SOIL BIOLOGY

A.J. Franzluebbers,
USDAAgricultural Research Service, Watkinsville, GA, USA

Keywords: Actinomycetes, bacteria, biological nitrogen fixation, bioremediation, carbon cycle, earthworms, fungi, microbial biomass, mycorrhizae, nematodes, nitrogen cycle, organic matter, protozoa, rhizosphere

Contents

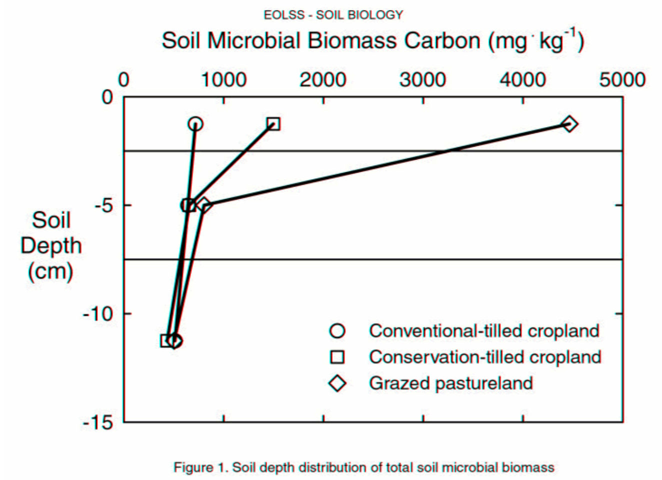
Summary

Soil biology represents a diverse group of organisms that reside during at least a part of their life cycle in the soil. These organisms vary widely in size from macrofauna > 10 mm in length (earthworms, spiders, beetles, mice, moles, etc.) to micro and mesofauna <10 mm in length (protozoa, nematodes, collembola, etc.) to microscropic forms of bacteria, fungi, and algae. Soil organisms can be primary producers of organic materials (e.g., phototrophic algae and bacteria), but more commonly are heterotrophic consumers of preformed organic materials. These heterotrophic organisms are essential in the cycling of nutrients and transfer of energy following the senescence of plant materials. Soil organisms also play major roles in soil formation and soil structural development by forming biotic pores, transforming soil minerals and organic matter into stable aggregates, and catalyzing mineral weathering processes. Ecologically, soil organisms perform many key environmental functions, including (1) regulation of carbon cycling from plant detritus back to the atmosphere, (2) provision of inorganic nitrogen to plants through decomposition and biological nitrogen fixation, (3) transformation of nitrate via denitrification to mitigate water contamination, (4) biodegradation of natural and synthetic contaminants in soil, and (5) purification of water percolating through soil into groundwater. Soil biology is recognized as a key component along with other soil disciplines for the understanding and development of land management systems by human society to help sustain and improve ecosystem functioning on local, regional, and global scales.

1. Soil organisms

Organisms living in the soil develop an active, diverse, and yet often under-appreciated ecosystem. The soil ecosystem is dynamic and composed of biotic (i.e., plant roots, microorganisms, and macroorganisms) and abiotic components (i.e., mineral particles, water, gases, nutrients, and nonliving organic matter). Soil organisms can be broadly separated into two groups, i.e., microflora and fauna. Microflora are a very diverse group of organisms that are generally not visible to the unaided eye, i.e., <200 μm. Microflora are classified in the Kingdom Protista, which lack the ability to form distinct tissue or organs for performing specific functions, and include bacteria, actinomycetes, fungi, and algae. Fauna are classified in the Kingdom Animalia and include such diverse organisms as protozoa, nematodes, mites, collembola, arthropods, earthworms, beetles, ants, and termites. Fauna can be further divided by size of body into microfauna (<0.2 mm length, <0.1 mm width), mesofauna (0.2 to 10 mm length, 0.1 to 2 mm width), and macrofauna (>10 mm length, >2 mm width).

Soils can be very different in the diversity of organisms present, but in general fungi dominate the soil biomass with 103 to 106 colony-forming units g-1 soil, while bacteria are most abundant in numbers. Types, numbers, and biomass of organisms vary not only from soil to soil, but also within the same soil type both spatially (i.e., vertically and horizontally due to resource allocation) and temporally (i.e., daily based on plant development and water availability, seasonally based on climatic conditions, and annually based on land use). The basic requirements for life [i.e., a suitable temperature, water, space, time, a terminal electron acceptor (e.g., O2 for aerobic organisms), an energy source, carbon source, nutrients, and a suitable pH] select for organisms tolerant or capable of activity under the specific set of environmental conditions. An example of depth changes in total soil microbial biomass in a pasture is shown in Figure 1, where plant litter and animal dung deposited at the soil surface provide much of the organic substrates for proliferation of microorganisms. An example of seasonal changes in dung beetle populations in a managed grassland is illustrated in Figure 2.



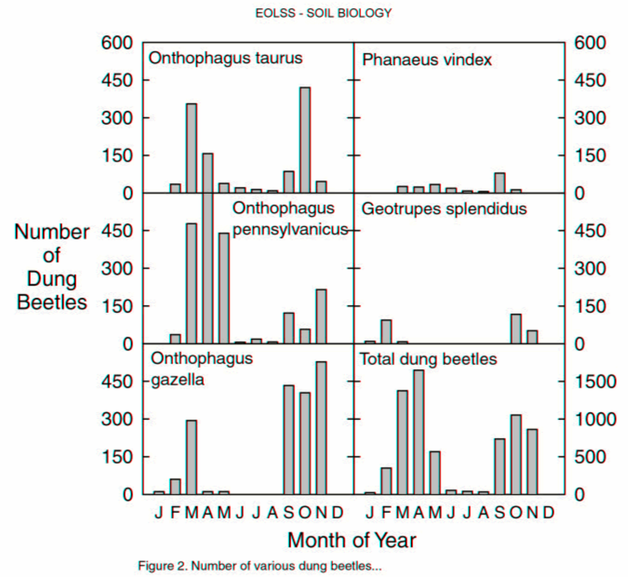


Figure 1. Soil depth distribution of total soil microbial biomass... Figure 2. Number of various dung beetles...

Soil microorganisms can be classified ecologically based on growth dynamics. Autochthonous species grow at a slow, steady rate, tend to be indigenous or native species, and undergo dormant stages to resist extinction. Zymogenous species have resistant stages, but become active quickly when food sources become available, such as on senescent roots following rainfall preceded by a long drought. Allochthonous species are invaders of an environment, enter the soil ecosystem through precipitation, manure, sewage, or diseased plant tissue, do not participate in a sustained way to the soil community, and may die off with time.

In addition, soil microorganisms can be classified nutritionally based on the nature of the energy source for generating adenosine triphospate (ATP) and the nature of the principal carbon source used for cell growth (Table 1).

Table 1. Classification of organisms based on metabolic sources of energy and carbon.

1.1. Bacteria

Bacteria can be found in nearly all soil environments. Bacteria are prokaryotic organisms, defined as cellular organisms without a nucleus. Bacteria vary widely in size (typically 0.5 μm in diameter to 8 μm in length) and shape (typically rod, sphere, or spiral, as well as pleomorphic that change shape during growth). Major groups of bacteria are classified according to shape, cell wall structure (i.e., by gram stain), motility, and metabolic capabilities (Table 2). Depending upon oxygen status of the soil, particular groups of bacteria will proliferate, including obligate aerobes (requiring O2 to grow), obligate anaerobes (can not grow in presence of O2), and facultative anaerobes (can grow in presence of absence of O2).

Table 2. Major groups of bacteria.

In a typical soil environment, bacteria form spores and form microcolonies. Soil conditions that favor heterotrophic bacteria are abundant water (at least 50% of the pore space occupied by water), neutral pH, relatively high temperature (30 to 40 EC), and abundant organic matter.

Cyanobacteria (or formerly blue-green algae) are capable of fixing atmospheric nitrogen. The cyanobacterium, Anabaena, forms a symbiotic association with the aquatic fern, Azolla. This association is an important mechanism for nitrogen fixation in flooded rice soils.

1.2. Actinomycetes

Actinomycetes give soil its musty or earthy odor through production of geosmin. They are unicellular, aerobic bacteria that resemble fungi in that they produce slender (0.5 to 2 μm diameter), y-branched hyphae, which often fragment and divide as a means of asexual sporulation. Hyphae of actinomycetes are thinner than those of fungi. Actinomycetes develop best under relatively dry and warm conditions and neutral soil pH. Most are heterotrophic, slower growing than most other bacteria (i.e., autochthonous), and utilize organic compounds more resistant to breakdown (e.g., cellulose, pectin, and chitin). Actinomycetes are a source of many antibiotics, including streptomycin, which is produced by one of the most common actinomycetes in soil, Streptomyces.

1.3. Fungi

Fungi are typically multicellular (although yeasts are unicellular) eukaryotes that do not contain chlorophyll, but produce a wide variety of spore and resting structures, including mushrooms, sclerotia, conidia, and rhizomorphs. Typical fungi have hyphae of 5 μm in diameter and <100 μm in length, are heterotrophic aerobes, grow from hyphal tips without extracellular enzymes, and predominate in acidic soils (pH<5.5). Many plant pathogens are fungi, but only a few fungi are pathogens. A special group of fungi particularly beneficial in agriculture are those that form a mycorrhizal symbiosis with plant roots, as described later in Section 1.5.

Fungi are split into five major groups:

Myxomycetes (slime molds), which are morphologically similar to protozoa, i.e., without cell walls in the vegetative state (although spores do contain cell walls). An example is Physarum.

Phycomycetes, which are non-septate and have no specialized spore structure. Examples are Pythium and Rhizopus.

Ascomycetes, which are septate with sexual spores in an ascus. An example is Saccharomyces.

Basidiomycetes, which are septate with sexual spores in a basidium. Examples are Boletus and Tricholoma.

Deuteromycetes (fungi imperfecti), which are septate with no sexual spores. Examples are Fusarium and Penicillium.

1.4. Algae

Algae are pioneers that often are the first to inhabit soils following disasters. Algae are photoautotrophic eukaryotes with various pigments and storage products used to distinguish among groups. The most common algae in soil are greens, diatoms, and yellow-greens, which derive inorganic nutrients and water from soil. In soil, most algae grow near or on the surface to capture sunlight for energy, although some can be found at more than a meter depth because they are facultative photoautotrophs obtaining energy from sunlight or inorganic compounds. Algae form various spores. Vegetative forms (2 to 50 μm in size) can be unicellular, colonial, filamentous, folious, tubular, blade-like, or leafy. Algal blooms occur because of their ability to form dormant spores or cysts under unfavorable conditions and then germinate upon return of favorable conditions.

1.5. Mycorrhizae

Mycorrhizae are symbiotic associations between plant roots and fungi. The association is very widespread and beneficial in natural ecosystems as well as in agriculture. Fungi receive carbohydrates and other organic compounds from the plant and fungi provide the plant with enhanced capabilities to acquire nutrients (especially phosphorus and several micronutrients) and water from soil. The smaller diameter of fungal hyphae and extension of these hyphae into surrounding soil increase the surface area of the plant root system so that more nutrients can be extracted from the soil, which is especially important in relatively infertile soils.

There are two general mycorrhizal associations, i.e., endomycorrhizae where fungal colonization is within root cells and ectomycorrhizae where fungal colonization is between cells of the root. The fungal symbiont in endomycorrhizal associations are Phycometes. The most important endomycorrhizae are the arbuscular mycorrhizae, which infect many of the important agronomic crops of the world. Arbuscules are club-like, branched filaments within root cells where the transfer of energy and nutrients takes place. Many arbuscular mycorrhizae also contain vesicles within cells, which contain storage lipids and are probably important for reproduction. Fungal hyphae can extend several centimeters from the root, accessing nutrients and water, decomposing organic matter, and improving soil structure.

Ectomycorrhizae are important to woody plants, especially in the Fagaceae and Pinaceae families. The fungal symbiont in ectomycorrhizal associations are Basidiomycetes, which form mushrooms such as truffles. Fungi do not penetrate root cells in this association, but rather form a mantle around the root and form a web of hyphae (hartig net) between epidermal cells. Fungal hyphae can extend several meters into the surrounding soil. Hyphae in this association also enhance nutrient uptake, decompose organic matter, and improve soil structure. Many fungal symbionts in the ectomycorrhizal association can be cultured apart from the host plant, while fungi of the endomycorrhizal association are obligate symbionts not cultured apart from host plants.

1.6. Lichens

Lichens are a symbiotic association between fungi and algae or fungi and cyanobacteria. In these relationships, the algae or cyanobacteria are primary producers, capturing energy from the sun and carbon from atmospheric CO2, and fungi (either ascomycetes or basidiomycetes) are consumers. Fungi provide protection from the environment and obtain inorganic nutrients and growth factors for the association. Lichens grow very slowly, resist direct sunlight, and are able to colonize habitats unsuitable for other microorganisms by producing organic acids to solubilize rock minerals. Some lichens are able to fix atmospheric nitrogen because of the capabilities of cyanobacteria such as Peltigera and Nostoc.

1.7. Microfauna

Microfauna is a group of small animals (<200 μm length, <100 μm width) including protozoa, rotifers, and nematodes. Protozoa are eukaryotic organisms that are typically motile, single-celled, and nonphotosynthetic. Soil protozoa typically range in size from 25 to 200 μm and are grouped as naked amoebae, testate amoebae, ciliates, and flagellates based on mode of locomotion. Protozoa proliferate in the surface of moist soils, feeding on bacteria and other soil organisms especially near the roots of plants. Cysts are formed during dormancy as a result of depletion of food source or soil drying. Number of protozoa in a surface soil is often inversely related to number of bacteria, i.e., high population following consumption and decreasing quantities of bacteria.

Rotifers can be found in soils that are continually moist, but are typically aquatic organisms and, therefore, not a major soil organism.

Nematodes (also called roundworms, threadworms, or eelworms) are some of the most numerous multicellular organisms in a wide range of soils. They proliferate in the water-filled pores of soil, as do protozoa and rotifers. The rhizosphere is a particularly active area for nematode proliferation. Most nematodes are saprophytic, i.e., feeding on decaying organic matter. Other nematodes feed on bacteria, fungi, plant roots, and other nematodes.

1.8. Mesofauna

Mesofauna is a group of organisms (0.2 to 10 mm length, 0.1 to 2 mm width) including tartigrades, collembola, and mites. Tartigrades (or water bears) range in size from 0.05 to 1.2 mm. They have similarities to both nematodes and microarthropods with bilateral symmetry having four pairs of legs. Tartigrades have cryptobiotic capabilities, i.e., undergoing dormancy induced by environmental stress and reactivating up to several years later. They are found typically in the top few centimeters of soil, feeding on algae, other microorganisms and particulate organic matter.

Collembola (or springtails) are small (0.2 to 5 mm in length), primitive insects. Many species jump by means of a furcula attached to the bottom of the abdomen. Most collembola eat decaying vegetation and fungi, although they have also been observed to consume nematodes and plant roots throughout the soil profile. Collembola are opportunistic microarthropods (r-strategy), capable of rapid individual and population growth when conditions are favorable. They may be important biological control agents for crops by consuming pathogenic fungi. Eggs are laid in groups, and therefore, populations occur in aggregations rather than at random. Collembola can be important food sources for predacious mites, beetles, and ants.

Mites are some of the most abundant microarthropods in many soils. Soil mites are a very diverse assemblage of spiders, divided into four major groups, i.e., oribatids, prostigmatics, mesostigmatics, and astigmatics. Oribatid mites are often most numerous in soils, are morphologically distinct between juvenile and adult stages, reproduce relatively slowly (k-strategy), and typically feed on detritus and fungi. Unlike most other microarthropods, oribatid mites have a calcareous exoskeleton. Prostigmatic mites feed on fungi, algae, and other soil organisms. Fungal-feeding prostigmatics are r-stategists, capable of rapid response to shifts in resources. Mesostigmatic mites are not particularly abundant in soil and are mostly predators of nematodes and other microarthropods. Astigmatic mites are the least common mites in soil and are found primarily in moist soil high in organic matter.

Other mesofauna that are less numerous, but present in many soils are protura (wingless insects lacking antennae and eyes that live near plant roots and litter), diplurans (elongate, delicate insects with long antennae and two abdominal cerci that feed either on decaying vegetation or predacious on nematodes, collembola, and enchytraeids), pseudoscorpions (small scorpions lacking tails and stingers that feed on nematodes, microarthropods, and enchytraeids), symphylids (white, eyeless, elongate, many-legged invertebrates resembling centipedes that feed on vegetation and soft soil animals), pauropoda (colorless, many-legged insects with branched antennae that feed on fungi and other soil organisms), and enchytraeids (or potworms, similar to earthworms, except smaller, that feed on fungi and possibly algae, bacteria, and other soil organisms).

1.9. Macrofauna

Macrofauna is a group of relatively large organisms (>10 mm length, >2 mm width) including isopods, millipedes, centipedes, scorpions, spiders, termites, ants, beetles, earthworms, and various other soil-dwelling animals (sometimes called megafauna) including mice, moles, groundhogs, etc. Isopods are cryptozoans, i.e., surface soil dwellers under stones, bark, or litter layers, which emerge at night to forage and otherwise roll into balls to avoid desiccation. They feed on roots, vegetation, and decaying plant litter, resulting in considerable fragmentation of organic matter.

Millipedes are saprophagous feeders, i.e., consuming dead or decaying organic debris, with a calcareous exoskeleton, and therefore important in calcium cycling. Leaf litter high in polyphenols tend to be avoided by millipedes, while litter with high calcium content is preferred. Microorganisms that develop in feces of millipedes help decompose organic matter, with subsequent consumption of feces by millipedes.

Centipedes are elongate, flattened, and active predators of various microarthropods in soil and surface litter.

Scorpions are typical cryptozoans in warm, dry ecosystems. They are mobile predators of other arthropods, lizards, mice, and birds.

Spiders in soil and surface litter layers are typically predators of soil insects.

Termites are social insects organized into castes. They have the ability to digest cellulose in wood because of intestinal colonization with various microorganisms (different species harbor either protozoans, bacteria, or fungi). Three groups of termites are distinguished by their feeding habits, i.e., on wood, on plant debris and humus, and on fungi. In the tropics, certain types of termites can move enormous quantities of soil from lower depths to form above-ground mounds several meters high. Termites are important agents of decomposition in tropical grasslands and temperate forests.

Ants are widespread throughout most terrestrial ecosystems. They are social insects that often nest in soil and consume a variety of foods, depending upon species such as microarthropods, decaying organic debris, seeds, plant secretions, and aphid secretions. Ants forming surface mounds are important in mixing soil from lower depths with surface soil.

Solitary wasps construct nests in soil and prey on other insects or spiders to feed developing eggs.

Beetles are the most diverse insect family, and in the soil can be divided into predacious, leaf feeding, and saprophagous. Ground beetles, rove beetles, and tiger beetles are predators of other insects. Dung beetles feed typically on large-animal feces. Wireworms are larvae that feed on roots in many ecosystems.

Earthworms are the most famous of the soil fauna, because of their size and tremendous ability to consume and organize soil mineral and organic constituents. Two well-studied species are Lumbricus terrestris, which burrows vertically deep into the soil, and Allolobophora caliginosa, which dwells mainly at the soil surface. Burrows loosen soil, allowing roots and other soil animals to colonize this space. Earthworm casts are often enriched in organic matter, microbial populations, and nutrient content, which improves nutrient cycling to associated vegetation.

2. Soil biological processes

The soil is the host environment for a number of extremely important processes that affect life on earth. These include decomposition of organic substances, transformation and cycling of nutrients, and promotion of soil aggregation and porosity. A variety of organisms work together structured as a food web to make an ecosystem function with time either naturally (e.g., native grasslands, forests, deserts, tundra, wetlands, etc.) or with management, as in agriculture (Figure 3).

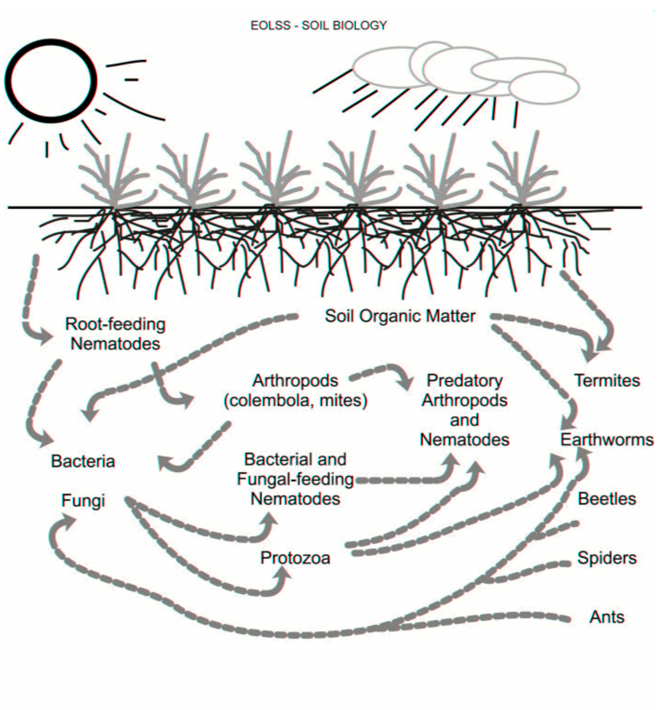


Figure 3. Generalized diagram of a food web with interactions among biotic components.

Figure 3. Generalized diagram of a food web with interactions among biotic components.

Primary producers (i.e., photosynthetic organisms such as plants and algae) feed this web of life by fixing atmospheric CO_2 into organic carbon molecules:

$$2H_2O + CO_2 + \text{light energy } 6\ (HC\text{-}HO) + O_2 + H_2O \qquad (1)$$

Primary consumers are those organisms that feed directly on plants (herbivores), such as root-feeding nematodes and insect larvae, mites, and earthworms. Secondary consumers are those organisms that feed on primary consumers and tertiary consumers are carnivores that feed on primary and secondary consumers. Ants may be tertiary consumers of centipedes, which may be secondary consumers of nematodes, which may be primary consumers of plant roots. Groups of organisms are not always in the same position in the food chain. For example, bacteria can be primary consumers of plant litter, but also tertiary consumers of dead secondary consumers, and the food source for protozoa or earthworms acting as secondary consumers.

2.1. Decomposition

All heterotrophic organisms are involved in the consumption and breakdown of organic materials. Decomposition of organic matter is an integral part of the global carbon cycle, where photosynthesis and respiration are dominant fluxes (Figure 4). Soil mesofauna and macrofauna often fragment plant and animal residues, which increases the surface area and exposes internal constituents to soil microfauna and microflora for further attack. Larger soil organisms, therefore, stimulate soil microbial activity and also distribute smaller organisms within soil as a result of their generally greater range of mobility. In addition, larger soil organisms such as earthworms, ants, and beetles physically move organic substrates from the soil surface to within the soil, which can enhance decomposition by placement in a more favorable zone for microbial attack because of less extreme moisture and temperature variations.

Factors affecting decomposition in soil are environmental conditions (i.e., temperature, aeration, moisture, supply of nutrients, pH, and redox potential) and chemistry of the substrate (i.e., distribution of easily decomposable and resistant fractions, particle size and surface area, presence of microbial inhibitors, and content of non-carbonaceous nutrients such as nitrogen and phosphorus). In general, water and oxygen need to be balanced for most rapid decomposition (Figure 5). However, halogenated compounds such as vinyl chloride and various solvents decompose more rapidly when exposed to alternating aerobic and anaerobic environments. When inorganic nitrogen is low in soil and residues with high carbon-to-nitrogen ratio are incorporated in soil, microbial activity is limited by the availability of nitrogen for growth of soil organisms (Figure 6).

Incomplete decomposition of organic matter can lead to accumulation of resistant compounds in soil, collectively termed humus. Rate of decomposition of primary plant constituents follows the order: water soluble components > cellulose, hemicellulose, and fats > lignin and waxes.

Cellulose is a carbohydrate composed of a linear chain of ß 1-4 linked glucose units. Cellulose decomposition occurs under both aerobic and anaerobic conditions. Aerobically, various fungi and some facultatively anaerobic bacteria convert cellulose to carbon dioxide, water, and cell biomass with the aid of three types of enzymes, i.e., C1, Cx, and ß glucosidase. Hemicellulose is a polysaccharide composed of pentoses, hexoses, and/or uronic acids. A variety of fungi and bacteria produce both endoenzymes (which cleave bonds within the polymer) and exoenzymes (which cleave monomers and dimers from the end of the polymer). Decomposition products of hemicellulose include carbon dioxide, water, cell biomass, and a variety of small carbohydrates. Chitin is an amino sugar found in fungal cell walls and insect skeletons. Chitin is decomposed by various fungi and bacteria with the aid of chitinase enzymes into N-acetylglucosamine and chitosan. Lignin is an aromatic compound composed of repeating benzene rings that are branched and complex. The aromatic structure of lignin makes it difficult to decompose. Only a few fungi and bacteria have the capability to decompose lignin, requiring first depolymerization into smaller aromatic acids and alcohols, side chain removal and methoxyl group oxidation, and finally ring opening.

Xenobiotic molecules are man-made molecules foreign to natural biological systems. Most synthetic organic molecules have natural counterparts or are sufficiently similar to naturally occurring compounds to be subjected to microbial metabolism. However, some compounds have molecular structures and chemical bond sequences not recognized by existing degradation enzymes, which make them slow to decompose. Recalcitrant xenobiotics are often a result of unusual substitutions (such as halogens), unusual bond sequences, excessive size (such as plastics), lack of microbial permease, toxicity, insolubility, and sorption of compounds to soil particles.

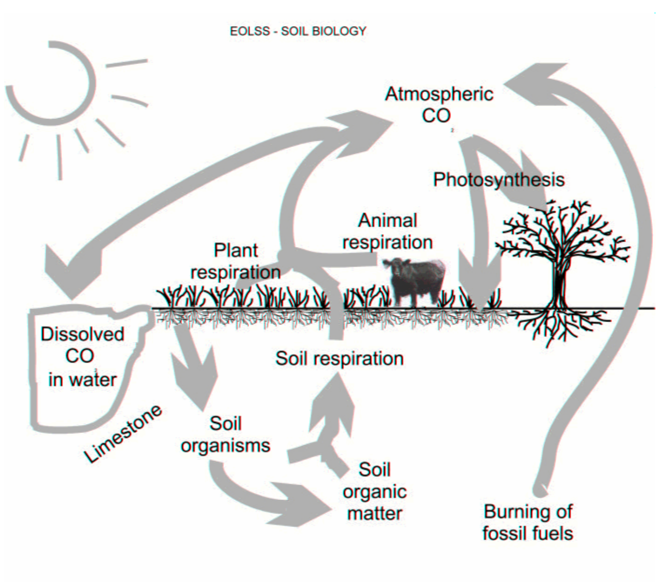


Figure 4. Simplified diagram of the global carbon cycle

Figure 4. Simplified diagram of the global carbon cycle.

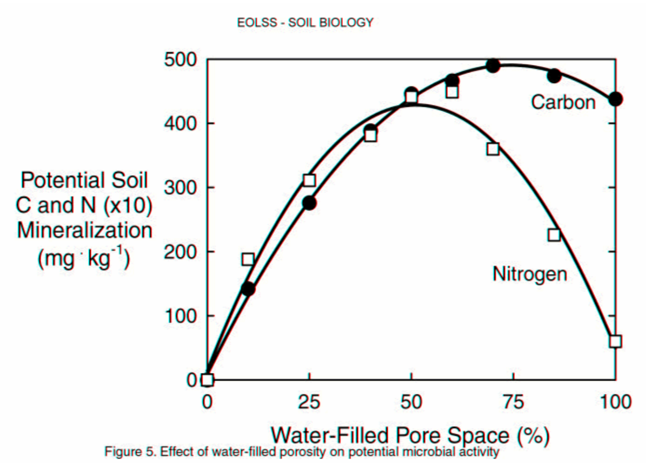


Figure 5. Effect of water-filled porosity on potential microbial activity...

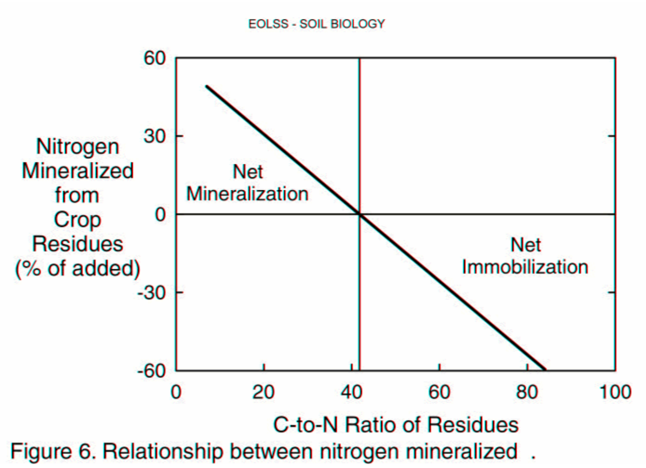


Figure 6. Relationship between nitrogen mineralized from crop residues...

2.2. Mineralization-immobilization

Mineralization is a heterotrophic process of organic matter breakdown into mineral constituents. The process of carbon mineralization (oxidate respiration) releases organically bound carbon to the atmosphere as CO_2:

$$C_6H_{12}O_6 + 6O_2 \; 6 \; 6CO_2 + 6H_2O + \text{energy} \qquad (2)$$

Many other organically bound nutrients are mineralized by soil heterotrophic organisms, including nitrogen through a series of oxidative reactions:

$$R\text{-}NH_2 + H_2O \; 6 \; R\text{-}OH + NH_3 \qquad (3)$$

$$NH_3 + H^+ + O_2 \; 6 \; NO_2! + 4H^+ \qquad (4)$$

$$2NO_2! + O_2 \; 6 \; 2NO_3! \qquad (5)$$

Immobilization of nitrogen (as well as other nutrients such as phosphorus and sulfur) is the biological uptake of inorganic nitrogen (particularly $NO_3!$ and NH_4^+) by soil microorganisms to meet their metabolic growth demands. Mineralization and immobilization occur simultaneously in soil. Net mineralization occurs when the product of mineralization exceeds that of immobilization. Significant net immobilization of inorganic soil N can occur when fresh organic substrates are added to the soil, because of very high soil microbial activity and subsequent microbial biomass growth with high nutrient demand (Figure 7). Carbon-to-nitrogen ratio of added organic substrate can be an indication of when and how long net nitrogen immobilization might occur in soil (Figure 8).

Figure 7. Mineralization and immobilization of nitrogen...

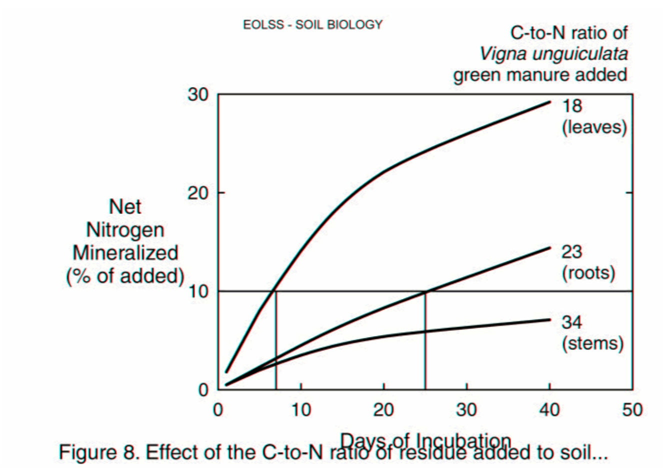


Figure 8. Effect of the C-to-N ratio of residue added to soil...

2.3. Nitrification

Nitrification is a very specific oxidative process, whereby ammonia (NH_3) is converted to nitrate in two steps by only a few specific chemolithotropic bacteria. Oxidation of ammonia to nitrite is carried out by Nitrosomonas, Nitrosococcus, Nitrospira, and Nitrosolubus:

$$2NH_3 + 3O_2 \; 6 \; 2HNO_2 + 2H_2O + \text{energy} \qquad (6)$$

In most soils, the second step of oxidation from nitrite to nitrate by either Nitrobacter or Nitrococcus quickly follows the first step, since it is uncommon to detect significant nitrite in soil solution, which is toxic to plants and mammals:

$$2HNO_2 + O_2 \; 6 \; 2HNO_3 + \text{energy} \qquad (7)$$

Nitrifying bacteria are obligate autotrophs (obtain carbon from CO_2), aerobic, sensitive to desiccation, and prefer moderate soil temperature and neutral pH. Extreme drying of soil can result in a lag in nitrate formation following rewetting, such as in arid ecosystems.

Especially in modern agricultural systems with inorganic fertilizer applications to achieve high yield of crops, excessive nitrate in soil can be leached beyond the root zone and eventually enter groundwater. One approach to limit loss of nitrogen in agricultural systems has been to apply a nitrification inhibitor along with ammoniacal fertilizer to keep more of the nitrogen as ammonia, which is less susceptible to losses via leaching and denitrification.

2.4. Denitrification

Denitrification is the microbial reduction of nitrate through anaerobic respiration to yield gaseous products such as NO, N_2O, and N_2:

$$5C_6H_{12}O_6 + 24KNO_3 \; 6 \; 30CO_2 + 18H_2O + 24KOH + 12N_2 + \text{energy} \qquad (8)$$

This process is limited to only a few bacterial genera, including Pseudomonas and Bacillus, which use nitrate and nitrite as electron acceptors under anoxic conditions. Many denitrifying bacteria are facultative anaerobes that utilize O_2 as an electron acceptor when present, but use NO_3! and NO_2! when necessary. Denitrification is most rapid at temperatures between 25 and 35 EC, with abundant nitrate and readily oxidizable carbon, and when O_2 in soil is at a low level.

Most denitrifiers convert nitrate all the way to N_2, but some stop at N_2O. When soil pH is <6 more N_2O and NO are formed as end products than N_2. Nitrous oxide (N_2O) contributes to development of acid rain when products of N_2O oxidation react with water to form nitric acid (HNO_3). Nitrous oxide also destroys ozone (O_3) in the stratosphere, where ozone protects the earth by filtering ultraviolet radiation from the sun. Nitrous oxide concentration in the atmosphere has risen from ca. 295 nL L^{-1} in 1950 to ca. 310 nL L^{-1} in 2000. Although this increase is relatively small compared with the rise in atmospheric CO_2 concentration during this same period (i.e., rising from 300 to 380 µL L^{-1}), the global warming potential of nitrous oxide is 310 times greater than that of carbon dioxide.

2.5. Biological nitrogen fixation

Biological nitrogen fixation requires high activation energy to split the double bond of N2:

$$N_2 + 3H_2 + \text{energy } 6\ 2NH_3 \quad (9)$$

Various soil microorganisms are able to fix atmospheric nitrogen (N2) into biologically available forms when (1) the substrate N2 is present, (2) there is sufficient energy from ATP, (3) there is a source of electrons (e.g., ferridoxan), (4) the enzyme nitrogenase is present, and (5) there is protection of nitrogenase from O2. Biological nitrogen fixation can be symbiotic with various plants, associative with plants, or asymbiotic.

Symbiotic nitrogen fixation is most notable between the bacteria Rhizobium and Bradyrhizobium and many leguminous plant species of the family Fabaceae. Bradyrhizobium fixes nitrogen within relatively large root nodules under the economically important crop, Glycine max (soybean). Typical clovers and alfalfa (Trifolium spp. and Melilotus spp.) have roots colonized in small club-shaped nodules with Rhizobium trifolii and Rhizobium meliloti, respectively. Pea (Pisum sativum), sweet pea (Lathyrus odoratus), and broad bean (Vicia faba) have associations with R. leguminosarum, while dry beans (Phaseolus spp.) have associations with R. phaseoli. Bradyrhizobium and Rhizobium can survive as free-living heterotrophs in soil for a few years, but free-living communities do not fix atmospheric nitrogen.

Symbiotic nitrogen fixation by microorganisms in association with non-leguminous plants also occurs between the actinomycete, Frankia, and various plants including Alnus, Casuarina, Ceanothus, Coriaria, Dryas, Elaeagnus, Hippophae, and Myrica. The blue-green algae, Nostoc and Anabaena, are able to fix atmospheric nitrogen in nodules on the stems of Gunnera and in the leaf pores of Azolla, respectively.

Rhizosphere bacteria such as Azospirillum and Azotobacter are able to utilize the root exudates of various grasses as sources of energy for their associative nitrogen-fixing activities. Free-living or nonsymbiotic forms of two bacterial genera, Azotobacter and Beijerinckia, can fix atmospheric nitrogen in aerobic soils. The bacterium, Clostridium, can fix atmospheric nitrogen in anaerobic soils.

2.6. Rhizosphere processes

The rhizosphere is a 1- to 2-mm zone surrounding roots that encompasses the ectorhizoplane (i.e., on the root surface) and the endorhizoplane (i.e., within root cells or between epidermal cells). The rhizosphere is characterized by high microbial activity due to the rich supply of organic carbon compounds derived from the root, such as exudates (compounds of low molecular weight that passively leak from intact cells into the soil), secretions (compounds of low and high molecular weight that are actively released into soil), mucilages (sloughed root cells and hydrolysates of root cell walls), mucigels (gelatinous combination of root cell byproducts, microbial cells and their byproducts, and soil colloidal, mineral, and organic matter), and lysates (compounds released from autolysis of older epidermal cells). Microbial populations in the rhizosphere may be 10 to 100 times higher than in the bulk mineral soil.

Several beneficial interactions occur with the close association between roots and soil microorganisms, including:

increased plant nutrient availability because of greater rates of mineralization of carbon, nitrogen, phosphorus, and sulfur from more active microbial poplulations and because of lower partial pressure of oxygen that increases iron and manganese solubility

release by microorganisms of plant growth regulators such as indole acetic acid, gibberellic acid, auxin, and allelopathic substances

production of mucigel, which helps maintain contact of root with soil and water

symbiotic and associative biological nitrogen fixation

mycorrhizae formation, which improves plant root acquisition of water and nutrients, especially phosphorus

removal of hydrogen sulfide (H2S) produced by flooded rice roots, by the microaerophilic sulfur-oxidizing bacteria, Beggiatoa

protection from potential plant pathogens through predation, parasitism, antibiotic production, and competition

Negative interactions between roots and soil microorganisms can also occur, including:

production of organic compounds by microorganisms that are detrimental to plant growth such as antibiotics and auxins

utilization of the limited amount of inorganic nutrients by microorganisms through immobilization and denitrification

proliferation of soil-borne plant pathogens that can infect roots

2.7. Soil structure formation

Soil structure formation is a complex biogeochemical process of interactions among mineral, organic, air, and water components of soil through time. Chemically, the presence of polyvalent cations (such as Ca2+, Mg2+, Fe2+ and Al3+) encourage flocculation and formation of stable microaggregates. Physically, soil structure is influenced by freezing/thawing, wetting/drying, and deformation and compression by roots and soil fauna. Biologically, soil microorganisms, soil fauna, and plant roots influence soil structure by providing organic matter, creating specific binding agents such as polysaccharides and gums, mixing organic materials with mineral components, and transforming organic material into stable organo-mineral complexes.

Several types of soil structural forms are recognized, including platy, prismatic, columnar, blocky, subangular blocky, granular, and crumb. The type of soil structure present can vary with depth and among similar soils due to management because of differences in temperature, moisture, chemical composition, organic matter inputs, biological activity, and mechanical forces (e.g., vehicular traffic).

Soil structure has two major components, aggregates and pores. Aggregates can be viewed in a hierarchical level of organization. Microaggregates (<0.25-mm diameter) are formed from clay- and silt-sized particles bound together by electrostatic forces and persistent organo-mineral complexes. Association of various microaggregates into larger macroaggregates (>0.25-mm diameter) occurs through transient binding agents (e.g., microbial- or plant-derived polysaccharides) and temporary binding agents (e.g., roots and fungal hyphae). Specific biological binding agents are recognized, including carbohydrates produced by various microorganisms, glomalin (a glycoprotein produced by arbuscular mycorrhizae), muramic acid produced by bacteria, and glucosamine produced by fungi.

Soil pores can be grouped into micropores and macropores. Micropores (<0.06-mm diameter) are often filled with water for long periods of time. Macropores (>0.06-mm diameter) allow ready movement of air and percolating water. Soil organic matter and the activity of soil biota are important agents for increasing the volume of macropores, which aid in rooting and improving aeration at lower soil depths.

3. State of the art in soil biology

Numerous advances have been made in the study of soil biology during the latter decades of the 20th century. Modern techniques are available to better characterize soil populations, biologically-mediated processes, and social implications of soil biological functions. The following describes some of the current topics in soil biology and associated measurement techniques receiving attention.

3.1. Soil microbial diversity

Traditionally, soil organisms have been observed directly either with the naked eye for macrofauna or with the aid of a microscope for microorganisms. Characterization of microbial isolates from soil has also been possible by identifying colonies cultured on petri plates with a specific growth medium. Direct methods are time consuming and culture methods are specific to growth media selected. Further, most of the bacteria observed with a fluorescent microscope cannot be cultured on laboratory media, because of very specific growth requirements. Earlier the specificity of growth requirements was considered a limitation for interpreting bacterial plate counts, but the development of substrate utilization techniques, such as BIOLOG using multiple growth media, has led to a systematic manner for characterizing the diversity of soil organisms.

Cultured and purified microorganism isolates can be classified biochemically with a range of techniques, including protein profiles, plasmid profiles, phospholipid profiles, intrinsic antibiotic resistance, and metabolic activity. Fatty-acid methyl esters (FAME) can be analyzed following transformation from soil of extracted phospholipid fatty acids, which are stable components of cell walls. FAMEs provide an estimate of community structure by providing relative types and numbers of organisms without the need to culture organisms.

Other emerging techniques to characterize soil organism diversity include total DNA extraction, amplification of specific fractions of DNA with polymerase chain reactions (PCR), fluorescence in situ hybridization (FISH), ribotyping of ribosomal RNA, and pulsed-field gel electrophoresis.

Ribotyping and other genotypic techniques are proving useful in identifying the source of fecal-borne pathogens in the environment. These techniques are able to discriminate among subspecies of a bacterium according to its association with a particular host.

3.2. Enzymes

Soil enzymes are primarily derived from microorganisms, but can also originate from animals and plants. Enzymes are protein molecules that catalyze biochemical reactions by reducing the activation energy required to perform the transformation. Six major classes of enzymes include oxidoreductases (important in fermentation and respiration pathways), transferases (transfer of molecular substitutions from one molecule to another), hydrolases (hydrolysis of various chemical linkages), lyases (removal of molecular groups from their substituents without hydrolysis), isomerases (intramolecular conversions), and ligases (repair of DNA molecules by linking together molecules). There is a wide variety of enzymes that have been studied, especially with regard to carbon cycling [e.g., amylase (conversion of starch and glycogen to maltose plus glucans), cellulase (conversion of cellulose to smaller glucans), lipase (conversion of neutral lipids to fatty acids plus glycerol), glucosidases, and invertase (conversion of sucrose to glucose plus fructose)]; nitrogen cycling [e.g., proteases, amidases, urease (conversion of urea to carbon dioxide and ammonia), and deaminase]; phosphorus cycling [e.g., phosphatases such as ATPase (conversion of ATP to ADP plus inorganic phosphorus) and phytase (conversion of phytic acid to inositol plus inorganic phosphorus)]; and sulfur cycling [e.g., arylsulfatase].

Enzymes can be intracellular (acting within cells) or extracellular (acting outside of cells). Dehydrogenase is an intracellular enzyme of broad significance in the transfer of hydrogen during organic matter decomposition. Extracellular enzymes are either excreted by microorganisms during cell growth and division, attached to cell debris and dead cells, or leaked into soil solution from lysed cells. Enzymes are extremely specific to a particular reaction, and therefore, are good indicators of specific soil biological functions.

Two general groups of enzymes have been classified based on their formation, i.e., constitutive (always produced by the cell) and adaptive (produced only when specific substrates are present). Adaptive enzymes allow conservation of energy and adaptation to different environmental conditions. Adaptive enzymes are often extracellular.

3.3. Soil organic matter characterization

Soil organic matter is extremely diverse in chemical composition, size and location, and biological availability. Soil organic matter has been chemically divided into non-humic and humic substances. Non-humic substances are constituents of plants, animals, and microorganisms, including proteins, carbohydrates, lignins, fats, waxes, resins, pigments, tannins, and other low-molecular weight compounds. Humic substances are highly processed, amorphous, dark-colored, hydrophilic, acidic, partly aromatic, chemically complex compounds of high-molecular weight. Humic substances have often been procedurally separated into fulvic acid, humic acid, and humin. There is a gradient between non-humic and humic substances in soil, because humus formation is largely a biochemical process, in which microorganisms decompose organic compounds, while at the same time chemical reactions in soil create new polymers. The major chemical constituents of soil organic matter include nitrogenous compounds (amino acids, amino sugars), carbohydrates, aromatic structures, fats, waxes, resins, organic phosphorus and sulfur compounds, and metal-organic complexes. There are a variety of methods used to chemically characterize soil organic matter, including proximate analysis, elemental analysis, ultraviolet and infrared spectroscopy, nuclear magnetic and electron spin resonance, pyrolysis, radiocarbon dating, and x-ray analysis.

Physically, soil organic matter can be described as to its location and size within soil through methods of disruption, separation, and subsequent analysis. The location and particle size of organic matter are important attributes that control access of resources to soil biota. Disruption techniques yield organic matter that can be separated into particle size fractions (i.e., sand-, silt-, and clay-sized particles) or aggregates (dry-stable or water-stable aggregate fractions). Separation techniques use sieving, sedimentation, or densitometry to isolate soil organic matter.

Biologically, soil organic matter can be described as to its susceptibility to decomposition, either under ideal or varying environmental conditions. Mathematical descriptions of the rate of decomposition (e.g., CO_2 evolution, oxygen uptake, or nutrient mineralization) are often used to distinguish among the pools of organic matter. For example, many current models now recognize at least three pools of organic matter (i.e., active, passive, and slow) with turnover times of days-weeks, months-years, and decades-centuries, respectively.

Soil organic matter content at the end of decades to centuries of a particular management system within an environment has been effectively predicted using models such as CENTURY, Roth-C, CANDY, and ICBM. Many of these models consider the quantity and quality (i.e., substrate attributes such as N concentration, phenolics, and particle size) of carbon inputs and the environmental conditions that control decomposition (i.e., temperature, moisture, oxygen, pH, nutrient availability, soil disturbance, and decomposer community) during time. Active, passive, and slow pools of soil organic matter can be mathematically described with non-linear equations as a function of time exposed to decomposition:

$$C_t = C_a(1 ! e!k_a t) + C_p(1 ! e!k_p t) + C_s(1 ! e!k_s t) \qquad (10)$$

where, Ct is the C level at time t; Ca, Cp, and Cs are C inputs in the active, passive, and slow pools, respectively; and ka, kp, and ks are the non-linear rate coefficients of the active, passive, and slow pools, respectively.

3.4. Quantification of soil microbial biomass

Soil organisms have long been recognized as the agents of nutrient transformations, and therefore play a key role in soil fertility and ecosystem functioning. In order to determine pools and fluxes of nutrients, knowledge of the quantity and activity of soil microbial biomass is needed. Size of the soil microbial biomass pool has implications on microbial growth efficiencies, immobilization of carbon, nitrogen, and other nutrients, rates of turnover of soil microbial biomass, microbial energetics, and modeling of soil organic matter dynamics.

Measurement of soil microbial biomass, while always of interest to soil microbiologists, became an ever-increasing topic of scientific investigations with the development of relatively simple and rapid, yet integrative protocols, specifically chloroform fumigation-incubation (measures the flush of CO2 or inorganic nitrogen during a 10-day incubation by surviving organisms following killing of most organisms with exposure to chloroform), substrate-induced respiration (measures the immediate response in respiration of CO2 to an easily decomposable substrate such as glucose), and adenosine triphosphate (measures the ATP content of soil organisms as an indicator of potential metabolic activity). These methods were the first to holistically quantify the entire soil microbial population as a single entity. Previously, labor-intensive methods were used to quantify soil microbial biomass, including plate counting and direct observation under a microscope. Since the development of these holistic methods in the 1970s, numerous other biochemical approaches have been developed to either improve the characterization of the more active portion of the microbial community, to reduce analysis time, or to quantify other nutrient components within the biomass, e.g., arginine ammonification, chloroform fumigation-extraction, rehydration-extraction, microwave irradiation-extraction, hot water extraction, and rehydration-mineralization.

3.5. Bioremediation

Concern with the pollution of air, water, and soil resources from industrial activities increased in the second half of the 20th century and continues today. Bioremediation techniques have been developed to enhance the decomposition of synthetic organic pollutants that would otherwise decompose very slowly, either due to their high concentration, unique chemical nature, or location in unfavorable environmental conditions. The applications for bioremediation techniques are diverse, just like the pollutants and the environmental conditions in which they have been spread. The process of bioremediation is essentially microbiologically driven through heterotrophic decomposition, but effective application of the process is supplemented with knowledge of chemical behavior, environmental toxicology, natural resource assessment, and environmental engineering.

Several conditions are necessary for biodegradation of an organic pollutant: (1) presence of organisms with the necessary enzymes to bring about biodegradation, (2) accessability of the pollutant to the organisms having the requisite enzymes for biodegradation, and (3) conducive environmental conditions for the microorganisms to proliferate throughout the course of biodegradation.

Pollutants that have been investigated for bioremediation include agricultural pesticides (e.g., trifluralin, tordon, paraquat, lindane, DDT, dicamba, chlordane, etc.), manufacturing by-products (e.g., pentachlorophenol, polychlorinated biphenyl, polyaromatic hydrocarbons, etc.), industrial chemicals (e.g., oil, gasoline, toluene, trinitrotoluene, etc.), and to a lesser extent, the combination of natural organic compounds with synthetic compounds such as chlorine in water treatment.

3.6. Decomposition

Decomposition is an important biological process on the global and local scale that balances many elemental cycles dependent upon photosynthesis. Elements bound in organic molecules produced by plants are released back to the environment through the heterotrophic activity of soil organisms. Decomposition is important on a local scale for nutrient cycling in agricultural systems to supply nitrogen, phosphorus, and secondary elements to plants, but also on a global scale for environmental quality of soil, air, and water resources by controlling soil carbon transformations, greenhouse gas emissions, and nutrient losses.

Decomposition can be measured as mass loss of organic substrates such as crop residues and animal feces. Ultimately, decomposition of organic molecules leads to mineralization of elemental constituents to CO2-C, NH4-N, PO4-P, etc., which can be measured as cumulative estimates of decomposition. The role of soil fauna in decomposition of organic residues is mainly as shredders and comminuters to facilitate further decomposition by microorganisms. The impact of soil fauna on decomposition can be measured with the use of litter bags with mesh openings to restrict certain sizes of organisms. Microbial decomposition can be measured through indicators of CO2 production, oxygen uptake, or net mineralization of nitrogen, phosphorus, and other elements.

3.7. Soil quality

Soil is a critical component of the earths biosphere, allowing us to produce food and fiber and to maintain environmental quality. The biological components of soil, perhaps more so than the physical and chemical components, can be either threatened or enhanced, depending upon how we use this resource. Soil quality assessment is an attempt to identify and characterize the management systems that elicit change in soil functions. The concept of soil quality recognizes that soil integratively affects plant productivity, environmental quality, and human and animal health. The concept also recognizes that caretakers of the soil resource have the ability to alter soil properties with time through the selection of land use and management, which ultimately affect the balance among these functions.

Soil quality implies that management can cause change in soil properties. Indicators of these changes may be physical, chemical, or biological in nature. Biological indicators that may relate to changes in soil function include, soil microbial biomass carbon and nitrogen pools, potentially mineralizable carbon and nitrogen, the presence and activity of certain soil faunal groups, soil enzyme activity, presence of fecal-borne bacteria, and microbial diversity.

3.8. Soil carbon sequestration

Carbon sequestration has become a topic of great interest as a means to mitigate the rising concentration of atmospheric CO2, a greenhouse gas, which could contribute to global warming. Soil organisms play a major role in the global carbon cycle, as they are the primary decomposers of plant-derived organic compounds. Plants fix CO2 into organic compounds and microorganisms convert these energy-rich compounds into either (1) organic byproducts, which can be stabilized in soil as humus, (2) soil microbial biomass, or (3) CO2, which is recycled back to the atmosphere.

Land management strategies are being sought that effectively increase the quantity of carbon fixed by plants and reduce the activity of soil microorganisms, in order to increase soil organic carbon. Some key principles that help define appropriate strategies are (1) promotion of active plant growth during as much of the year as possible (e.g., double cropping, relay cropping, intercropping, and planting both warm- and cool-season forages), (2) reduction in soil disturbance (e.g., conservation tillage and permanent vegetation), (3) application of organic amendments to the land when possible (e.g., animal manures, sludge, and compost), and (4) diversification of plant communities (e.g., crop rotations and mixed-stand forages).

4. Concluding remarks

The study of soil biology has had a relatively short history in comparison with other fields of soil science. Many advances have been made in the characterization of processes mediated by soil organisms, yet much remains to be accomplished to fully understand the complexity of interactions between soil organisms and with changes in environmental conditions.

It is estimated that a mere 10% of the population of organisms in soil has currently been identified to species level, suggesting that much more work is needed in identification and classification of soil organisms. New methods to detect functional groups of organisms will improve our ability to understand the many biotic interactions in and among ecosystems.

Soil biology needs to be a key component of ecosystem investigations in order to obtain a more thorough understanding of the mechansims of control for why ecosystems are degrading, being stabilized, or are aggrading. The critical role of soil organisms in ecosystem productivity, environmental quality, and human and animal health needs to be appreciated.

Related Chapters

Click Here To View The Related Chapters

Glossary

Adenosine triphosphate (ATP): Common energy-donating molecule in biochemical reactions. Also an important compound in transfer of phosphate groups.
Aerobic: (i) Having molecular oxygen as a part of the environment, (ii) growing only in the presence of molecular oxygen, as in aerobic organisms, or (iii) occurring only in the presence of molecular oxygen, as in certain chemical or biochemical processes such as aerobic respiration.
Anaerobic: (i) The absence of molecular oxygen, (ii) growing in the absence of molecular oxygen, or (iii) occurring in the absence of molecular oxygen.
Autochthonous: Microorganisms and/or substances indigenous to a given ecosystem; the true inhabitants of an ecosystem; referring to the common microbiota of the body of soil microorganisms that tend to remain constant despite fluctuations in the quantity of fermentable organic matter.
Biodegradation: Decomposition of a substance by biological processes.
Bioremediation: The use of biological agents to reclaim soil and water polluted by substances hazardous to the environment or human health.
Conidia: Nonmotile, asexual spores resulting from mitotic nuclear division and formed from the ends or sides of a hypha; produced in abundant numbers by the asexual phase of soil fungi in the phyla Ascomycota and Basidiomycota.
Decomposition: Chemical breakdown of a compound into simpler compounds, often accomplished by microbial metabolism.
Denitrification: Reduction of nitrogen oxides (usually nitrate and nitrite) to molecular nitrogen or nitrogen oxides with a lower oxidation state of nitrogen by bacterial activity.
Ecosystem: Community of organisms and the environment in which they live.
Halogen: Any of the five elements F, Cl, Br, I, and At that form part of group VII A of the periodic table.
Heterotroph: An organism able to derive carbon and energy for growth and cell synthesis by utilizing organic compounds.
Humus: Total of the organic compounds in soil exclusive of undecayed plant and animal tissues, their partial decomposition products, and the soil biomass.
K-strategy: Ecological strategy where organisms depend on physiological adaptations to environmental resources. K strategists are usually stable and permanent members of the community.
Mesofauna: Nematodes, oligochaete worms, smaller insect larvae, and microarthropods.
Microbial biomass: The total mass of living microorganisms in a given volume or mass of soil.
Microfauna: Protozoa, nematodes, and arthropods of microscopic size.
Microflora: Bacteria (including actinomycetes), fungi, algae, and viruses.
Obligate: (i) Adjective referring to an environmental factor (for example, oxygen) that is always required for growth or (ii) organism that can grow and reproduce only by obtaining carbon and other nutrients from a living host, such as obligate symbiont.
Phototroph: An organism that uses light as a source of energy and CO2 or carbonates as the source of carbon for cell biosynthesis.
R-strategy: Ecological strategy where organisms rely on high reproductive rates for continued survival within the community. Populations of r-strategists are subject to extreme fluctuations.
Rhizomorph: Mass of fungal hyphae organized into long, thick strands usually with a darkly pigmented outer rind and containing specialized tissues for absorption and water transport.
Rhizosphere: The zone of soil immediately adjacent to plant roots in which the kinds, numbers, or activities of microorganisms differ from that of the bulk soil.
Saprophyte: Nonparasitic nutritional mechanism by which an organism obtains its food exclusively from the degradation of nonliving organic material.
Sclerotia: Modified fungal hyphae that form compact, hard vegetative resting structures with a thick pigmented outer rind.
Soil ecology: The study of organisms in soil and their relationship to the environment and each other.
Zymogenous: Opportunistic organisms found in soils in large numbers immediately following addition of a readily decomposable organic substrate.

Bibliography

Alexander M.A. (1994). Biodegradation and Bioremediation. 302 pp. San Diego, CA, USA: Academic Press [An excellent description of the processes and technologies of bioremediation].
Brussard L., Kooistra M.J. (1993). Soil Structure/Soil Biota Interrelationships. 829 pp. Amsterdam, Netherlands: Elsevier [A thorough review of established and innovative methods of soil ecological study and assessment at the microscopic scale].
Coleman D.C., Crossley D.A.Jr. (1996). Fundamentals of Soil Ecology. 205 pp. San Diego, CA, USA: Academic Press [A very good description of the types of organisms in soil, their interactions with the soil environment, and the processes they mediate].
Crossley D.A.Jr., Coleman D.C., Hendrix P.F., Cheng W., Wright D.H., Beare M.H., Edwards C.A. (Eds). (1991). Modern Techniques in Soil Ecology. 510 pp. Amsterdam, Netherlands: Elsevier [A recent compilation of methods describing soil microbial and faunal characteristics under various conditions].
Darbyshire J.F., (Ed). (1994). Soil Protozoa. 209 pp. Wallingford, Oxon, UK: CAB International [The only recent publication that describes in detail the types and activities of soil protozoa].
Dindal D.L. (1990). Soil Biology Guide. 1349 pp. New York, NY, USA: Wiley Press [Extensive classification key to the most common organisms found in soil].
Doran J.W., Coleman D.C., Bezdicek D.F., Stewart B.A. (1994). Defining Soil Quality for a Sustainable Environment. 244 pp. Madison, WI, USA: Soil Science Society of America [A collection of perspectives on defining soil quality, identifying soil quality indices, and assessing the biological importance of soil quality].
Paul E.A., Clark F.E. (1996). Soil Microbiology and Biochemistry. 340 pp. San Diego, CA, USA: Academic Press [Textbook devoted to the classical study of soil microbiology and its role in the environment].
Sylvia D.M., Fuhrmann J.J., Hartel P.G., Zuberer D.A. (1998). Principles and Applications of Soil Microbiology. 550 pp. Upper Saddle River, NJ, USA: Prentice-Hall [Excellent textbook devoted to the comprehensive coverage of soil microbiology].
Weaver R.W., Angle J.S., Bottomley P.S. (Eds). (1994). Methods of Soil Analysis, Part 2: Microbiological and Biochemical Properties. 1121 pp. Madison, WI, USA: Soil Science Society of America [Describes why and how procedures are used by soil scientists for the investigation of soil microbial properties].

Web sites of relevance to soil biology

International Union of Soil Science, http://www.icsu.org/Membership/SUM/iuss.html
Soil Ecology Society, http://www.wcsu.ctstateu.edu/ses/conference.html
Soil Science Society of America, http://www.soils.org with link to Division S-3 Soil Biology and Biochemistry
International Society for Microbial Ecology, http://microbes.org/index.htm
American Society for Microbiology, http://www.asmusa.org
Digital Learning Center for Microbial Ecology, http://commtechlab.msu.edu/sites/dlc-me

Biographical Sketch

Alan J. Franzluebbers has been a Research Soil Ecologist with the U.S. Department of AgricultureAgricultural Research Service in Watkinsville, Georgia, USA since 1996. He has a Ph.D. in soil science from Texas A&M University and graduated with a M.S. and B.S. in agronomy and horticulture from the University of Nebraska. He served one year as a Canadian Government Visiting Fellow in Beaverlodge, Alberta, Canada in 1995. He is the lead scientist for a base-funded project entitled "Enhancing soil-water-nutrient processes in Southern Piedmont pasture and crop systems". His scientific interests are in developing sustainable pasture and crop management systems and determining their impacts on the soil environment. Biochemical and biophysical properties of soils are of special interest. He has authored/coauthored 65 peer-reviewed publications and 101 non-peer-reviewed proceedings and abstracts. Alan serves as Joint-Editor-in-Chief of Soil & Tillage Research, is an associate editor of Soil Science Society of America Journal, and has served as a subject editor for Soil Biology & Biochemistry. He has been a reviewer of >300 manuscripts in 18 different agricultural and environmental journals.

Table 1. Classification of organisms based on metabolic sources of energy and carbon.

Classification	Energy source for generating ATP	Source of carbon for cell growth
Photoautotroph	Light	CO_2
Photoheterotroph	Light	CO_2, simple organic compounds
Chemoautotroph	inorganic compounds	CO_2
Heterotroph	organic matter	organic matter

EOLSS - SOIL BIOLOGY

Table 2. Major groups of bacteria**.**

Group	Characteristic
Phototrophs	Utilize light as energy source; including Cyanobacteria
Gram negative chemolithotrophs	Nitrogen or sulfur oxidizers; including *Nitrobacter*
Methanogens	Methane production under anaerobic conditions
Gram negative aerobes	Important in elemental cycling; including *Rhizobium*
Gram negative facultative anaerobes	Including *Escherichia, Salmonella, Klebsiella, Erwinia*
Gram negative anaerobes	Important in elemental cycling; including *Desulfovibrio*
Gram positive cocci	Form irregular clusters; including *Staphylococcus*
Endospore forming rods and cocci	Resist environmental stress; including *Bacillus*
Gliding bacteria	Gliding motility; Form macroscopic fruiting structure
Sheathed bacteria	Morphologically resemble filamentous algae or fungi
Budding and/or appendaged bacteria	Appendages that concentrate metallic oxides
Spirochetes, spirals, and curved bacteria	Helically coiled or spiral morphology
Gram positive asporogenous rod-shaped	Similar to actinomycetes; including *Lactobacillus*
Actinomycetes and related organisms	Form branching filaments; including *Frankia*
Rickettsias	Obligate parasites that lack ATP production capability
Mycoplasmas	Only bacteria to lack cell wall