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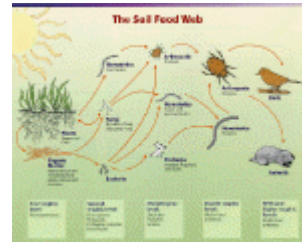
Soil Biology

The Soil Biology Primer

Chapter 1: THE SOIL FOOD WEB

By Elaine R. Ingham

SOIL BIOLOGY AND THE LANDSCAPE

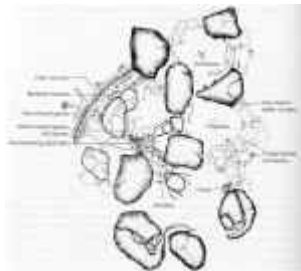


A Soil Food Web Glossary	
Autotrophs	These are animals with chlorophyll. They include trees, grasses, shrubs, and other plants.
Bacteria	Microscopic organisms that are usually not visible to the naked eye. They include many species of bacteria, including those that are beneficial to plants and animals.
Fungi	These include mushrooms, yeasts, and molds. They are important for decomposing organic matter and for their role in the soil food web.
Invertebrates	These are animals without a backbone. They include nematodes, insects, and earthworms.
Vertebrates	These are animals with a backbone. They include birds, mammals, and reptiles.
Decomposers	Organisms that break down dead organic matter into simpler substances that can be used by plants and animals.
Microbes	These are organisms that are too small to be seen with the naked eye. They include bacteria, fungi, and protozoa.
Producers	These are organisms that produce their own food through photosynthesis.
Consumers	These are organisms that eat other organisms for energy.
Herbivores	These are consumers that eat plants.
Carnivores	These are consumers that eat other animals.
Top-level	These are the highest level of consumers in a food web.

An incredible diversity of organisms make up the soil food web. They range in size from the tiniest one-celled bacteria, algae, fungi, and protozoa, to the more complex nematodes and micro-arthropods, to the visible earthworms, insects, small vertebrates, and plants.

As these organisms eat, grow, and move through the soil, they make it possible to have clean water, clean air, healthy plants, and moderated water flow.

There are many ways that the soil food web is an integral part of landscape processes. Soil organisms decompose organic compounds, including manure, plant residue, and pesticides, preventing them from entering water and becoming pollutants. They sequester nitrogen and other nutrients that might otherwise enter groundwater, and they fix nitrogen from the atmosphere, making it available to plants. Many organisms enhance soil aggregation and porosity, thus increasing infiltration and reducing runoff. Soil organisms prey on crop pests and are food for above-ground animals.



The soil environment. Organisms live in the microscale environments within and between soil particles. Differences over short distances in pH, moisture, pore size, and the types of food available create a broad range of habitats.

Credit: S. Rose and E.T. Elliott

THE FOOD WEB: ORGANISMS AND THEIR INTERACTION

The soil food web is the community of organisms living all or part of their lives in the soil. A food web diagram shows a series of conversions (represented by arrows) of energy and nutrients as one organism eats another (see food web diagram).

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All food webs are fueled by the primary producers: the plants, lichens, moss, photosynthetic bacteria, and algae that use the sun's energy to fix carbon dioxide from the atmosphere. Most other soil organisms get energy and carbon by consuming the organic compounds found in plants, other organisms, and waste by-products. A few bacteria, called chemoautotrophs, get energy from nitrogen, sulfur, or iron compounds rather than carbon compounds or the sun.

As organisms decompose complex materials, or consume other organisms, nutrients are converted from one form to another, and are made available to plants and to other soil organisms. All plants – grass, trees, shrubs, agricultural crops – depend on the food web for their nutrition.



WHAT DO SOIL ORGANISMS DO?

Growing and reproducing are the primary activities of all living organisms. As individual plants and soil organisms work to survive, they depend on interactions with each other. By-products from growing roots and plant residue feed soil organisms. In turn, soil organisms support plant health as they decompose organic matter, cycle nutrients, enhance soil structure, and control the populations of soil organisms including crop pests. (See table of functions of soil organisms.)

ORGANIC MATTER FUELS THE FOOD WEB

Soil organic matter is the storehouse for the energy and nutrients used by plants and other organisms. Bacteria, fungi, and other soil dwellers transform and release nutrients from organic matter (see photo).



These microshredders, immature oribatid mites, skeletonize plant leaves. This starts the nutrient cycling of carbon, nitrogen, and other elements.

Collohmannia sp. **Credit:** Roy A. Norton, College of Environmental Science & Forestry, State University of New York

Organic matter is many different kinds of compounds – some more useful to organisms than others. In general, soil organic matter is made of roughly equal parts humus and active organic matter. Active organic matter is the portion available to soil organisms. Bacteria tend to use simpler organic compounds, such as root exudates or fresh plant residue. Fungi tend to use more complex compounds, such as fibrous plant residues, wood and soil humus.

Intensive tillage triggers spurts of activity among bacteria and other organisms that consume organic matter (convert it to CO₂), depleting the active fraction first. Practices

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that build soil organic matter (reduced tillage and regular additions of organic material) will raise the proportion of active organic matter long before increases in total organic matter can be measured. As soil organic matter levels rise, soil organisms play a role in its conversion to humus—a relatively stable form of carbon sequestered in soils for decades or even centuries.

FOOD SOURCES FOR SOIL ORGANISMS

“Soil organic matter” includes all the organic substances in or on the soil. Here are terms used to describe different types of organic matter.

Living organisms: Bacteria, fungi, nematodes, protozoa, earthworms, arthropods, and living roots.

Dead plant material; organic material; detritus; surface residue: All these terms refer to plant, animal, or other organic substances that have recently been added to the soil and have only begun to show signs of decay. Detritivores are organisms that feed on such material.

Active fraction organic matter: Organic compounds that can be used as food by microorganisms. The active fraction changes more quickly than total organic matter in response to management changes.

Labile organic matter: Organic matter that is easily decomposed.

Root exudates: Soluble sugars, amino acids and other compounds secreted by roots.

Particulate organic matter (POM) or Light fraction (LF) organic matter: POM and LF have precise size and weight definitions. They are thought to represent the active fraction of organic matter which is more difficult to define. Because POM or LF is larger and lighter than other types of soil organic matter, they can be separated from soil by size (using a sieve) or by weight (using a centrifuge).

Lignin: A hard-to-degrade compound that is part of the fibers of older plants. Fungi can use the carbon ring structures in lignin as food.

Recalcitrant organic matter: Organic matter such as humus or lignin-containing material that few soil organisms can decompose.

Humus or humified organic matter: Complex organic compounds that remain after many organisms have used and transformed the original material. Humus is not readily decomposed because it is either physically protected inside of aggregates or chemically too complex to be used by most organisms. Humus is important in binding tiny soil aggregates, and improves water and nutrient holding capacity.

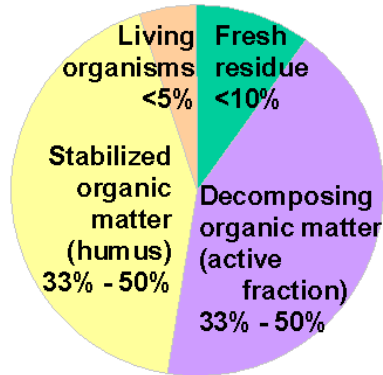
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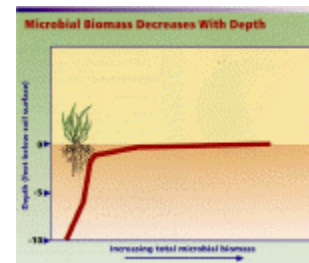
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Components of Soil Organic Matter



WHERE DO SOIL ORGANISMS LIVE?

The organisms of the food web are not uniformly distributed through the soil. Each species and group exists where they can find appropriate space, nutrients, and moisture. They occur wherever organic matter occurs – mostly in the top few inches of soil (see figure), although microbes have been found as deep as 10 miles (16 km) in oil wells.



Soil organisms are concentrated:

Around roots. The rhizosphere is the narrow region of soil directly around roots (see photo). It is teeming with bacteria that feed on sloughed-off plant cells and the proteins and sugars released by roots. The protozoa and nematodes that graze on bacteria are also concentrated near roots. Thus, much of the nutrient cycling and disease suppression needed by plants occurs immediately adjacent to roots.



Bacteria are abundant around this root tip (the rhizosphere) where they decompose the plentiful simple organic substances.
Credit: No. 53 from Soil Microbiology and Biochemistry Slide Set. 1976 J.P. Martin, et al., eds. SSSA, Madison WI.

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In litter. Fungi are common decomposers of plant litter because litter has large amounts of complex, hard-to-decompose carbon. Fungal hyphae (fine filaments) can “pipe” nitrogen from the underlying soil to the litter layer. Bacteria cannot transport nitrogen over distances, giving fungi an advantage in litter decomposition, particularly when litter is not mixed into the soil profile. However, bacteria are abundant in the green litter of younger plants which is higher in nitrogen and simpler carbon compounds than the litter of older plants. Bacteria and fungi are able to access a larger surface area of plant residue after shredder organisms such as earthworms, leaf-eating insects, millipedes, and other arthropods break up the litter into smaller chunks.

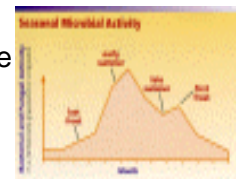
On humus. Fungi are common here. Much organic matter in the soil has already been decomposed many times by bacteria and fungi, and/or passed through the guts of earthworms or arthropods. The resulting humic compounds are complex and have little available nitrogen. Only fungi make some of the enzymes needed to degrade the complex compounds in humus.

On the surface of soil aggregates. Biological activity, in particular that of aerobic bacteria and fungi, is greater near the surfaces of soil aggregates than within aggregates. Within large aggregates, processes that do not require oxygen, such as denitrification, can occur. Many aggregates are actually the fecal pellets of earthworms and other invertebrates.

In spaces between soil aggregates. Those arthropods and nematodes that cannot burrow through soil move in the pores between soil aggregates. Organisms that are sensitive to desiccation, such as protozoa and many nematodes, live in water-filled pores. (See Figure page 1.)

WHEN ARE THEY ACTIVE?

The activity of soil organisms follows seasonal patterns, as well as daily patterns. In temperate systems, the greatest activity occurs in late spring when temperature and moisture conditions are optimal for growth (see graph). However, certain species are most active in the winter, others during dry periods, and still others in flooded conditions.



Not all organisms are active at a particular time. Even during periods of high activity, only a fraction of the organisms are busily eating, respiring, and altering their environment. The remaining portion are barely active or even dormant.

Many different organisms are active at different times, and interact with one another, with plants, and with the soil. The combined result is a number of beneficial functions including nutrient cycling, moderated water flow, and pest control.

THE IMPORTANCE OF THE SOIL FOOD WEB

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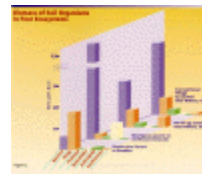
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The living component of soil, the food web, is complex and has different compositions in different ecosystems. Management of croplands, rangelands, forestlands, and gardens benefits from and affects the food web. The next unit of the Soil Biology Primer, “The Food Web & Soil Health,” introduces the relationship of soil biology to agricultural productivity, biodiversity, carbon sequestration and to air and water quality. The remaining six units of the Soil Biology Primer describe the major groups of soil organisms: bacteria, fungi, protozoa, nematodes, arthropods, and earthworms. For more information about the diversity within each organism group, see the list of readings at the end of “The Food Web & Soil Health” unit.

Chapter 2: THE FOOD WEB & SOIL HEALTH

By Elaine R. Ingham

HOW DO FOOD WEBS DIFFER?



Each field, forest, or pasture has a unique soil food web with a particular proportion of bacteria, fungi, and other groups, and a particular level of complexity within each group of organisms. These differences are the result of soil, vegetation, and climate factors, as well as land management practices. (See figure of food webs in different ecosystems.)

TYPICAL FOOD WEB STRUCTURES

The “structure” of a food web is the composition and relative numbers of organisms in each group within the soil system. Each type of ecosystem has a characteristic food web structure (see table of typical numbers of organisms in soil). Some features of food web structures include:

The ratio of fungi to bacteria is characteristic to the type of system. Grasslands and agricultural soils usually have bacterial-dominated food webs – that is, most biomass is in the form of bacteria. Highly productive agricultural soils tend to have ratios of fungal to bacterial biomass near 1:1 or somewhat less. Forests tend to have fungal-dominated food webs. The ratio of fungal to bacterial biomass may be 5:1 to 10:1 in a deciduous forest and 100:1 to 1000:1 in a coniferous forest.

Organisms reflect their food source. For example, protozoa are abundant where bacteria are plentiful. Where bacteria dominate over fungi, nematodes that eat bacteria are more numerous than nematodes that eat fungi.

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Management practices change food webs. For example, in reduced tillage agricultural systems, the ratio of fungi to bacteria increases over time, and earthworms and arthropods become more plentiful.

HOW IS THE FOOD WEB MEASURED?

The measurement techniques used to characterize a food web include:

Counting. Organism groups, such as bacteria, protozoa, arthropods, etc.; or subgroups, such as bacterial-feeding, fungal-feeding, and predatory nematodes, are counted and through calculations, can be converted to biomass.

Direct counts – counting individual organisms with the naked eye or with a microscope. All organisms can be counted, or only the active ones that take up a fluorescent stain (Figure 3).

Plate counts – counting the number of bacterial or fungal colonies that grow from a soil sample.

Measuring activity levels. Activity is determined by measuring the amount of by-products, such as CO₂, generated in the soil, or the disappearance of substances, such as plant residue or methane used by a large portion of the community or by specific groups of organisms.

These measurements reflect the total “work” the community can do. Total biological activity is the sum of activities of all organisms, though only a portion are active at a particular time.

Respiration – measuring CO₂ production. This method does not distinguish which organisms (plants, pathogens, or other soil organisms) are generating the CO₂.

Nitrification rates – measuring the activity of those species involved in the conversion of ammonium to nitrate.

Decomposition rates – measuring the speed of disappearance of organic residue or standardized cotton strips.

Measuring cellular constituents. The total biomass of all soil organisms or specific characteristics of the community can be inferred by measuring components of soil organisms such as the following.

Biomass carbon, nitrogen, or phosphorus – measure the amount of nutrients in living cells, which can then be used to estimate the total biomass of organisms. Chloroform

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fumigation is a common method used to estimate the amount of carbon or nitrogen in all soil organisms.

Enzymes – measure enzymes in living cells or attached to soil. Assays can be used to estimate potential activity or to characterize the biological community.

Phospholipids and other lipids – provide a “fingerprint” of the community, and quantify the biomass of groups such as fungi or actinomycetes.

DNA and RNA – provide a “fingerprint” of the community, and can detect the presence of specific species or groups.

WHAT IS COMPLEXITY?

Food web complexity is a factor of both the number of species and the number of different kinds of species in the soil. For example, a soil with ten species of bacterial-feeding nematodes is less complex than a soil with ten nematode species that includes bacterial-feeders, fungal-feeders, and predatory nematodes.



Complexity can be determined, in part, from a food web diagram such as Figure 4 (see diagram), which represents the soil in an old-growth Douglas fir forest. Each box of the food web diagram represents a functional group of organisms that perform similar roles in the soil system. Transfers of energy are represented by the arrows on the diagram and occur when one organism eats another. Complex ecosystems have more functional groups and more energy transfers than simple ecosystems.

The number of functional groups that turn over energy before the energy leaves the soil system is different (and characteristic) for each ecosystem (Figure 5). In the Douglas fir system (Figure 4), energy may undergo more than twenty transfers from organism to organism, or between functional groups. In contrast, a cave or low-residue cultivated system is not likely to include a large variety of higher predators on the right-hand side of a soil food web diagram. Energy and nutrients will be cycled through fewer types of organisms.

Land management practices can alter the number of functional groups – or complexity – in the soil. Intensively managed systems, such as cropland, have varied numbers of functional groups. Crop selections, tillage practices, residue management, pesticide use, and irrigation alter the habitat for soil organisms, and thus alter the structure and complexity of the food web.

BENEFITS OF COMPLEXITY

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Biological complexity of a soil system can affect processes such as nutrient cycling, the formation of soil structure, pest cycles, and decomposition rates. Researchers have yet to define how much and what kind of food web complexity in managed ecosystems is optimal for these soil processes.

Nutrient cycling. When organisms consume food, they create more of their own biomass and they release wastes. The most important waste for crop growth is ammonium (NH_4^+). Ammonium and other readily utilized nutrients are quickly taken up by other organisms, including plant roots. When a large variety of organisms are present, nutrients may cycle more rapidly and frequently among forms that plants can and cannot use.

Nutrient retention. In addition to mineralizing or releasing nitrogen to plants, the soil food web can immobilize or retain nitrogen when plants are not rapidly growing. Nitrogen in the form of soil organic matter and organism biomass is less mobile and less likely to be lost from the rooting zone than inorganic nitrate (NO_3^-) and ammonium (NH_4^+).

Improved structure, infiltration, and water-holding capacity. Many soil organisms are involved in the formation and stability of soil aggregates. Bacterial activity, organic matter, and the chemical properties of clay particles are responsible for creating microaggregates from individual soil particles. Earthworms and arthropods consume small aggregates of mineral particles and organic matter, and generate larger fecal pellets coated with compounds from the gut. These fecal pellets become part of the soil structure. Fungal hyphae and root hairs bind together and help stabilize larger aggregates. Improved aggregate stability, along with the burrows of earthworms and arthropods, increases porosity, water infiltration, and water-holding capacity.

Disease suppression. A complex soil food web contains numerous organisms that can compete with disease-causing organisms. These competitors may prevent soil pathogens from establishing on plant surfaces, prevent pathogens from getting food, feed on pathogens, or generate metabolites that are toxic to or inhibit pathogens.

Degradation of pollutants. An important role of soil is to purify water. A complex food web includes organisms that consume (degrade) a wide range of pollutants under a wide range of environmental conditions.

Biodiversity. Greater food web complexity means greater biodiversity. Biodiversity is measured by the total number of species, as well as the relative abundance of these species, and the number of functional groups of organisms.

MANAGEMENT AND SOIL HEALTH

A healthy soil effectively supports plant growth, protects air and water quality, and ensures human and animal health. The physical structure, chemical make-up, and

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biological components of the soil together determine how well a soil performs these services.

In every healthy system or watershed, the soil food web is critical to major soil functions including:

1. sustaining biological activity, diversity, and productivity;
2. regulating the flow of water and dissolved nutrients;
3. storing and cycling nutrients and other elements; and
4. filtering, buffering, degrading, immobilizing and detoxifying organic and inorganic materials that are potential pollutants.

The interactions among organisms enhance many of these functions.

Successful land management requires approaches that protect all resources, including soil, water, air, plants, animals and humans. Many management strategies change soil habitats and the food web, and alter soil quality, or the capacity of soil to perform its functions. Examples of some practices that change the complexity and health of the soil community include:

- Compared to a field with a 2-year crop rotation, a field with a 4 crops grown in rotation may have a greater variety of food sources (i.e., roots and surface residue), and therefore is likely to have more types of bacteria, fungi, and other organisms.
- A cleanly-tilled field with few vegetated edges may have fewer habitats for arthropods than a field broken up by grassed waterways, terraces, or fence rows.
- Although the effect of pesticides on soil organisms varies, high levels of pesticide use will generally reduce food web complexity. An extreme example is the repeated use of methyl bromide which has been observed to eliminate most soil organisms except a few bacteria species.

THE FOOD WEB AND CARBON SEQUESTRATION

Land management practices can be chosen to increase the amount of carbon sequestered as soil organic matter and reduce the amount of CO₂, a greenhouse gas, released to the atmosphere.

As the soil food web decomposes organic material, it releases carbon into the atmosphere as CO₂ or converts it to a variety of forms of soil organic matter. Labile or active fractions of organic matter stay in the soil for a few years. Stable forms reside in the soil for decades or hundreds of years. Physically stabilized organic matter is protected inside soil aggregates that soil organisms help create. Humified organic matter is stable because bacteria and fungi have helped form molecules that are too complex and large for soil organisms to decompose.

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LOOKING FORWARD

The functions of the food web are essential to plant growth and environmental quality. Good resource management will integrate food web-enhancing strategies into the regular activities of farms, ranches, forests, or in backyard gardens. Needed research will examine food web functions within whole systems, and will support technology development. Technology to assess and maintain the functions of soil food webs will be developed to assist land managers and researchers as they strive towards soil productivity and stewardship. In the coming years, we can expect progress at answering soil biology questions such as the following.

What is a healthy food web? What measurements or observations can be used to determine whether a particular biological community is desirable for the intended land use? What level of complexity is optimal for highly productive and sustainable crop, range or forest lands?

Is it more useful to count species, or types of organisms? The Soil Biology Primer divides food web organisms into six groups. Achieving an optimal balance of these groups is one approach to managing the food web. Alternatively, identifying the species and complexity present within a group may provide other useful information about the health and productive potential of a soil.

How should the biology of the soil be managed? In the future, land managers may be able to more precisely predict the effect of management decisions such as the timing of tillage, the application of a certain kind of compost, or the use of a particular pesticide. They may choose practices with the intent of making specific changes to the composition of the soil food web.

What are the costs and benefits of managing for soil biological functions? The costs to achieve a highly diverse, or complex, soil community need to be identified. These can be compared to the benefits of biological services provided, such as nutrient cycling, disease suppression, and soil structure enhancement.

Chapter 3: BACTERIA

By Elaine R. Ingham

THE LIVING SOIL: BACTERIA

Bacteria are tiny, one-celled organisms – generally 4/100,000 of an inch wide (1 μm) and somewhat longer in length. What bacteria lack in size, they make up in numbers. A

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teaspoon of productive soil generally contains between 100 million and 1 billion bacteria.
That is as much mass as two cows per acre.

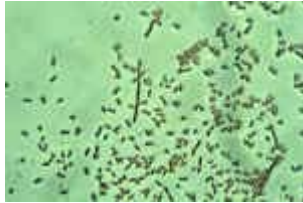


Figure 1: A ton of microscopic bacteria may be active in each acre of soil.

Credit: Michael T. Holmes, Oregon State University, Corvallis.



Figure 2: Bacteria dot the surface of strands of fungal hyphae.

Credit: R. Campbell. In R. Campbell. 1985. Plant Microbiology. Edward Arnold; London. P. 149. Reprinted with the permission of Cambridge University Press.

Bacteria fall into four functional groups. Most are decomposers that consume simple carbon compounds, such as root exudates and fresh plant litter. By this process, bacteria convert energy in soil organic matter into forms useful to the rest of the organisms in the soil food web. A number of decomposers can break down pesticides and pollutants in soil. Decomposers are especially important in immobilizing, or retaining, nutrients in their cells, thus preventing the loss of nutrients, such as nitrogen, from the rooting zone.

A second group of bacteria are the *mutualists* that form partnerships with plants. The most well-known of these are the nitrogen-fixing bacteria. The third group of bacteria is the *pathogens*. Bacterial pathogens include *Xymomonas* and *Erwinia* species, and species of *Agrobacterium* that cause gall formation in plants. A fourth group, called *lithotrophs* or *chemoautotrophs*, obtains its energy from compounds of nitrogen, sulfur, iron or hydrogen instead of from carbon compounds. Some of these species are important to nitrogen cycling and degradation of pollutants.

WHAT DO BACTERIA DO?

Bacteria from all four groups perform important services related to water dynamics, nutrient cycling, and disease suppression. Some bacteria affect water movement by producing substances that help bind soil particles into small aggregates (those with diameters of 1/10,000-1/100 of an inch or 2-200 μ m). Stable aggregates improve water infiltration and the soil's water-holding ability. In a diverse bacterial community, many organisms will compete with disease-causing organisms in roots and on aboveground surfaces of plants.

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A FEW IMPORTANT BACTERIA

Nitrogen-fixing bacteria form symbiotic associations with the roots of legumes like clover and lupine, and trees such as alder and locust. Visible nodules are created where bacteria infect a growing root hair (Figure 4). The plant supplies simple carbon compounds to the bacteria, and the bacteria convert nitrogen (N_2) from air into a form the plant host can use. When leaves or roots from the host plant decompose, soil nitrogen increases in the surrounding area.

Nitrifying bacteria change ammonium (NH_4^+) to nitrite (NO_2^-) then to nitrate (NO_3^-) – a preferred form of nitrogen for grasses and most row crops. Nitrate is leached more easily from the soil, so some farmers use nitrification inhibitors to reduce the activity of one type of nitrifying bacteria. Nitrifying bacteria are suppressed in forest soils, so that most of the nitrogen remains as ammonium.

Denitrifying bacteria convert nitrate to nitrogen (N_2) or nitrous oxide (N_2O) gas. Denitrifiers are anaerobic, meaning they are active where oxygen is absent, such as in saturated soils or inside soil aggregates.

Actinomycetes are a large group of bacteria that grow as hyphae like fungi (Figure 3). They are responsible for the characteristically “earthy” smell of freshly turned, healthy soil. Actinomycetes decompose a wide array of substrates, but are especially important in degrading recalcitrant (hard-to-decompose) compounds, such as chitin and cellulose, and are active at high pH levels. Fungi are more important in degrading these compounds at low pH. A number of antibiotics are produced by actinomycetes such as *Streptomyces*.



Figure 3: Actinomycetes, such as this *Streptomyces*, give soil its "earthy" smell.
Credit: No. 14 from Soil Microbiology and Biochemistry Slide Set. 1976. J.P. Martin, et al., eds. SSSA, Madison, WI



Figure 4: Nodules formed where *Rhizobium* bacteria infected soybean roots.
Credit: Stephen Temple, New Mexico State University

WHERE ARE BACTERIA?

Various species of bacteria thrive on different food sources and in different microenvironments. In general, bacteria are more competitive when labile (easy-to-metabolize) substrates are present. This includes fresh, young plant residue and the

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compounds found near living roots. Bacteria are especially concentrated in the rhizosphere, the narrow region next to and in the root. There is evidence that plants produce certain types of root exudates to encourage the growth of protective bacteria.

Bacteria alter the soil environment to the extent that the soil environment will favor certain plant communities over others. Before plants can become established on fresh sediments, the bacterial community must establish first, starting with photosynthetic bacteria. These fix atmospheric nitrogen and carbon, produce organic matter, and immobilize enough nitrogen and other nutrients to initiate nitrogen cycling processes in the young soil. Then, early successional plant species can grow. As the plant community is established, different types of organic matter enter the soil and change the type of food available to bacteria. In turn, the altered bacterial community changes soil structure and the environment for plants. Some researchers think it may be possible to control the plant species in a place by managing the soil bacteria community.

BUG BIOGRAPHY: Bacteria That Promote Plant Growth

By Ann Kennedy, USDA Agricultural Research Service, Pullman, WA

Certain strains of the soil bacteria *Pseudomonas fluorescens* have anti-fungal activity that inhibits some plant pathogens. *P. fluorescens* and other *Pseudomonas* and *Xanthomonas* species can increase plant growth in several ways. They may produce a compound that inhibits the growth of pathogens or reduces invasion of the plant by a pathogen. They may also produce compounds (growth factors) that directly increase plant growth.

These plant growth-enhancing bacteria occur naturally in soils, but not always in high enough numbers to have a dramatic effect. In the future, farmers may be able to inoculate seeds with anti-fungal bacteria, such as *P. fluorescens*, to ensure that the bacteria reduce pathogens around the seed and root of the crop.

Chapter 4: SOIL FUNGI

By Elaine R. Ingham

THE LIVING SOIL: FUNGI

Fungi are microscopic cells that usually grow as long threads or strands called hyphae, which push their way between soil particles, roots, and rocks. Hyphae are usually only several thousandths of an inch (a few micrometers) in diameter. A single hyphae can

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span in length from a few cells to many yards. A few fungi, such as yeast, are single cells.

Hyphae sometimes group into masses called mycelium or thick, cord-like “rhizomorphs” that look like roots. Fungal fruiting structures (mushrooms) are made of hyphal strands, spores, and some special structures like gills on which spores form. (See figure) A single individual fungus can include many fruiting bodies scattered across an area as large as a baseball diamond.

Fungi perform important services related to water dynamics, nutrient cycling, and disease suppression. Along with bacteria, fungi are important as decomposers in the soil food web. They convert hard-to-digest organic material into forms that other organisms can use. Fungal hyphae physically bind soil particles together, creating stable aggregates that help increase water infiltration and soil water holding capacity.

Soil fungi can be grouped into three general functional groups based on how they get their energy. *Decomposers* – saprophytic fungi – convert dead organic material into fungal biomass, carbon dioxide (CO₂), and small molecules, such as organic acids. These fungi generally use complex substrates, such as the cellulose and lignin, in wood, and are essential in decomposing the carbon ring structures in some pollutants. A few fungi are called “sugar fungi” because they use the same simple substrates as do many bacteria. Like bacteria, fungi are important for immobilizing, or retaining, nutrients in the soil. In addition, many of the secondary metabolites of fungi are organic acids, so they help increase the accumulation of humic-acid rich organic matter that is resistant to degradation and may stay in the soil for hundreds of years.

Mutualists – the mycorrhizal fungi – colonize plant roots. In exchange for carbon from the plant, mycorrhizal fungi help solubilize phosphorus and bring soil nutrients (phosphorus, nitrogen, micronutrients, and perhaps water) to the plant. One major group of mycorrhizae, the *ectomycorrhizae* (Figure 3), grow on the surface layers of the roots and are commonly associated with trees. The second major group of mycorrhizae are the *endomycorrhizae* that grow within the root cells and are commonly associated with grasses, row crops, vegetables, and shrubs. Arbuscular mycorrhizal (AM) fungi (Figure 4) are a type of endomycorrhizal fungi. Ericoid mycorrhizal fungi can be either ecto- or endomycorrhizal.

The third group of fungi, *pathogens* or *parasites*, cause reduced production or death when they colonize roots and other organisms. Root-pathogenic fungi, such as *Verticillium*, *Pythium*, and *Rhizoctonia*, cause major economic losses in agriculture each year. Many fungi help control diseases. For example, nematode-trapping fungi that parasitize disease-causing nematodes, and fungi that feed on insects may be useful as biocontrol agents.

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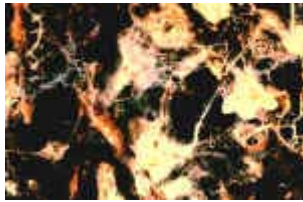


Figure 1: Many plants depend on fungi to help extract nutrients from the soil. Tree roots (brown) are connected to the symbiotic mycorrhizal structure (bright white) and fungal hyphae (thin white strands) radiating into the soil.

Credit: Randy Molina, Oregon State University, Corvallis

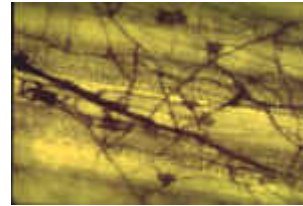


Figure 2: Fungus beginning to decompose leaf veins in grass clippings.

Credit: No. 48 from Soil Microbiology and Biochemistry Slide Set. 1976. J.P. Martin, et al., eds. SSSA, Madison WI.



Figure 3: Ectomycorrhizae are important for nutrient absorption by tree and grape roots. The fungus does not actually invade root cells but forms a sheath that penetrates between plant cells. The sheath in this photo is white, but they may be black, orange, pink, or yellow.

Credit: USDA, Forest Service, PNW Research Station, Corvallis, Oregon

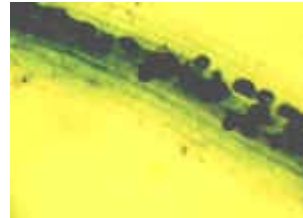


Figure 4: The dark, round masses inside the cells of this clover root are vesicles for the arbuscular mycorrhizal fungus (AM).

Credit: Elaine R. Ingham

WHERE ARE FUNGI?

Saprophytic fungi are commonly active around woody plant residue. Fungal hyphae have advantages over bacteria in some soil environments. Under dry conditions, fungi can bridge gaps between pockets of moisture and continue to survive and grow, even when soil moisture is too low for most bacteria to be active. Fungi are able to use nitrogen up from the soil, allowing them to decompose surface residue which is often low in nitrogen.

Fungi are aerobic organisms. Soil which becomes anaerobic for significant periods generally loses its fungal component. Anaerobic conditions often occur in waterlogged soil and in compacted soils.

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Fungi are especially extensive in forested lands. Forests have been observed to increase in productivity as fungal biomass increases.



Figure 5: In arid rangeland systems, such as southwestern deserts, fungi pipe scarce water and nutrients to plants.

Credit: Jerry Barrow, USDA-ARS Jornada Experimental Range, Las Cruces, NM.



Figure 6: Mushrooms, common in forest systems, are the fruiting bodies made by a group of fungi called basidiomycetes. Mushrooms are "the tip of the iceberg" of an extensive network of underground hyphae.

Credit: Ann Lewandowski, NRCS Soil Quality Institute

MYCORRHIZAL FUNGI IN AGRICULTURE

Mycorrhiza is a symbiotic association between fungi and plant roots and is unlike either fungi or roots alone. Most trees and agricultural crops depend on or benefit substantially from mycorrhizae. The exceptions are many members of the Cruciferae family (e.g., broccoli, mustard), and the Chenopodiaceae family (e.g. lambsquarters, spinach, beets), which do not form mycorrhizal associations. The level of dependency on mycorrhizae varies greatly among varieties of some crops, including wheat and corn.

Land management practices affect the formation of mycorrhizae. The number of mycorrhizal fungi in soil will decline in fallowed fields or in those planted to crops that do not form mycorrhizae. Frequent tillage may reduce mycorrhizal associations, and broad spectrum fungicides are toxic to mycorrhizal fungi. Very high levels of nitrogen or phosphorus fertilizer may reduce inoculation of roots. Some inoculums of mycorrhizal fungi are commercially available and can be added to the soil at planting time.



Figure 7: Mycorrhizal fungi link root cells to soil particles. In this photo, sand grains are bound to a root by hyphae from endophytes (fungi similar to mycorrhizae), and by

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polysaccharides secreted by the plant and the fungi.

Credit: Jerry Barrow, USDA-ARS Jornada Experimental Range, Las Cruces, NM.

Chapter 5: SOIL PROTOZOA

By Elaine R. Ingham

THE LIVING SOIL: PROTOZOA

Protozoa are single-celled animals that feed primarily on bacteria, but also eat other protozoa, soluble organic matter, and sometimes fungi. They are several times larger than bacteria – ranging from 1/5000 to 1/50 of an inch (5 to 500 μm) in diameter. As they eat bacteria, protozoa release excess nitrogen that can then be used by plants and other members of the food web.

Protozoa are classified into three groups based on their shape: *Ciliates* are the largest and move by means of hair-like cilia. They eat the other two types of protozoa, as well as bacteria. *Amoebae* also can be quite large and move by means of a temporary foot or “pseudopod.” Amoebae are further divided into *testate amoebae* (which make a shell-like covering) and *naked amoebae* (without a covering). *Flagellates* are the smallest of the protozoa and use a few whip-like flagella to move.



Figure 1: Protozoa play an important role in nutrient cycling by feeding intensively on bacteria. Notice the size of the speck-like bacteria next to the oval protozoa and large, angular sand particle.

Credit: Elaine R. Ingham



Figure 2: Bacteria ingested by an amoeba. *Credit: No. 35 from Soil Microbiology and Biochemistry Slide Set. 1976. J.P. Martin, et al., eds. SSSA, Madison, WI*

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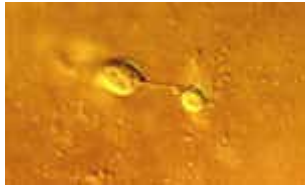


Figure 3: Flagellates have one or two flagella which they use to propel or pull their way through soil. A flagellum can be seen extending from the protozoan on the left. The tiny specks are bacteria.

Credit: Elaine R. Ingham

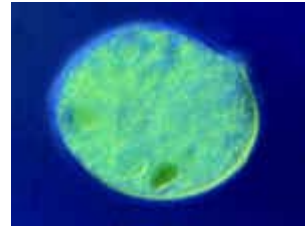


Figure 6: Ciliates are the largest of the protozoa and the least numerous. They consume up to ten thousand bacteria per day, and release plant available nitrogen. Ciliates use the fine cilia along their bodies like oars to move rapidly through soil.

Credit: Elaine R. Ingham

WHAT DO PROTOZOA DO?

Protozoa play an important role in mineralizing nutrients, making them available for use by plants and other soil organisms. Protozoa (and nematodes) have a lower concentration of nitrogen in their cells than the bacteria they eat. (The ratio of carbon to nitrogen for protozoa is 10:1 or much more and 3:1 to 10:1 for bacteria.) Bacteria eaten by protozoa contain too much nitrogen for the amount of carbon protozoa need. They release the excess nitrogen in the form of ammonium (NH₄⁺). This usually occurs near the root system of a plant. Bacteria and other organisms rapidly take up most of the ammonium, but some is used by the plant. (See figure for explanation of mineralization and immobilization.)



Another role that protozoa play is in regulating bacteria populations. When they graze on bacteria, protozoa stimulate growth of the bacterial population (and, in turn, decomposition rates and soil aggregation.) Exactly why this happens is under some debate, but grazing can be thought of like pruning a tree – a small amount enhances growth, too much reduces growth or will modify the mix of species in the bacterial community.

Protozoa are also an important food source for other soil organisms and help to suppress disease by competing with or feeding on pathogens.

WHERE ARE PROTOZOA?

Protozoa need bacteria to eat and water in which to move, so moisture plays a big role in determining which types of protozoa will be present and active. Like bacteria, protozoa are particularly active in the rhizosphere next to roots.

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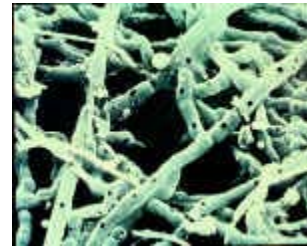
Typical numbers of protozoa in soil vary widely – from a thousand per teaspoon in low fertility soils to a million per teaspoon in some highly fertile soils. Fungal-dominated soils (e.g. forests) tend to have more testate amoebae and ciliates than other types. In bacterial-dominated soils, flagellates and naked amoebae predominate. In general, high clay-content soils contain a higher number of smaller protozoa (flagellates and naked amoebae), while coarser textured soils contain more large flagellates, amoebae of both varieties, and ciliates.

NEMATODES AND PROTOZOA

Protozoa and bacterial-feeding nematodes compete for their common food resource: bacteria. Some soils have high numbers of either nematodes or protozoa, but not both. The significance of this difference to plants is not known. Both groups consume bacteria and release NH_4^+ .

BUG BIOGRAPHY: Soil Dwelling Vampires

Most protozoa eat bacteria, but one group of amoebae, the vampyrellids, eat fungi. The perfectly round holes drilled through the fungal cell wall, much like the purported puncture marks on the neck of a vampire's victim, are evidence of the presence of vampyrellid amoebae. The amoebae attach to the surface of fungal hyphae and generate enzymes that eat through the fungal cell wall. The amoeba then sucks dry or engulfs the cytoplasm inside the fungal cell before moving on to its next victim.



Vampyrellids attack many fungi including root pathogens, such as *Gaeumannomyces graminis*, shown in the photo. This fungus attacks wheat roots and causes take-all disease.

Chapter 6: NEMATODES

By Elaine R. Ingham

THE LIVING SOIL: NEMATODES

Nematodes are non-segmented worms typically 1/500 of an inch (50 μm) in diameter and 1/20 of an inch (1 mm) in length. Those few species responsible for plant diseases have received a lot of attention, but far less is known about the majority of the nematode community that plays beneficial roles in soil.

An incredible variety of nematodes function at several trophic levels of the soil food web. Some feed on the plants and algae (first trophic level); others are grazers that feed on bacteria and fungi (second trophic level); and some feed on other nematodes (higher trophic levels).

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Free-living nematodes can be divided into four broad groups based on their diet. *Bacterial-feeders* consume bacteria. *Fungal-feeders* feed by puncturing the cell wall of fungi and sucking out the internal contents. *Predatory nematodes* eat all types of nematodes and protozoa. They eat smaller organisms whole, or attach themselves to the cuticle of larger nematodes, scraping away until the prey's internal body parts can be extracted. *Omnivores* eat a variety of organisms or may have a different diet at each life stage. *Root-feeders* are plant parasites, and thus are not free-living in the soil.



Figure 1: Most nematodes in the soil are not plant parasites. Beneficial nematodes help control disease and cycle nutrients.
Credit: Elaine R. Ingham

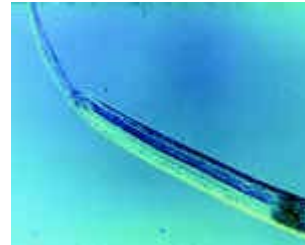


Figure 2: A predatory nematode consumes a smaller nematode.
Credit: Kathy Merrifield, Oregon State University, Corvallis.

WHAT DO NEMATODES DO?

Nutrient cycling. Like protozoa, nematodes are important in mineralizing, or releasing, nutrients in plant-available forms. When nematodes eat bacteria or fungi, ammonium (NH₄⁺) is released because bacteria and fungi contain much more nitrogen than the nematodes require.

Grazing. At low nematode densities, feeding by nematodes stimulates the growth rate of prey populations. That is, bacterial-feeders stimulate bacterial growth, plant-feeders stimulate plant growth, and so on. At higher densities, nematodes will reduce the population of their prey. This may decrease plant productivity, may negatively impact mycorrhizal fungi, and can reduce decomposition and immobilization rates by bacteria and fungi. Predatory nematodes may regulate populations of bacterial-and fungal-feeding nematodes, thus preventing over-grazing by those groups. Nematode grazing may control the balance between bacteria and fungi, and the species composition of the microbial community.

Dispersal of microbes. Nematodes help distribute bacteria and fungi through the soil and along roots by carrying live and dormant microbes on their surfaces and in their digestive systems.

Food source. Nematodes are food for higher level predators, including predatory nematodes, soil microarthropods, and soil insects. They are also parasitized by bacteria and fungi.

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Disease suppression and development. Some nematodes cause disease. Others consume disease-causing organisms, such as root-feeding nematodes, or prevent their access to roots. These may be potential biocontrol agents.



Figure 3: Fungal-feeding nematodes have small, narrow stylets, or spears, in their stoma (mouth) which they use to puncture the cell walls of fungal hyphae and withdraw the cell fluid. This interaction releases plant-available nitrogen from fungal biomass.

Credit: Elaine R. Ingham



Figure 4: This bacterial-feeding nematode, *Elaphonema*, has ornate lip structures that distinguish it from other nematodes. Bacterial-feeders release plant-available nitrogen when they consume bacteria.

Credit: Elaine R. Ingham



Figure 5: The *Pratylenchus*, or lesion nematode, has a shorter, thicker stylet in its mouth than the root feeder in Figure 6.

Credit: Kathy Merrifield, Oregon State University, Corvallis



Figure 6: Root-feeding nematodes use their stylets to puncture the thick cell wall of plant root cells and siphon off the internal contents of the plant cell. This usually causes economically significant damage to crops. The curved stylet seen inside this nematode is characteristic of the genus *Trichodorus*.

Credit: Elaine R. Ingham

WHERE ARE NEMATODES?

Nematodes are concentrated near their prey groups. Bacterial-feeders abound near roots where bacteria congregate; fungal-feeders are near fungal biomass; root-feeders are concentrated around roots of stressed or susceptible plants. Predatory nematodes are more likely to be abundant in soils with high numbers of nematodes.

Because of their size, nematodes tend to be more common in coarser-textured soils. Nematodes move in water films in large (>1/500 inch or 50 μm) pore spaces.

Agricultural soils generally support less than 100 nematodes in each teaspoon (dry gram) of soil. Grasslands may contain 50 to 500 nematodes, and forest soils generally

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hold several hundred per teaspoon. The proportion of bacterial-feeding and fungal-feeding nematodes is related to the amount of bacteria and fungi in the soil. Commonly, less disturbed soils contain more predatory nematodes, suggesting that predatory nematodes are highly sensitive to a wide range of disturbances.

NEMATODES AND SOIL QUALITY

Nematodes may be useful indicators of soil quality because of their tremendous diversity and their participation in many functions at different levels of the soil food web. Several researchers have proposed approaches to assessing the status of soil quality by counting the number of nematodes in different families or trophic groups.* In addition to their diversity, nematodes may be useful indicators because their populations are relatively stable in response to changes in moisture and temperature (in contrast to bacteria), yet nematode populations respond to land management changes in predictable ways. Because they are quite small and live in water films, changes in nematode populations reflect changes in soil microenvironments.

*Blair, J. M. et al. 1996. Soil invertebrates as indicators of soil quality. In *Methods for Assessing Soil Quality*, SSSA Special Publication 49, pp. 273-291.

BUG BIOGRAPHY: Nematode Trappers

One group of fungi may be a useful biological control agent against parasitic nematodes. These predatory fungi grow through the soil, setting out traps when they detect signs of their prey. Some species use sticky traps, others make circular rings of hyphae to constrict their prey. When the trap is set, the fungi put out a lure, attracting nematodes that are looking for lunch. The nematode, however, becomes lunch for the fungus.

Chapter 7: ARTHROPODS

By Andrew R. Moldenke, Oregon State University

THE LIVING SOIL: ARTHROPODS

Many bugs, known as arthropods, make their home in the soil. They get their name from their jointed (arthros) legs (podos). Arthropods are invertebrates, that is, they have no backbone, and rely instead on an external covering called an exoskeleton.



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Figure 1: The 200 species of mites in this microscope view were extracted from one square foot of the top two inches of forest litter and soil. Mites are poorly studied, but enormously significant for nutrient release in the soil.

Credit: Val Behan-Pelletier, Agriculture and Agri-Food Canada

Arthropods range in size from microscopic to several inches in length. They include insects, such as springtails, beetles, and ants; crustaceans such as sowbugs; arachnids such as spiders and mites; myriapods, such as centipedes and millipedes; and scorpions.

Nearly every soil is home to many different arthropod species. Certain row-crop soils contain several dozen species of arthropods in a square mile. Several thousand different species may live in a square mile of forest soil.

Arthropods can be grouped as shredders, predators, herbivores, and fungal-feeders, based on their functions in soil. Most soil-dwelling arthropods eat fungi, worms, or other arthropods. Root-feeders and dead-plant shredders are less abundant. As they feed, arthropods aerate and mix the soil, regulate the population size of other soil organisms, and shred organic material.

SHREDDERS

Many large arthropods frequently seen on the soil surface are shredders. Shredders chew up dead plant matter as they eat bacteria and fungi on the surface of the plant matter. The most abundant shredders are millipedes and sowbugs, as well as termites, certain mites, and roaches. In agricultural soils, shredders can become pests by feeding on live roots if sufficient dead plant material is not present.



Figure 3: Millipedes are also called Diplopods because they possess two pairs of legs on each body segment. They are generally harmless to people, but most millipedes protect themselves from predators by spraying an offensive odor from their skunk glands. This desert-



Figure 4: Sowbugs are relatives of crabs and lobsters. Their powerful mouth-parts are used to fragment plant residue and leaf litter.

Credit: Gerhard Eisenbeis and Wilfried Wichard. 1987. Atlas on the Biology of Soil Arthropods. Springer-Verlag, New York. P.

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dwelling giant millipede is about 8 inches long. 111.

Orthoporus ornatus.

Credit: David B. Richman, New Mexico State University, Las Cruces.

PREDATORS

Predators and micropredators can be either generalists, feeding on many different prey types, or specialists, hunting only a single prey type. Predators include centipedes, spiders, ground-beetles, scorpions, skunk-spiders, pseudoscorpions, ants, and some mites. Many predators eat crop pests, and some, such as beetles and parasitic wasps, have been developed for use as commercial biocontrols.



Figure 7: This 1/8 of an inch long spider lives near the soil surface where it attacks other soil arthropods. The spider's eyes are on the tip of the projection above its head.
Walckenaera acuminata.
Credit: Gerhard Eisenbeis and Wilfried Wichard. 1987. Atlas on the Biology of Soil Arthropods. Springer-Verlag, New York. P. 23.

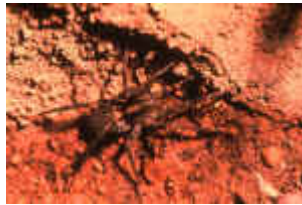


Figure 8: The wolf-spider wanders around as a solitary hunter. The mother wolf-spider carries her young to water and feeds them by regurgitation until they are ready to hunt on their own.
Credit: Trygve Steen, Portland State University, Portland, Oregon.

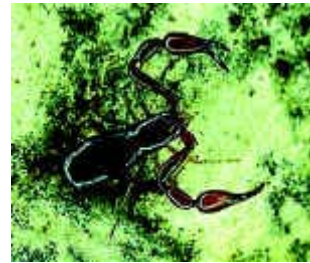


Figure 9: The pseudoscorpion looks like a baby scorpion, except it has no tail. It produces venom from glands in its claws and silk from its mouth parts. It lives in the soil and leaf litter of grasslands, forests, deserts and croplands. Some hitchhike under the wings of beetles.
Credit: David B. Richman, New Mexico State University, Las Cruces

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Figure 10: Long, slim centipedes crawl through spaces in the soil preying on earthworms and other soft-skinned animals. Centipede species with longer legs are familiar around homes and in leaf litter.

Credit: No. 40 from Soil Microbiology and Biochemistry Slide Set. 1976. J.P. Martin, et al., eds. SSSA, Madison, WI



Figure 11: Predatory mites prey on nematodes, springtails, other mites, and the larvae of insects. This mite is 1/25 of an inch (1mm) long. *Pergamasus sp.*

Credit: Gerhard Eisenbeis and Wilfried Wichard. 1987. Atlas on the Biology of Soil Arthropods. Springer-Verlag, New York. P. 83.



Figure 12: The powerful mouthparts on the tiger beetle (a carabid beetle) make it a swift and deadly ground-surface predator. Many species of carabid beetles are common in cropland.

Credit: Cicindlla campestris. D.I. McEwan/Aguila Wildlife Images

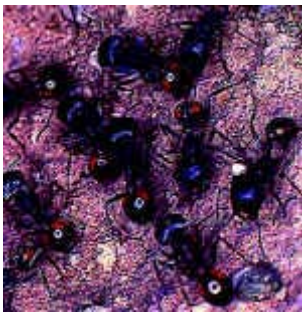


Figure 13: Rugose harvester ants are scavengers rather than predators. They eat dead insects and gather seeds in grasslands and deserts where they burrow 10 feet into the ground. Their sting is 100 times more powerful

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than a fire ant sting.

Pogonomyrmex rugosus

Credit: David B. Richman,

New Mexico State

University, Las Cruces.

HERBIVORES

Numerous root-feeding insects, such as cicadas, mole-crickets, and anthomyiid flies (root-maggots), live part of all of their life in the soil. Some herbivores, including rootworms and symphylans, can be crop pests where they occur in large numbers, feeding on roots or other plant parts.



Figure 14: The symphylan, a relative of the centipede, feeds on plant roots and can become a major crop pest if its population is not controlled by other organisms.

Credit: Ken Gray Collection, Department of Entomology, Oregon State University, Corvallis.

FUNGAL FEEDERS

Arthropods that graze on fungi (and to some extent bacteria) include most springtails, some mites, and silverfish. They scrape and consume bacteria and fungi off root surfaces. A large fraction of the nutrients available to plants is a result of microbial-grazing and nutrient release by fauna.



Figure 17: This pale-colored and blind springtail is typical of fungal-feeding springtails that live deep in the surface layer of natural and agricultural soils throughout the world.

Figure 18: Oribatid turtle-mites are among the most numerous of the microarthropods. This millimeter-long species feeds on fungi.

Euzetes globulus

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*Credit: Andrew R. Moldenke, Oregon
State University, Corvallis*

*Credit: Gerhard Eisenbeis and Wilfried
Wichard. 1987. Atlas on the Biology of Soil
Arthropods. Springer-Verlag, New York. P.
103*

WHAT IS IN YOUR SOIL?

If you would like to see what kind of organisms are in your soil, you can easily make a pitfall trap to catch large arthropods, and a Burlese funnel to catch small arthropods.

Make a pitfall trap by sinking a pint- or quart-sized container (such as a yogurt cup) into the ground so the rim is level with the soil surface. If desired, fashion a roof over the cup to keep the rain out, and add 1/2 of an inch of non-hazardous antifreeze to the cup to preserve the creatures and prevent them from eating one another. Leave in place for a week and wait for soil organisms to fall into the trap.

To make a Burlese funnel, set a piece of 1/4 inch rigid wire screen in the bottom of a funnel to support the soil. (A funnel can be made by cutting the bottom off a plastic soda bottle.) Half fill the funnel with soil, and suspend it over a cup with a bit of anti-freeze or ethyl alcohol in the bottom as a preservative.

Suspend a light bulb about 4 inches over the soil to drive the organisms out of the soil and into the cup. Leave the light bulb on for about 3 days to dry out the soil. Then pour the alcohol into a shallow dish and use a magnifying glass to examine the organisms.

WHAT DO ARTHROPODS DO?

Although the plant feeders can become pests, most arthropods perform beneficial functions in the soil-plant system.

Shred organic material. Arthropods increase the surface area accessible to microbial attack by shredding dead plant residue and burrowing into coarse woody debris. Without shredders, a bacterium in leaf litter would be like a person in a pantry without a can-opener – eating would be a very slow process. The shredders act like can-openers and greatly increase the rate of decomposition. Arthropods ingest decaying plant material to eat the bacteria and fungi on the surface of the organic material.

Stimulate microbial activity. As arthropods graze on bacteria and fungi, they stimulate the growth of mycorrhizae and other fungi, and the decomposition of organic matter. If grazer populations get too dense the opposite effect can occur – populations of bacteria and fungi will decline. Predatory arthropods are important to keep grazer populations under control and to prevent them from over-grazing microbes.

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Mix microbes with their food. From a bacterium's point-of-view, just a fraction of a millimeter is infinitely far away. Bacteria have limited mobility in soil and a competitor is likely to be closer to a nutrient treasure. Arthropods help out by distributing nutrients through the soil, and by carrying bacteria on their exoskeleton and through their digestive system. By more thoroughly mixing microbes with their food, arthropods enhance organic matter decomposition.

Mineralize plant nutrients. As they graze, arthropods mineralize some of the nutrients in bacteria and fungi, and excrete nutrients in plant-available forms.

Enhance soil aggregation. In most forested and grassland soils, every particle in the upper several inches of soil has been through the gut of numerous soil fauna. Each time soil passes through another arthropod or earthworm, it is thoroughly mixed with organic matter and mucus and deposited as fecal pellets. Fecal pellets are a highly concentrated nutrient resource, and are a mixture of the organic and inorganic substances required for growth of bacteria and fungi. In many soils, aggregates between 1/10,000 and 1/10 of an inch (0.0025mm and 2.5mm) are actually fecal pellets.

Burrow. Relatively few arthropod species burrow through the soil. Yet, within any soil community, burrowing arthropods and earthworms exert an enormous influence on the composition of the total fauna by shaping habitat. Burrowing changes the physical properties of soil, including porosity, water-infiltration rate, and bulk density.

Stimulate the succession of species. A dizzying array of natural bio-organic chemicals permeates the soil. Complete digestion of these chemicals requires a series of many types of bacteria, fungi, and other organisms with different enzymes. At any time, only a small subset of species is metabolically active – only those capable of using the resources currently available. Soil arthropods consume the dominant organisms and permit other species to move in and take their place, thus facilitating the progressive breakdown of soil organic matter.

Control pests. Some arthropods can be damaging to crop yields, but many others that are present in all soils eat or compete with various root- and foliage-feeders. Some (the specialists) feed on only a single type of prey species. Other arthropods (the generalists), such as many species of centipedes, spiders, ground-beetles, rove-beetles, and gamasid mites, feed on a broad range of prey. Where a healthy population of generalist predators is present, they will be available to deal with a variety of pest outbreaks. A population of predators can only be maintained between pest outbreaks if there is a constant source of non-pest prey to eat. That is, there must be a healthy and diverse food web.

A fundamental dilemma in pest control is that tillage and insecticide application have enormous effects on non- target species in the food web. Intense land use (especially monoculture, tillage, and pesticides) depletes soil diversity. As total soil diversity

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declines, predator populations drop sharply and the possibility for subsequent pest outbreaks increases.

WHERE DO ARTHROPODS LIVE?

The abundance and diversity of soil fauna diminishes significantly with soil depth. The great majority of all soil species are confined to the top three inches. Most of these creatures have limited mobility, and are probably capable of “cryptobiosis,” a state of “suspended animation” that helps them survive extremes of temperature, wetness, or dryness that would otherwise be lethal.

As a general rule, larger species are active on the soil surface, seeking temporary refuge under vegetation, plant residue, wood, or rocks. Many of these arthropods commute daily to forage within herbaceous vegetation above, or even high in the canopy of trees. (For instance, one of these tree-climbers is the caterpillar-searcher used by foresters to control gypsy moth). Some large species capable of true burrowing live within the deeper layers of the soil.

Below about two inches in the soil, fauna are generally small – 1/250 to 1/10 of an inch. (Twenty-five of the smallest of these would fit in a period on this page.) These species are usually blind and lack prominent coloration. They are capable of squeezing through minute pore spaces and along root channels. Sub-surface soil dwellers are associated primarily with the rhizosphere (the soil volume immediately adjacent to roots).

ABUNDANCE OF ARTHROPODS

A single square yard of soil will contain 500 to 200,000 individual arthropods, depending upon the soil type, plant community, and management system. Despite these large numbers, the biomass of arthropods in soil is far less than that of protozoa and nematodes.

In most environments, the most abundant soil dwellers are springtails and mites, though ants and termites predominate in certain situations, especially in desert and tropical soils. The largest number of arthropods are in natural plant communities with few earthworms (such as conifer forests). Natural communities with numerous earthworms (such as grassland soils) have the fewest arthropods. Apparently, earthworms out-compete arthropods, perhaps by excessively reworking their habitat or eating them incidentally. However, within pastures and farm lands arthropod numbers and diversity are generally thought to increase as earthworm populations rise. Burrowing earthworms probably create habitat space for arthropods in agricultural soils.

BUG BIOGRAPHY: Springtails

Springtails are the most abundant arthropods in many agricultural and rangeland soils. populations of tens of thousands per square

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yard are frequent. When foraging, springtails walk with 3 pairs of legs like most insects, and hold their tail tightly tucked under the belly. If attacked by a predator, body fluid rushes into the tail base, forcing the tail to slam down and catapult the springtail as much as a yard away. Springtails have been shown to be beneficial to crop plants by releasing nutrients and by feeding upon diseases caused by fungi.

Chapter 8: EARTHWORMS

by Clive A. Edwards, The Ohio State University

THE LIVING SOIL: EARTHWORMS

Of all the members of the soil food web, earthworms need the least introduction. Most people become familiar with these soft, slimy, invertebrates at a young age. Earthworms are hermaphrodites, meaning that they exhibit both male and female characteristics.

They are major decomposers of dead and decomposing organic matter, and derive their nutrition from the bacteria and fungi that grow upon these materials. They fragment organic matter and make major contributions to recycling the nutrients it contains.

Earthworms occur in most temperate soils and many tropical soils. They are divided into 23 families, more than 700 genera, and more than 7,000 species. They range from an inch to two yards in length and are found seasonally at all depths in the soil.

In terms of biomass and overall activity, earthworms dominate the world of soil invertebrates, including arthropods.



Figure 1: Earthworms generate tons of casts per acre each year, dramatically altering soil structure.

Credit: Clive A. Edwards, The Ohio State University, Columbus.



Figure 2: A corn leaf pulled into a night crawler burrow.

Credit: Soil and Water Management Research Unit, USDA-Agricultural Research Service, St. Paul, Minnesota.

WHAT DO EARTHWORMS DO?

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Earthworms dramatically alter soil structure, water movement, nutrient dynamics, and plant growth. They are not essential to all healthy soil systems, but their presence is usually an indicator of a healthy system. Earthworms perform several beneficial functions.

Stimulate microbial activity. Although earthworms derive their nutrition from microorganisms, many more microorganisms are present in their feces or casts than in the organic matter that they consume. As organic matter passes through their intestines, it is fragmented and inoculated with microorganisms. Increased microbial activity facilitates the cycling of nutrients from organic matter and their conversion into forms readily taken up by plants.

Mix and aggregate soil. As they consume organic matter and mineral particles, earthworms excrete wastes in the form of casts, a type of soil aggregate. Charles Darwin calculated that earthworms can move large amounts of soil from the lower strata to the surface and also carry organic matter down into deeper soil layers. A large proportion of soil passes through the guts of earthworms, and they can turn over the top six inches (15 cm) of soil in ten to twenty years.

Increase infiltration. Earthworms enhance porosity as they move through the soil. Some species make permanent burrows deep into the soil. These burrows can persist long after the inhabitant has died, and can be a major conduit for soil drainage, particularly under heavy rainfall. At the same time, the burrows minimize surface water erosion. The horizontal burrowing of other species in the top several inches of soil increases overall porosity and drainage.

Improve water-holding capacity. By fragmenting organic matter, and increasing soil porosity and aggregation, earthworms can significantly increase the water-holding capacity of soils.

Provide channels for root growth. The channels made by deep-burrowing earthworms are lined with readily available nutrients and make it easier for roots to penetrate deep into the soil.

Bury and shred plant residue. Plant and crop residue are gradually buried by cast material deposited on the surface and as earthworms pull surface residue into their burrows.

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Figure 3: A mixture of soil and organic matter within an earthworm burrow. Earthworms incorporate large amounts of organic matter into the soil.

Credit: Clive A. Edwards, The Ohio State University, Columbus.

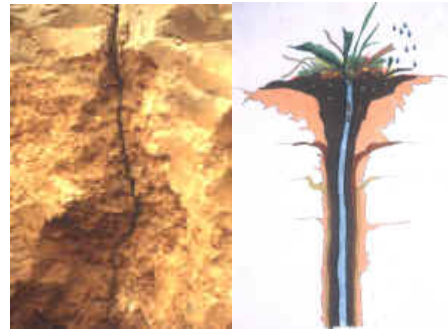


Figure 4: Some worms live in permanent vertical burrows such as these. Others move horizontally near the surface, filling their burrow with casts as they move.

Credit: North Appalachian Experimental Watershed, USDA-Agricultural Research Service, Coshocton, Ohio.

WHERE ARE EARTHWORMS?

Different species of earthworms inhabit different parts of the soil and have distinct feeding strategies. They can be separated into three major ecological groups based on their feeding and burrowing habits. All three groups are common and important to soil structure.

Surface soil and litter species – Epigeic species. These species live in or near surface plant litter. They are typically small and are adapted to the highly variable moisture and temperature conditions at the soil surface. The worms found in compost piles are epigeic and are unlikely to survive in the low organic matter environment of soil.

Upper soil species – Endogeic species. Some species move and live in the upper soil strata and feed primarily on soil and associated organic matter (geophages). They do not have permanent burrows, and their temporary channels become filled with cast material as they move through the soil, progressively passing it through their intestines.

Deep-burrowing species – Anecic species. These earthworms, which are typified by the “night crawler,” *Lumbricus terrestris*, inhabit more or less permanent burrow systems that may extend several meters into the soil. They feed mainly on surface litter that they pull into their burrows. They may leave plugs, organic matter, or cast (excreted soil and mineral particles) blocking the mouth of their burrows.

LOOKING FOR EARTHWORMS?

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It is easy to determine whether you have an adequate population of earthworms in your soil. Look for their casts in the forms of little piles of soil, mineral particles, or organic matter at the soil surface. They can be seen moving over the soil surface or even breeding, particularly on warm, damp nights. Dump a spadeful of moist soil into a bucket or onto a sheet of plastic, and sort through for earthworms. Can you identify different species? To find the deep burrowing species, pour a dilute mustard solution onto the soil. Many will quickly come to the soil surface in response to this irritant.

ABUNDANCE AND DISTRIBUTION OF EARTHWORMS

The majority of temperate and many tropical soils support significant earthworm populations. A square yard of cropland in the United States can contain from 50-300 earthworms, or even larger populations in highly organic soils. A similar area of grassland or temperate woodlands will have from 100-500 earthworms. Based on their total biomass, earthworms are the predominant group of soil invertebrates in most soils.

The family of earthworms that is most important in enhancing agricultural soil is Lumbricidae, which includes the genera *Lumbricus*, *Aporrectodea*, and several others. Lumbricids originated in Europe and have been transported by human activities to many parts of the world. The United States has only one or two known native species of lumbricids. Others were brought to this country by settlers (probably in potted plants from Europe), and were distributed down the waterways.

Generally, lumbricids are much more common in the north and east than in the drier south and west of the United States. They tend to be more abundant in loam and clay loam and even in silty soil, than in sandy soil and heavy clay. Populations also build up in irrigated soil. Earthworm populations tend to increase with soil organic matter levels and decrease with soil disturbances, such as tillage and potentially harmful chemicals.



Figure 5: Casts at the soil surface are evidence that earthworms are shredding, mixing, and burying surface residue.

Credit: Soil and Water Management Research Unit, USDA-Agricultural Research Service, St. Paul, Minnesota.



Figure 6: This earthworm burrow is an opening in an otherwise crusted soil surface.

Credit: Clive A. Edwards, The Ohio State University, Columbus.

INTERACTIONS OF EARTHWORMS WITH OTHER MEMBERS OF THE FOOD WEB

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The lives of earthworms and microbes are closely intertwined. Earthworms derive their nutrition from fungi, bacteria, and possibly protozoa and nematodes, and they promote the activity of these organisms by shredding and increasing the surface area of organic matter and making it more available to small organisms.

Earthworms also influence other soil-inhabiting invertebrates by changing the amount and distribution of organic matter and microbial populations. There is good evidence that earthworm activity affects the spatial distribution of soil microarthropod communities in the soil.

Earthworms have few invertebrate enemies, other than flatworms and a species of parasitic fly. Their main predators are a wide range of birds and mammals that prey upon them at the soil surface.

EARTHWORMS AND WATER QUALITY

Earthworms improve water infiltration and water holding capacity because their shredding, mixing, and defecating enhances soil structure. In addition, burrows provide quick entry for water into and through soil. High infiltration rates help prevent pollution by minimizing runoff, erosion, and chemical transport to surface waters.

There is concern that burrows may increase the transport of pollutants, such as nitrates or pesticides, into groundwater. However, the movement of potential pollutants through soil is not a straightforward process and it is not clear when earthworm activity will or will not have a negative impact on groundwater quality.

Whether pollutants reach groundwater depends on a number of factors, including the location of pollutants on the surface or within soil, the quantity and intensity of rain, how well water moves into and through other parts of the soil, and characteristics of the burrows. The horizontal burrows of endogeic earthworms (such as *Aporrectodea tuberculata*, which are common in Midwestern fields) do not transport water and solutes as deeply as the vertical burrows of night crawlers (*L. terrestris*) and other anecic species. Even vertical burrows, however, are not direct channels for water movement. They have bends and turns and are lined with organic matter that adsorbs many potential pollutants from the water.

Although there is much more to learn about how earthworms affect water movement through soil, they clearly help minimize pollution of surface waters by improving infiltration rates and decreasing runoff.

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Figure 7: A mound of organic matter was moved aside to expose the entrance to a burrow. *L. terrestris* will quickly replug its burrow if its mound is removed.

Credit: North Appalachian Experimental Watershed, USDA-Agricultural Research Service, Coshocton, Ohio.



Figure 8: *L. terrestris* mating, and earthworm cocoons. Earthworms mate periodically throughout the year, except when environmental conditions are unfavorable. The worms form slime tubes to help adhere to each other during copulation which may take as long as an hour. After the worms separate, they each produce a cocoon. One or two worms will hatch from a cocoon after several weeks. *L. terrestris* cocoons are about a quarter inch long.

Credit: Clive A. Edwards, The Ohio State University, Columbus.

BUG BIOGRAPHY: Night Crawlers and Tillage

The substitution of conventional tillage by no-till or conservation tillage is increasingly common and widely adopted in the United States and elsewhere. In these situations, earthworms, particularly the “night crawler,” *Lumbricus terrestris* L., are especially important. Earthworms become the main agent for incorporating crop residue into the soil by pulling some into their burrows and by slowly burying the remainder under casts laid on the soil surface.

In reduced tillage systems, surface residue builds up and triggers growth in earthworm populations. Earthworms need the food and habitat provided by surface residue, and they eat the fungi that become more common in no-till soils. As earthworm populations increase, they pull more and more residue into their burrows, helping to mix organic matter into the soil, improving soil structure and water infiltration.

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