix atmospheric nitrogen in symbiosis with host legumes (Fred et al., 1932; Giller, 2001). Nitrogen-fixing bacteria, such as *Azospirillum* and *Azotobacter*, also form endophytic or associative relationships within or in close association with plant roots (Boddy et al., 2003), and there are many free-living  $N_2$  fixing bacterial species as well (Dobbelaere et al., 2003). BNF is discussed in more detail in Chapter 12. Most soil fauna meet their energy, cell biomass C, and mineral nutrient requirements from consuming other organisms as either grazers or as predators.

The availability of mineral elements is not the only important aspect; so are the relative proportions or ratios of mineral elements in relation to an organism's needs. A soil may be high in P, Mg, Ca, and S, for example, but if nitrogen availability is low, then the growth of soil organisms will be limited by the lack of this element. This concept is known as Liebig's "Law of the Minimum," where the growth of any organism is restricted by whatever nutrient element is in the shortest supply in its environment relative to its needs (von Liebig, 1843; van der Ploeg, et al., 1999). This concept is important to bear in mind. No matter how much of a given mineral nutrient is added to a soil, this will not improve crop yield or microbial growth if this is not a factor that is limiting production (Thies et al., 1991).

### 5.1.6 Adaptations to Stress

Given the high spatial variability in soil properties, the microorganisms that live in soil must be capable of rapidly adapting to continually changing surroundings. Soil organisms respond to stress by varying their use of  $O_2$ , by forming resting structures, by increasing intracellular solute concentrations, by producing polyols and heat-shock proteins, and/or by altering membrane structure, to name a few of the possible mechanisms.

Microorganisms vary in their need for or tolerance of  $O_2$ . We referred above to the two major groups in terms of their functional relationship to  $O_2$ : aerobes and anaerobes. Aerobes are species capable of growing at the  $O_2$  concentration found in the atmosphere (21%), and they typically use  $O_2$  as a terminal electron acceptor in the respiratory electron transport chain. There are three main types of aerobes: obligate, facultative, and microaerophilic. Obligate aerobes require the presence of  $O_2$  for their survival; their type of metabolism is aerobic respiration. While facultative aerobes do not require  $O_2$ , they grow much better if  $O_2$  is present. These versatile bacteria have the capacity to respire either aerobically or anaerobically. Microaerophiles require  $O_2$ , but they can function at much lower levels than atmospheric concentrations. Their form of metabolism is aerobic respiration (Atlas and Bartha, 1998).

Anaerobes, on the other hand, do not or cannot use  $O_2$  as a terminal electron acceptor. There are two basic types of anaerobes: aerotolerant anaerobes and obligate anaerobes. The first do not use  $O_2$  for their metabolism, but they are not harmed by its presence. These organisms depend on a fermentative type of metabolism for their energy. Obligate or strict anaerobes, in contrast, are harmed by the presence of  $O_2$ . These organisms metabolize various substrates to derive energy either by fermentation or anaerobic respiration.

Facultative aerobes, microaerophiles, and aerotolerant anaerobes are better able to persist in the soil environment since they have the ability to adapt readily to the often rapid changes in  $O_2$  availability that invariably occur in the soil. The capacity of facultative aerobes for use compounds other than  $O_2$  as terminal electron acceptors in anaerobic

respiration, for example, allows them to continue to respire C substrates and to generate the energy-storing molecule ATP via the electron transport chain when O<sub>2</sub> supply is reduced or cut. Nitrate (NO<sub>3</sub><sup>-</sup>) and sulfate (SO<sub>4</sub><sup>2-</sup>) are commonly used as alternative electron acceptors in anaerobic respiration.

The capacity to form spores or cysts is another type of adaptation that can enhance an organism's persistence in soil during periods of low water availability. Bacterial endospores are very durable, thick-walled dehydrated bodies that are formed inside the bacterial cell. When released into the environment, they can survive extreme heat, desiccation, and exposure to toxic chemicals. Bacteria, such as *Bacillus* and *Clostridium* that form endospores, and actinomycetes and true fungi, that commonly reproduce by conidia and spores, are well represented in the soil community. Their capacity to form spores gives these species an obvious survival advantage in the soil environment. The much larger protozoa and nematodes (Chapter 10) which feed on bacteria and fungi can both form cysts or thick-walled resting structures that enable them to survive when conditions are not favorable for growth. Once conditions become favorable, such as after a rain or when prey populations increase, the cysts germinate and these protozoa and nematodes then resume feeding, growing, and reproducing.

Other adaptations also enhance the capacity for organisms to survive in the ever-changing soil environment. Examples include producing polyols (alcohols with three or more hydroxyl groups) and heat-shock proteins; increasing intracellular solute concentrations; altering the membrane composition as seen in many Archaea (a prokaryotic lineage distinct from the Bacteria); and producing heat-stable proteins as seen in the thermophiles. In the last two decades, there has been a great increase in our knowledge of the survival strategies and mechanisms of soil biota which make possible the existence of the plethora of species that we are now coming to know, through molecular methods, are present in the soil.

### 5.1.7 Build It and They Will Come

When the physical and chemical characteristics of a soil are within optimal ranges, biological activity generally follows suit. For example, if soil texture and structure allow for a good balance between adequate drainage vs. moisture retention with sufficient gas exchange, conditions will generally be conducive for microbial growth and activity. If the soil is compacted or water-saturated, it rapidly becomes anaerobic. Under such conditions, fermentative metabolism may predominate, and organic acids and alcohols are produced. Practices that improve SOM content, water-stable aggregation, and drainage, such as growing cover crops and retaining residues (Chapter 30), applying compost (Chapter 31), and reducing tillage (Chapters 22 and 24) all help promote abundant, active soil biological communities.

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## 5.2 Classifying Organisms Within the Soil Food Web

### 5.2.1 The Soil Food Web as a System

When one thinks of any ecosystem, generally the first things that come to mind are the organisms — plants, animals, and microbes — that live within it and provide a variety of ecosystem services. In ecological terms, these are classified either as producers (plants, algae, and autotrophic bacteria) or consumers (herbivores, predators, and decomposers). The primary producers, most often plants in terrestrial ecosystems, form the base of

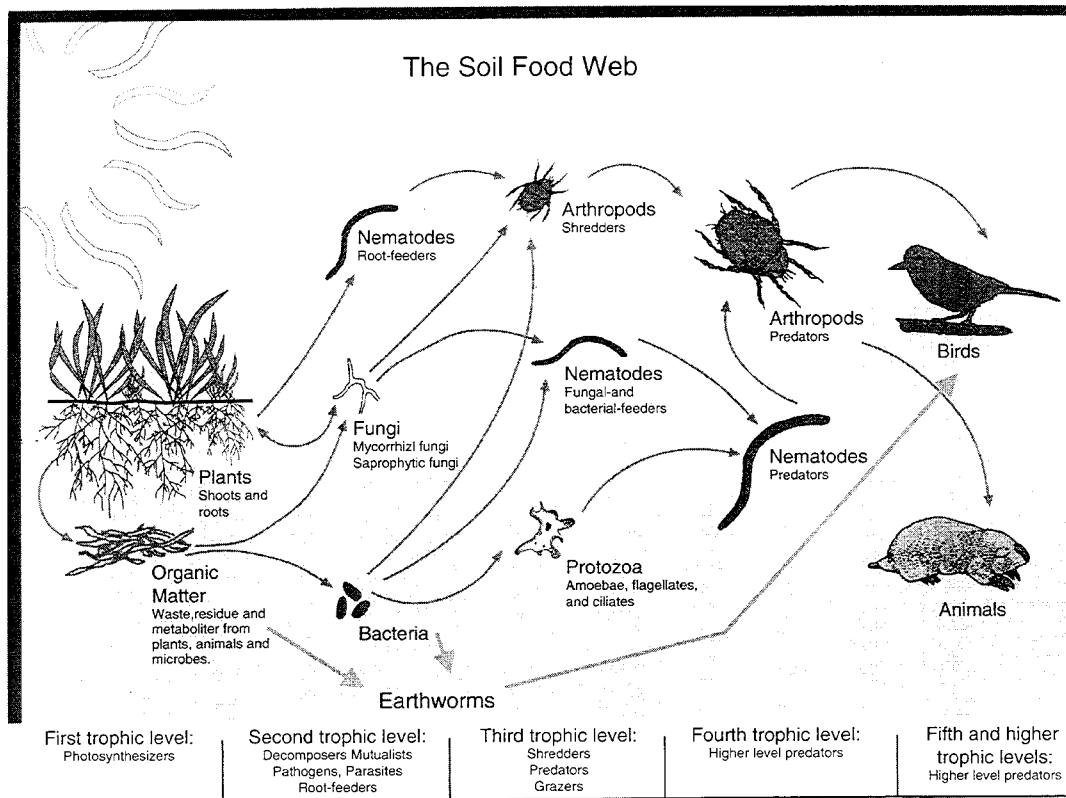


the food chain, or more accurately, the food web — a vast network of feeding interactions between and among organisms within the system. Primary producers capture energy from sunlight through the process of photosynthesis. This captured energy, stored in chemical bonds, provides the energy for most other organisms within the food web.

Trophic (feeding) interactions can be quite complex, especially below ground. Primary producers, generally plants, are consumed by herbivores, which are the primary consumers. Herbivores are in turn consumed by predators, which are considered secondary consumers within the system. Predators are then consumed by higher-order predators, the tertiary consumers within the system and on upwards. A simplified diagram of the soil food web is given in Figure 5.1.

Consumption is an energetically inefficient process. A rule of thumb is that only 10% of the energy contained at the first trophic level persists as usable energy at the next trophic level. Thus, up to 90% of the energy contained in primary producers, when consumed, becomes unavailable for metabolic work, being mostly lost from the system in the form of heat. This inefficiency of energy flow from one trophic level to the next has important consequences for the structure of ecosystems. The biomass that can be supported at any particular trophic level depends on the amount and availability of biomass in organisms at the trophic level immediately below it, upon which it feeds.

In aboveground systems, the largest biomass will be that of the primary producers. As one moves to higher trophic levels in the food web, both the biomass and often the number of organisms that can be supported decrease. This leads to the concept of a pyramid of biomass, or a pyramid of energy. This shape suggests how the size of successive



**FIGURE 5.1**

A simplified soil food web emphasizing trophic (feeding) relationships and functional roles of the soil biota. Adapted from SWCS (2000).

populations in any food web, i.e., their number and biomass, will decrease. Food webs will have, necessarily, a finite number of trophic levels as the total energy available for metabolic work at higher levels is consecutively dissipated as heat.

Organisms in all ecosystems are dependent on a source of energy that can be captured to do metabolic work, discussed in more detail in Chapter 6. Whether they capture it themselves through photo- or chemosynthesis or rely on preformed organic compounds, such as plant or animal tissue from other organisms, is a distinction that becomes very important when we consider the biota within an ecosystem's soil subsystem. The biological system beneath the soil surface operates on the same principles as those above ground, but with some distinct and important differences. The key difference is that primary production is extremely limited below ground since it is not continuously driven by abundant solar energy. This makes the whole subterranean subsystem energy-limited. Root-derived soluble C compounds, sloughing of root cells, and root death below ground, plus litter and animal waste deposited above ground, are the primary sources of energy for the belowground community (Wardle, 2002).

### 5.2.2 Energy and Carbon as Key Limiting Factors

The necessary goal for any organism is to obtain enough energy, cell biomass C, and mineral nutrients to produce the cellular constituents that are necessary for survival, growth, and reproduction. Metabolism refers to the biochemical processes occurring within living cells that make it possible for organisms to carry out what is necessary to maintain life. Microorganisms can be differentiated, and are categorized, based on three important metabolic requirements: (1) their source of energy; (2) their source of cell biomass C; and (3) their source of electrons or reducing equivalents.

- Phototrophs obtain energy from light, whereas chemotrophs obtain their energy from the chemical bonds in reduced organic or inorganic compounds.
- Autotrophs obtain their cell carbon from either  $\text{CO}_2$  or  $\text{HCO}_3^-$ , whereas heterotrophs obtain their cell C from organic compounds.
- Lithotrophs derive electrons from reduced inorganic compounds such as  $\text{NH}_4^+$ , whereas organotrophs derive them from reduced organic compounds.

Four main groups are typically identified based on their sources of energy and cell C: photoautotrophs, photoheterotrophs, chemoautotrophs, and chemoheterotrophs (Atlas and Bartha, 1998). Photoautotrophs, as noted above, include plants, cyanobacteria, and other photosynthetic bacteria that use the process of photosynthesis to convert light energy from the sun into chemical energy. The chemical energy captured is subsequently used for carbon fixation.

Organisms such as the nitrifying bacteria that use ammonium ( $\text{NH}_4$ ) as a source of energy and reducing potential to fix  $\text{CO}_2$  into cell biomass are known as chemoautotrophs. Those bacteria and fungi, protozoa and soil fauna that rely on plant and animal residues and SOM as sources of both energy and cell biomass C are classified as chemoheterotrophs, or simply as heterotrophs. Photoheterotrophs are a small and unusual group of photosynthetic bacteria, the green nonsulfur and purple nonsulfur bacteria that use light as a source of energy and organic compounds as their source of cell C.

The activity of heterotrophic soil organisms depends on the availability of degradable organic C compounds. Since primary production below ground is limited by a lack of light, soil heterotrophs must depend on the activity and success of aboveground photoautotrophs, mainly plants, for their survival. In a healthy soil, heterotrophs meet

their needs for energy and cell biomass C from the continuous addition of plant and animal residues, from the secretion of organic compounds by plant roots, and from the slow turnover of SOM, which includes the microbial biomass that continually dies off as new microorganisms come to life.

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### 5.3 Primary Producers

#### 5.3.1 Energy Capture in Plants Drives the Soil Community

Plants as primary producers capture energy by in their aerial leaf systems, and much of that energy is transferred below ground to plant roots through the phloem, part of the plant's vascular system specialized for this purpose. Plant roots provide a special, highly energized habitat for microorganisms living next to them in the surrounding soil, referred to as the rhizosphere, discussed below. Some microorganisms are endophytic, inhabiting the interior tissues of roots as mutualists rather than as parasites. Hence, it is sometimes difficult to delineate where the realm of the plant root ends and that of soil organisms begins.

Carbon compounds released by roots serve as the primary source of energy for most heterotrophic soil organisms. Belowground herbivores, plant-parasitic nematodes and pathogenic fungi feed directly on living root tissues, thus reducing plant productivity. However, the vast majority of organisms in the rhizosphere that feed on root-derived compounds are decomposers. In most cases, their presence around the roots is highly beneficial to plant growth, particularly when their activities release mineral nutrients that plants can subsequently acquire, thus creating a positive feedback loop between plants and the rhizosphere microbial community.

Another major source of energy for soil heterotrophs is dead plant material (litter) and animal residues. In woodlands, this would be primarily in the form of leaf fall and tissues of dead plants, plus animal excrement and carcasses. In agricultural systems, much of the plant material is removed during harvests and not returned to the soil. This is an undesirable management practice, however, because it runs down the energy status of the soil, depleting the energy needed by microorganisms to perform their many beneficial functions.

In addition to vascular plants, other primary producers that may be present in surface soil are photosynthetic bacteria, cyanobacteria, and algae. However, their energy contribution to soil is comparatively small. Cyanobacteria, a large and diverse group of photosynthetic bacteria coming in an assortment of shapes and sizes, were previously, mistakenly, called blue-green algae. Ranging from 1 to 10  $\mu\text{m}$  in diameter, they are found as filaments, colonies of numerous shapes, and as single cells. Many of the filamentous cyanobacteria are able to fix atmospheric  $\text{N}_2$  within specialized thick-walled cells, called heterocysts. Cyanobacteria, other photosynthetic bacteria, and algae use light energy and generally require high moisture levels; hence, they are not active below the first few millimeters in soil. Some cyanobacteria and algae do, however, form important partnerships with fungi called lichens. Lichens are resistant to desiccation and colonize rock surfaces, tree bark, and other organic and inorganic surfaces. In some ecosystems, such as in the Arctic and very arid environments, lichens and cyanobacterial soil crusts may be the dominant primary producers (Belnap, 2003). Their contribution to soil function in arable lands is not substantial in comparison to vascular plants, however, and we will not consider them further here.

The soil biota are limited mainly by the amount of energy that can be produced and stored by aboveground organisms that is ultimately transferred below ground. Gross and

net rates of primary production vary greatly from one plant species to the next due mainly to the photosynthetic pathway used (C3, C4, and CAM) and to abiotic factors such as variations in light, soil moisture, temperature, and nutrient availability. The highest capacities for photosynthesis are seen in plants possessing the C4 photosynthetic pathway such as maize, sorghum, and sugarcane; the lowest capacity is found in plants relying on crassulacean acid metabolism (CAM), such as desert succulents. Variations in photosynthetic capacity have a direct impact on the amount of fixed C that reaches the soil and becomes available for use by heterotrophic soil organisms. Of the total C fixed by photo- or chemosynthetic organisms (gross primary production [GPP]), some portion is used to fuel their own cellular respiration. GPP minus respiration is called net primary production (NPP), or the accumulation of standing plant biomass (and that of other autotrophs). NPP is what fuels the soil subsystem, largely in the form of detritus and root exudates.

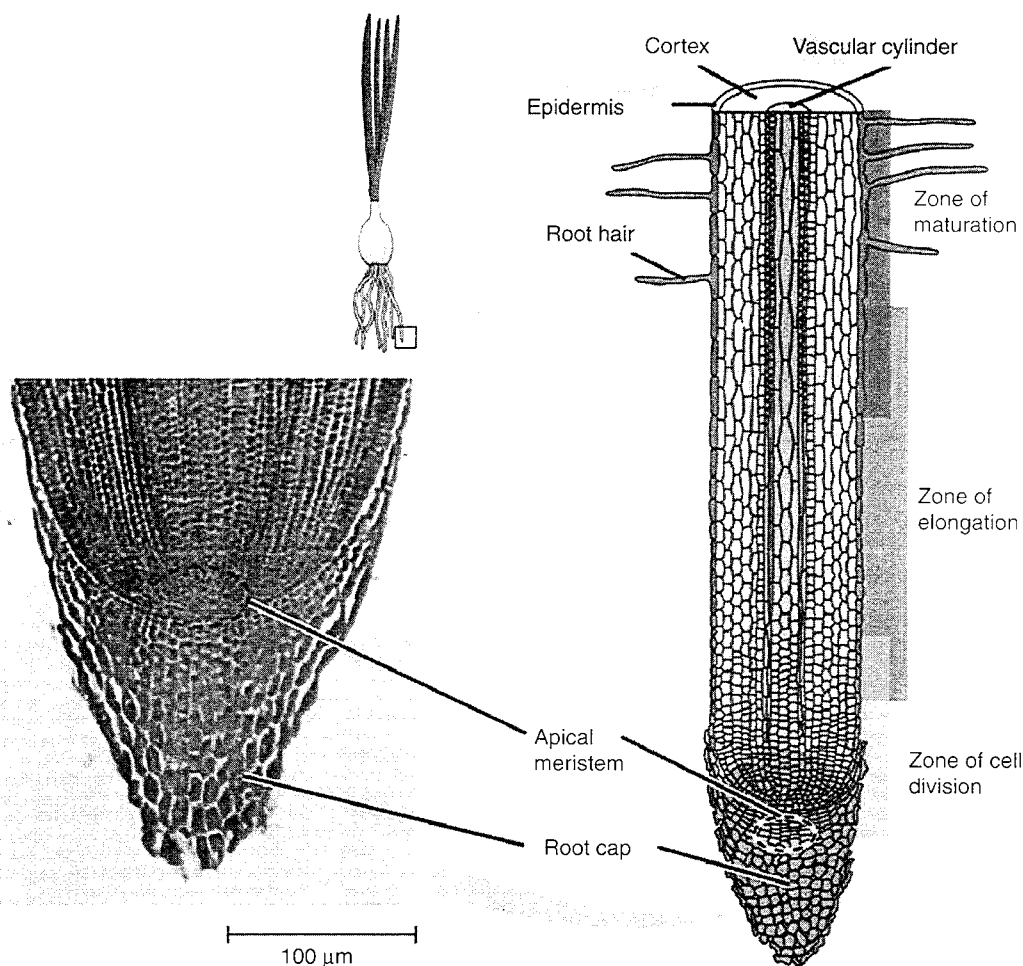
### 5.3.2 Roots

Processes that occur at or near the soil–root interface control the productivity of both plants and soil organisms. This interface is discussed in more detail in Chapter 7. Here, we consider briefly the roles and contributions of root systems as part of the soil food web. We note that roots also offer habitat for bacteria and fungi, referred to as endophytes, living within roots, performing mutualistic services such as documented in Chapter 8, while themselves being benefited by plant roots.

Root systems are composed of long thick roots that provide structural support and shorter, fine roots that are important in the uptake of nutrients and water. Soil biota are not evenly distributed along a single root system. Even though various root types within a single root system support very distinct distributions of both bacterial and fungal species (McCully, 1999), fine roots and root hairs (specialized epidermal cells) have often been neglected in soil ecology studies. Microbial population differences associated with roots of differing size and age need to be taken into account for understanding root–soil dynamics.

Through the roots, plants acquire the water and nutrients that they need for survival. Plant roots are not passive absorbers of nutrients and water, but actually active regulators maintaining complex signaling relationships between roots and shoots (Chapter 15). Features of an actively growing root are shown in Figure 5.2. Root hairs and the root cap are very influential in controlling rhizosphere microbial populations. Root hairs greatly increase the amount of soil that plants can explore and from which they can extract nutrients and water. Root hairs extend into the soil environment usually less than 10 mm and range from 20–70  $\mu\text{m}$  in diameter. They form on both the structural roots, as well as on the finer lateral roots. Root hairs initially grow straight, but when they encounter soil particles they curl, bend, and often develop branches, creating microhabitats in which microbes can reside. Root hairs are often the cells in which mutualistic relationships with mycorrhizal fungi and nitrogen-fixing rhizobia bacteria are initiated, discussed in Chapters 9 and 12.

The growing plant root has three distinct zones: the meristem, or zone of cell division, where new root cells are formed; the zone of elongation where these cells expand and lengthen; and the zone of maturation, or root hair zone, where these cells mature and from whence root hairs originate (Figure 5.2). As roots grow, root cap cells are continuously sloughed off into the soil, being replaced by the dividing meristem cells of the elongating root. Root cap cells secrete a dense mucilage of polysaccharides that serves several significant purposes, including providing a lubricant for the root to grow through the soil and for retaining moisture, thereby guarding root tissues against desiccation (Bengough and Kirby, 1999). Mucilage that undergoes continuous wetting and drying contributes to the formation of soil aggregates, which give the soil better structure and tilth.



**FIGURE 5.2**

Cross-section of a typical root showing different zones and organs. From Campbell, N.A. and Reece, J.B., *Biology*, 7th ed., Benjamin Cummings, San Francisco (2005). With permission.

The sloughed-off root cap cells and mucilage remain in the soil, covering the maturing root surface as it continues to grow into the soil environment. Some recent evidence suggests that these sloughed root cap cells may sometimes act as decoys, with potential pathogens colonizing these sloughed cells rather than the intact root cap cells, as the root tip grows away from the area. This process of sloughing off root cells, among other things, thus helps to protect the meristem from pathogen invasion.

### 5.3.3 The Rhizosphere

The root surface is referred to as the rhizoplane, whereas the rhizosphere is the biologically active area of soil that surrounds the root and is chemically, energetically, and biologically different from the surrounding bulk soil. It is the zone where plants have the most direct influence on their soil environment through root metabolic activities, such as respiring and excreting C-rich compounds, or through nonmetabolically mediated processes that cause cell contents to be released into the surrounding soil, such as cell abrasion or sloughing. The rhizosphere can extend outward up to 1 cm or

more from the root surface depending on the plant type and soil moisture and texture (for a comprehensive review, see Pinton et al., 2001). Here we discuss the rhizosphere in terms of the soil food web. A closer look at the components and functions of the rhizosphere is provided in Chapter 7, after considering energy flows in Chapter 6. Practical applications are seen in Chapter 39

Together, the rhizosphere and the rhizoplane provide diverse habitats for a wide assortment of microorganisms. Habitats on root surfaces are affected by differences in moisture, temperature, light exposure, plant age, root architecture, and root longevity. However, the primary way in which plants influence the communities of microorganisms that inhabit the rhizosphere is through their deposition of root-derived compounds. These are classified as root exudates (passive process), secretions (active process), mucigel (root/microbial byproduct mixtures), and lysates (contents of ruptured cells) (Rovira, 1969).

The accumulation of all these various substances put into the soil is called rhizodeposition, and represents the key process by which C is transferred from living plants into the soil subsystem of the larger ecosystem (Jones et al., 2004). Rhizodeposition increases the energy status of the surrounding soil and, consequently, the mass and activity of soil microbes and fauna that are found in the rhizosphere. This is reflected in the R/S ratio, i.e., the biomass of microbes in the rhizosphere (R) in relation to that in the bulk soil (S). This ratio is generally greater than one.

Microorganisms engage in a variety of activities in the rhizosphere. Beneficial interactions include fixing  $N_2$  (Chapters 12 and 27), solubilizing or enhancing uptake of less mobile nutrients (Chapters 13 and 37), promoting plant growth (Chapters 14, 32, 33, and 34), mutualistic symbioses (Chapters 9, 12, and 34), biocontrol (Chapter 41), antibiosis, aggregating and stabilizing soil, and improving water retention. Neutral or variable interactions include free enzyme release, bacterial attachment, competition for nutrients, and nutrient flux. Harmful activities include allelopathy (Chapter 16), phytotoxicity, and infection or pathogenesis. Complementing these positive, neutral, or negative functions are ones that occur within roots, associated with endophytic organisms such as discussed in Chapters 8 and 12.

Many activities of microbes in the rhizosphere are of benefit to plants. Indeed, some research findings have indicated that plants may select for, i.e., support, certain taxonomic or functional groups of organisms present in their rhizospheres; however, laboratory and field experiments have given inconsistent results (e.g., Grayston et al., 1998; Smalla and Wieland, 2001; Singh et al., 2004).

A central interest in soil ecology studies is enhancing or manipulating microbial populations found in the rhizosphere, including abundance and differential distribution of species. Many inoculation programs are aimed at changing species distributions in the rhizosphere either to enhance a particular process or to suppress plant pathogens. Inoculating legumes with specific strains of rhizobia aims to increase BNF (Chapter 12) or provide other benefits (Chapter 8), while inoculating with mycorrhizae is intended to increase plant uptake of poorly mobile nutrients (Chapters 9 and 33). Inoculating with *Trichoderma* (Chapter 34), plant growth-promoting rhizobacteria (Chapter 32), or applying compost (Chapter 31) may aid in suppressing plant pathogens in many systems.

Part III of this volume provides numerous examples of how managing to enhance beneficial populations in the rhizosphere and improving soil biological activity in general can yield significant benefits to plant productivity and soil quality (see especially Chapter 39). Favorable results, however, are contingent on many factors being aligned in certain ways, so this area of research continues to present many unresolved questions.

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## 5.4 Consumers

The soil biota have a number of important functional roles as consumers which include: C mineralization and OM turnover, nutrient cycling, vital mutualisms with plants and each other, causing and suppressing plant and animal diseases, improving soil structure, bioremediating contaminated soil (Chapter 42), and generating and consuming greenhouse gases (Susilo et al., 2004; and Chapter 43). For many years, the focus has been on measuring pools of nutrients or organic substrates without regard to the organisms responsible for the shifts between one pool and another. This has changed substantially in recent years as the focus has moved toward assessing the abundance, activity, and diversity of communities, populations, individuals, and gene sequences of interest.

### 5.4.1 Decomposers, Herbivores, Parasites, and Pathogens

The first consumer group of the soil food web, the primary consumers, contains decomposers, i.e., organisms that feed on root exudates and plant and animal residues, and numerous herbivores, parasites, and pathogens that feed on living root tissues. This trophic level encompasses many heterotrophic soil bacteria and fungi. These include the important mycorrhizal fungi and symbiotic rhizobia bacteria discussed in Chapters 8, 9, and 12, as well as several types of pathogenic fungi, oomycetes, and root-feeding nematodes (Figure 5.1). It includes also the larvae and adult stages of insects that feed on the roots and shoots of plants and whose life-cycles are largely carried out in the soil.

Heterotrophic soil bacteria have several functional roles in soil, most importantly as decomposers of dead organic matter. They can also be symbionts that live with plants and other organisms in the soil to mutual benefit, or pathogens that live at the expense of other organisms. Saprophytic bacteria, which feed on dead organic matter, are the most numerous of the decomposers. These bacteria produce, as a group, many different enzymes that give them broad capacities to degrade organic matter, enabling them to metabolize a vast array of C compounds to obtain energy and cell biomass C. Many heterotrophic bacteria facilitate key transformations of various nutrient elements that complete elemental cycling. A prime example is the fixation of  $N_2$  from the atmosphere by nitrogen-fixing bacteria and the return of  $N_2$  to the atmosphere during anaerobic respiration by facultative anaerobes through the process of denitrification, with the sequential reduction of nitrate ( $NO_3^-$ ) in the soil solution to  $N_2$  gas in the soil atmosphere.

Soil bacteria and fungi are important in developing and maintaining soil structure and aggregation. Bacteria improve soil structure by producing exopolysaccharides and other metabolites that help glue soil particles together. Fungi, by producing a network of hyphal filaments, also help to stabilize aggregates.

Some soil bacteria are important plant pathogens that colonize living plant tissue and cause disease. Common examples are crown gall caused by *Agrobacterium tumefaciens* and the black rot of crucifers caused by *Xanthomonas campestris*. Certain plant-pathogenic bacteria that colonize the rhizosphere produce metabolites that retard plant growth. It is possible for a bacterium that is considered to be plant growth-promoting under some soil conditions to become deleterious to the plant as environmental conditions change. A shift from aerobic respiration to fermentation under  $O_2$ -limited conditions, for example, can cause a shift in the endproducts of metabolism from  $CO_2$  to acids and alcohols which may be damaging to roots.

An important mutualism between soil fungi and plants is that of the mycorrhizal fungi. Ectomycorrhizae associate largely with tree species, inhabiting root surfaces and extending

their hyphae from there, while endomycorrhizae form associations with most crop plants, actually penetrating and inhabiting their cortical root cells as discussed in Chapter 9. In the relationship between these fungi and a host plant, the plant benefits by enhanced nutrient status, largely from increased uptake of phosphorous and micronutrients, protection from desiccation (through increased water uptake), and protection from pathogens and toxic metals by occupying the same niche or forming a protective layer on the root surface. Mycorrhizal fungi benefit in return by obtaining energy and fixed carbon directly from host plants.

The last of the primary consumers considered here are the plant-feeding nematodes. Infestation by parasitic nematodes causes millions of dollars in crop losses each year (Bird and Koltai, 2000). Most species of plant-feeding nematodes harbor a needle-shaped stylet or mouth part that enables them to pierce the plant cell wall and cell membrane and to feed on the cell contents. Maintaining large populations of beneficial soil organisms — the saprophytic and symbiotic bacteria and fungi, as well as free-living nematode species — is a promising means for reducing and preventing the spread of parasitic nematodes as they all compete for substrates and space within the rhizosphere. Nematodes as primary and secondary consumers within the food web are considered in more detail in Chapter 10.

#### 5.4.2 Organic Matter Decomposition

One of the more important functions of the primary decomposer group of microbes, saprophytic bacteria and fungi, is to break down complex organic materials into their component building blocks by the action of exoenzymes (Reynolds et al., 2003). Enzymes are proteins produced by living cells that facilitate (catalyze) chemical reactions by lowering the energy needed for activating these processes. Most enzymes are characterized by high specificity, which is largely a function of differences in enzyme-active sites.

Different soil bacteria and fungi produce an enormous variety of enzymes that are secreted into the surrounding environment, such as dehydrogenases, proteases, and cellulases. These exoenzymes reduce organic molecules and degrade proteins and cellulose, respectively, into their component parts outside the cells. The products are then taken up through the cell wall and cell membrane for use in metabolic reactions. Producing exoenzymes involves a high carbon cost to bacteria and fungi; hence, they become highly invested in the surfaces that they have colonized. Bacteria often form biofilms on surfaces that enable them to degrade organic compounds more efficiently (Davey and O'Toole, 2000).

Released nutrients are taken up by decomposers, which can result in the immobilization of nutrients within microbial biomass. Inorganic nutrient elements, such as N, P, S, K, and Mg, in excess of their needs, are released back into the soil environment and become available once again for uptake by plants. Since most plants cannot take up nutrients in organic forms, the decomposition of OM is an important source of inorganic nutrients for them. Through their respiration, soil decomposers also release CO<sub>2</sub> back into the atmosphere, making it available once again for plants to capture in the process of photosynthesis, thus completing the C cycle.

The rate and extent of decomposition is directly related to the nature of the OM that is being decomposed. Materials of different composition and energy status will decompose at different rates, and thus there is variation in the length of time that organic materials remain (reside) in the soil before being completely broken down. Many plant and animal residues, such as root exudates, leaf litter, frass (insect excrement), and manure, have very short residence times in soil, being completely decomposed in weeks, months, or at most



a few years. Carbon in this form is referred to as part of the labile C fraction. Microbial metabolites, humic acids, and highly lignified materials have lower mineral nutrient contents in relation to the carbon content or require highly specialized enzymes for their decomposition. Carbon in this form has a long residence time in soil on the order of years, decades, or more and is referred to as part of the recalcitrant carbon fraction (Paul and Clark, 1996).

The quality of OM inputs represents a primary limiting factor affecting the growth and reproduction of saprophytic organisms. If the available forms of carbon are high in energy and easily broken down (high quality), as is the case with many plant residues, then decomposers are likely to be both active and abundant. However, where SOM content is low, or when OM inputs consist of more recalcitrant materials, such as lignin and polyphenols (lower quality), microbial activity will be restricted, and the functioning of the whole ecosystem will be affected.

SOM has many key functional roles. Serving as the primary source of carbon and energy for the soil biota, it becomes the primary factor controlling microbial activity. It also influences soil water-holding capacity, air permeability, nutrient availability, and water infiltration rates. SOM content is very sensitive to soil management practices. For example, tillage exposes SOM previously occluded inside aggregates. Once exposed, SOM is rapidly mineralized by colonizing microbes, thus reducing the overall OM content of the soil. Many of the chapters in Part III focus on management practices that can help to conserve and increase SOM quantity and quality as a basic strategy for enhancing soil system functioning and sustainability. The quality, turnover, and functional significance of soil OM inputs are discussed in more detail in Chapters 6 and 18.

#### **5.4.3 Grazers, Shredders, and Predators**

The organisms at the next trophic level are the secondary consumers, which include the protozoa, bacterial- and fungal-feeding nematodes, and microarthropods such as mites and collembola. These organisms feed predominantly on soil bacteria and fungi, but also consume SOM. Feeding on live bacteria and fungi is commonly referred to as grazing. Grazers are critically important in the cycling of mineral nutrients since when they feed on nitrogen-rich bacteria, they excrete large amounts of inorganic nitrogen into soil (Bonkowski, 2004).

Grazers have adapted various methods of consuming their prey. Bacteria-feeding protozoa engulf their prey, whereas bacteria- and fungus-feeding nematodes have specialized mouth parts for piercing or penetrating. Those of bacteria-feeding nematodes sweep or suck bacteria off the surfaces of roots and soil particles, while fungus-feeding nematodes often have fine stylets that allow them to pierce the fungal cell walls and consume the cell contents, seen in Figures 10.1 and 10.2 in Chapter 10. Grazing, no matter the mechanism, results in more rapid nutrient turnover and release because the amount consumed is often in excess of the grazing organism's needs.

Unlike the plant-parasitic nematodes, the bacteria- and fungus-feeding nematodes are very beneficial within soil systems. Their grazing activity helps to regulate the size and structure of bacterial and fungal populations and accelerates nutrient cycling, making them the "good guys" within the soil nematode world. When soil nematicides or fumigants are used, all nematodes can be killed off, the beneficial as well as the deleterious species. This disrupts the functioning of the free-living nematodes and compromises their role in facilitating nutrient turnover (Ibekwe, 2004). More selective ways of dealing with plant-parasitic nematodes are needed, such as developing suppressive soils that enhance the beneficial nematode populations while controlling the plant-feeding species. Enhancing the populations of beneficial nematodes can help keep the deleterious ones

in check through several mechanisms, including stimulating induced systemic resistance (ISR) in plants by enhancing nutrient availability and competing for space and other resources. This is an active area of current research in soil ecology. The ecological roles of protozoa and nematodes are discussed further in Chapter 10.

The shredders and predators occupy several trophic levels, depending on the substrates or prey on which they feed. Mites and collembola fragment (shred) and ingest OM and thus are primary consumers, but some also graze on fungi, which makes them secondary consumers. Earthworms and enchytraeids fragment and ingest OM and so are primary consumers, but the OM is often covered with bacteria and fungi, thus they are simultaneously secondary consumers. As we move up the food chain, we find that the feeding relationships are not straightforward or distinct. Many organisms feed at multiple trophic levels, and this contributes to the complexity of trophic relationships and leads to efficient OM turnover and net nutrient release.

Collectively, the shredders are important for controlling microbial populations, shredding organic matter, and cycling nutrients. Shredding, also known as comminution, speeds up residue decomposition as it mixes bacteria and fungi with the residues and increases the surface area available for these decomposers to colonize. Mesofauna (mites, collembola, termites, and enchytraeid worms) and macrofauna (wood lice, millipedes, beetles, ants, earthworms, snails, and slugs) all contribute to the shredding and turnover of organic residues. Shredders also deposit partially digested residues, called frass or insect excrement, in the soil. Frass being very energy rich is an excellent substrate for decomposers. In addition to depositing nutrient-rich casts, earthworm activity also mixes the upper layers of the mineral soil with surface residues (bioturbation) and creates biopores or channels for water and roots to pass through.

The higher trophic levels in the soil food web (tertiary consumers and beyond) contain predatory nematodes and predatory arthropods, such as pseudoscorpions, centipedes, and species of spiders, beetles, and ants. From a soil ecology perspective, the life history and functions of the predators are important because they can help regulate important plant pest populations. Larger soil animals such as moles, while important members of the soil subsystem, are not considered here, but their ecological roles are discussed in Wolfe (2002). Ecological roles and functions of soil fauna are discussed further in Chapter 11.

#### **5.4.4 They All Interact Together**

Soil biota, through a continuous and highly interrelated set of feeding relationships, are key to liberating plant-available nutrients in the rhizosphere (Adl, 2003). Without the activities of soil biota, nutrients bound up in organic matter would remain immobilized, and the cycling of nutrients would be greatly limited. Instead, soil organisms mineralize OM, thus facilitating the release of inorganic nutrient elements and their continual cycling.

The effects of this process are not simple because the nutrients liberated are also available for uptake by bacteria, fungi, protozoa, nematodes, and microarthropods living on or in the vicinity of roots. All of these organisms compete with roots for uptake of these mineral nutrients. Soil saprophytes, while important in mineralizing organic matter, are equally important in immobilizing nutrients. Only when these elements are available in excess of what microbial communities need do they become freely available to plants. Immobilization of nutrients in the soil biota is not as negative a process as it sounds. It can actually be quite beneficial by retaining nutrients within the topsoil and rhizosphere, thereby preventing them from leaching into lower soil horizons, beyond the reach of plants unless there is very deep root growth.

Bacteria require more mineral nutrients in relation to their carbon requirements than do fungi or protozoa. Therefore, bacteria are more likely to immobilize mineral nutrients,

whereas the activities of fungi, protozoa, nematodes, and microarthropods are likely to result in greater release of available mineral nutrients into the soil solution.

The soil food web is thus an intricate set of interrelationships among a wide diversity of organisms. This web of interactions significantly influences all aspects of the soil environment. Without living organisms and other soil organic materials, the soil would be simply a compilation of minerals, gases, and water. Nutrient elements would not be recycled, and the system would rapidly wind down to lower fertility levels, unless all the elements are constantly replaced from external sources. The strategy adopted by the Green Revolution was essentially indifferent to the roles and contributions of soil biota, and this has contributed to impoverishment of the soil biota and SOM in many areas. To maintain a healthy soil food web is to conserve a self-renewing ecosystem capable of sustaining plant growth for long-term productivity. Ignoring and undermining the rich diversity of life in soil comes at a cost. Better to understand this highly complex community so that soil resources can be managed in more sustainable ways.

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## 5.5 Biological Diversity and Soil Fertility

There is still a continuing debate over whether increasing bacterial and fungal species diversity in the soil environment will lead to longer-term ecosystem sustainability. In particular, questions arise as to how changes in management practices that affect plant community diversity and productivity may have indirect impacts on below ground soil biotic communities and their functioning (Giller et al., 1997; Clapperton et al., 2003). It is still unclear how much soil biotic diversity is required for sustainable soil systems, or if simply having a representative set of organisms that give functional diversity is sufficient (Brussaard et al., 2004). It is well known that plant litter is critical in determining soil physical properties and also the quality and availability of substrates for microorganisms (Wardle et al., 2004). Although strong correlations do exist, many studies have shown that as long as litter quality is maintained, increasing the species richness of plant litter has no predictable effect on decomposition rates or biological activity (Wardle et al., 1997; Bardgett and Shine, 1999).

It will be of great value to determine more conclusively the significance of the operative relationships between soil biodiversity and fertility. Understanding these relationships could allow ecosystem managers to encourage the presence of organisms that are beneficial to soil systems intended for crop and animal production, as well as to overall ecosystem health as discussed in Parts II and III of this volume.

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## 5.6 Discussion

A good summary statement about soil systems by Martius et al. (2001) is cited in Chapter 13: "Soil comes to life through organic matter, which supports highly diverse communities of microorganisms and soil fauna that provide critical ecosystem services, most notably the recycling of nutrients." Soil management clearly needs to focus on managing, directly or indirectly, the soil biological communities for improved soil function and long-term sustainability. Soil is arguably our most precious global resource and one that has been sorely mistreated. This mismanagement has sacrificed millions of hectares of fertile soil through erosion and degradation, which occurred not just because of unwise physical

manipulation but due to a loss of the soil life that is needed to maintain its integrity and thus help it resist loss.

Analyzing the chemical and physical aspects of soil systems is much easier than delving into the complex realm of soil biology, and thus the analysis and evaluation of chemical and physical properties has dominated soil science for generations. Today, more soil research is examining soil biology, assisted by new methods for analysis as discussed in Chapter 46. These are overcoming previous limitations to our ability to classify, measure, and assess causal relationships. The chapters that follow in Part II give insights into the various agents and processes composing soil systems, with chapters in Part III then showing how such knowledge is being applied to make soil system management more effective and sustainable.

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