SOIL BIOLOGY AND TREE GROWTH

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Soil Biology

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Introduction

Forest soils harbor an enormous variety of life forms that principally derive their energy from organic matter produced by photosynthesis and shed from plant structures and from animals. The major biological components of forest soils are plant roots, microbes, and soil animals. As other articles deal with tree roots (*see* **Soils and Site**: Tree Roots and their Interaction with Soil) and the mycorrhizal and rhizosphere organisms associated with them (*see* **Soils and Site**: Soil Organic Matter), this article will concentrate on the freeliving microbial and faunal components of the soil biota. Together these organisms play a critical part in the function of forest ecosystems through their role in organic matter breakdown, decomposition, and release of materials to the soil environment and atmosphere. Through these processes they have a positive influence on the availability of nutrients for plant growth and on soil structure.

Forest Soil Biota

The structure of cells and the way they obtain energy gives rise to the fundamental classification of all life forms. Two domains, prokaryotes and eukaryotes, and six kingdoms are recognized. There are two kingdoms within the prokaryotes, bacteria and archaea; within the eukaryotes are the four kingdoms – protoctista (under revision), plantae, fungi, and animalia (**Table 1**). Viruses are less than 0.3 μm in size and make a negligible contribution to microbial biomass and ecology in forest soils; they are not discussed further here. All these life forms have representatives in forest soils; indeed it is thought that soils provide habitat for the majority of earth's biodiversity. The extent of microbial diversity in soil remains largely unknown (**Table 2**), mainly due to the difficulties of studying such small organisms that have simple morphology. Furthermore, only a small percentage of the soil microbial community responds to cultivation in laboratory media, so that only a small fraction of them has been isolated and cultured. The best evidence for the vast biodiversity among soil biota is derived from molecular techniques, some of which are listed in **Table 3**. Overall, there is an extremely high diversity of decomposer species in forest soils that is undoubtedly related to the heterogeneity of the forest soil environment. This diversity ensures the maintenance of matter and energy fluxes and it confers resistance against disturbances to decomposition. For example, both fungi and heterotrophic bacteria play a role in nitrification, particularly in acid forest soils.

Despite recent advances in our knowledge of the range of bacteria occurring in soils, we have little knowledge of the ecology and biogeography of most microorganisms in forest soils. The relatively recent application of rRNA sequence analyses in determining the phylogenetic relationships between organisms has led to some reclassification within and among microbial groups.

Prokaryotes

From an evolutionary point of view the prokaryotes were the first life form to appear, evolving about 3.5 billion years ago. Prokaryotes are molecules surrounded by a membrane and cell wall; they lack subcellular membrane-enclosed organelles.

Bacteria

The bacteria are single-celled prokaryotic organisms that lack a true nucleus, and at between 0.2 and 1 μm in length they are among the smallest forms of life in forest soils. They have rigid cell walls and, where motile, move by means of a flagellum. There are three basic cell shapes among the bacteria: cocci, rods, and spirals. Among the 12 or so phyla of bacteria, three are generally associated with forest soils: the purple bacteria, the Gram-positive bacteria,

Table 1 Overview of the major biota found in forest soils. The dashed line shows the division of biota according to size

Size group	*Cell type*	*Kingdom or domain*	*Important groups found in forest soils*	*Example subgroup or genus*
Microflora (0.1 μm–10 μm)	Prokaryotes	Archaea	Methanogenic archaea	*Methanobacterium, Methanococcus*
		Bacteria	Purple bacteria	Nitrifying bacteria
			Sporogenic bacilli	Bacillales
			Cyanobacteria	Nostocales
			Actinomycetes	Thermomonosporas
	Eukaryotes	Mycota or fungi	Zygomycota	Zygomycetes, *Mucor*
			Ascomycota	Ascomycetes, *Aspergillus*
			Basidiomycota	Mushrooms, *Agaricus, Gloeophyllum*
			Deuteromycota	Deuteromycetes, *Arthrobotrys*
		Protoctista	Algae	Chlorophyta, *Chlorella*
			Oomycetes	Saprolegionales, *Phythium*
Microfauna (body width< 100 μm)			Ciliophora	Ciliates, *Paramecium*
			Sarcomastigophora	Naked and testate amoebae
			Mycetozoa	*Dictyostellium*, *Acrasis*
		Animalia	Nematodes	Nematodes
Mesofauna (body width 100 μm to 2 μm)			Rotifers	Rotifers
			Microarthropods	Acari (mites)
				Collembola (springtails)
			Annelids	Enchytraeidae (enchytraeids)
Macrofauna (body size generally ranges from 2 mm to 20 mm, but may be greater)				Lumbricidae (earthworms)
			Macroarthropods	Megascolecidae (earthworms)
				Hymenoptera (ants)
				Isoptera (termites)
				Chilopoda (centipedes)
				Diplopoda (millipedes)
				Pauropoda (pauropods)
				Isopoda (crustaceans)
				Coleoptera (beetles/weevils)
				Mollusca (mollusks)
Macroflora		Plantae		Plant roots

Adapted from Coleman DC and Crossley DA (1996) *Fundamentals of Soil Ecology*. London: Academic Press and Lavelle P and Spain AV (2001) *Soil Ecology*. London: Kluwer.

Table 2 Known and estimated total species numbers

Group	*Known species*	*Estimated total species*	*Percentage known*
Vascular plants	220 000	270 000	81
Bryophytes	17 000	25 000	68
Algae	40 000	60 000	67
Fungi	69 000	1 500 000	5
Bacteria	3 000	30 000	10
Viruses	5 000	130 000	4

Adapted from Coleman DC and Crossley DA (1996) *Fundamentals of Soil Ecology*. London: Academic Press.

and the cyanobacteria. These bacterial groups are capable of exploiting a wide range of energy sources – a trait that is important in the functional processes of forest ecosystems. Overall, because bacteria are not able to penetrate organic material their progress as cellulose decomposers is limited to the surface erosion of substrates; their rate of substrate breakdown is proportional to the rate at which exoenzymes are produced and diffuse out from the bacterial colonies. The purple bacteria cover a diverse range of metabolism including aerobes, anaerobes, chemoautotrophs, chemoheterotrophs, and chemophototrophs. The Gram-positive bacteria include the actinomycetes and the sporogenic bacilli. Members of both these groups (including the free-living *Clostridium*) are able to fix atmospheric nitrogen. The cyanobacterial group comprises obligate photoautotrophs that occur in unicellular, colonial, and filamentous forms with cell diameters usually within 1.0 to 10 μm. The relatively recent development of 16S ribosomal RNA (rRNA) gene sequence studies has revealed evidence in soil of bacterial divisions not usually associated with soil, including green nonsulfur bacteria, planctomycetes, spirochaetes, and novel methane-producing archaea.

Table 3 Examples of current methods for analyzing microbial diversity in soils and their application

Method	*Comments*
Culturing of microbes	Generally not representative of biota present
16S rRNA gene sequence analysis with polymerase chain reaction amplification	Provides identification of members of a community
In situ hybridization	Can be used to identify metabolically active microorganisms
Substrate utilization	Measures metabolic diversity
Flow cytometry	Enumeration of microorganisms
Terminal restriction fragment length polymorphisms	Comparative analysis
Polymerase chain reaction amplification or expression cloning	Functional diversity targeted
RNA dot or slot block	Representation of metabolically active members of a community

Reproduced with permission from Rondon MR, Goodman RM, and Handelsman J (1999) The Earth's bounty: assessing and accessing soil microbial diversity. *Trends in Biotechnology* 17(10): 403–409.

Archaea

This group has generally been known as the archaeabacteria, with recent studies preferring to call them archaea because of significant differences in their cell structure compared with bacteria. Members of this classification are subdivided into a range of groups on the basis of photosynthetic ability, means of locomotion, and nature of the cell wall where one is present. The archaea lack a muramic acid component in their cell walls, which contain branch-chained, ether-linked lipids that differ greatly from cell walls in eukaryotes. This radically different cell wall structure has led some taxonomists to claim that, in evolutionary terms, archaeans are more distant from the bacteria than are animals. Although the group includes organisms capable of flourishing in extreme conditions not usually associated with forests (e.g., the extreme halophytes and extreme thermophiles), there are a few reports of archaea occurring in nonextreme environments in forest soils. In addition, a number of groups may be important under certain conditions in forest soils; among these are the methane-producing archaea (methanogens; e.g., *Methanobacterium, Methanococcus*) and the thermoacidophiles (*Sulpholobus, Acidothermus*). The latter group are chemoautotrophic sulfur archaea capable of transforming sulfur forms in soil. In boreal forest soils the first reports of the genetic diversity among archaea have begun appearing in the literature over the last 5 years.

Eukaryotes

The eukaryotes appeared about 1.5 billion years ago. The basic eukaryote cell consists of a plasma membrane, glycocalyx, cytoplasm, cytoskeleton, and membrane-enclosed subcellular organelles. All of the soil animals and fungi are eukaryotes.

Fungi

The fungi (Mycota) are eukaryotic organisms that have a mycelial structure formed from slender filaments or hyphae (2–10 μm in diameter) that may be unbranched or branched, septate or nonseptate and which are commonly multinucleate. The fungi are subdivided on differences in mycelium structure and method of reproduction. Some of the main classes common in forest soils include the chytridiomycetes, the zygomycetes, the ascomycetes, and the basidiomycetes. Despite the wide range of fungi they are all chemoheterotrophic and in forest soils most are aerobic. None of the fungi is capable of fixing nitrogen from the atmosphere. Fungi are particularly prevalent in forest soils because of their ability to decompose lignin, which is a major component of wood, and to tolerate a wide range of soil pH. Fungi use exoenzymes to decompose substrates and their filamentous habit allows them to invade and ramify through substrates, applying mechanical pressure with their elongating hyphae. In this way fungi are able to import nutrients to enable them to break down substrates. These life-form advantages of fungi in decomposition mean that only in anaerobic habitats, such as waterlogged soils, do the bacteria predominate over the fungi. Fungi are the most abundant decomposing organisms in aerated forest soils, with typical biomass ranges of 500–5000 $kg\,ha^{-1}$. In the forest floor the fungi can represent between 10% and 60% of the total biomass; only plant roots exceed them in terms of biomass in soil.

Soil Fauna

Based on body size, habitat preference, and food consumed, soil fauna are generally assigned to one of three functional groups – microfauna, mesofauna or macrofauna (**Table 1**). In forests, approximately 90% of the soil faunal biomass is usually found in the top 10 cm of humus and soil. The relative abundance of soil fauna changes among forests at different latitudes; macrofauna tend to be more abundant in the tropics than they are in temperate regions, while microfauna are often more common in temperate regions than in the tropics. The microfauna, of which nematodes and protozoa are the major taxa, are single-celled fauna with a body width of $<100\,\mu m$; they lack mitochondria and live in water-filled pores and water films around soil particles. Some are motile. Most are heterotrophic and feed by engulfing their prey, usually other soil microbes. They are predominantly restricted to the topsoil for this reason. Among the protozoa are a number of groups that are common in forest soils – the ciliates, the amoebae, and the slime molds. Ciliates (Phylum Ciliaphora) are mostly freeliving in water films in soil; they feed by grazing on bacteria and particulate organic matter. Amoebas (Subphylum Sarcodina) are either naked or shelled, with the encased or testate amoebae largely inhabiting freshwater and moist soils. Slime molds (Phylum Mycetozoa) are divided into cellular and true slime molds, both of which are found in moist soils where they feed on live bacteria. The mesofauna, including the microarthropods, such as mites, collembolans (wingless insects), and enchytraeid worms, have a body width of 100 μm to 2 mm. The mesofauna are litter-transformers that produce organic structures in the form of faecal pellets that act as incubators for microbial digestion; their effect on soil structure is minimal.

The macrofauna, often termed ecosystem engineers, include earthworms, ants, termites, myriapods (centipedes and millipedes), snails, and slugs. Their body size generally ranges from 2 to 20 mm but may be much greater, particularly in the case of earthworms. The macrofauna directly or indirectly modulate the availability of resources and microhabitats for other soil biota by causing physical changes to the soil environment and biotic materials. While the role of the larger soil animals such as earthworms in litter mixing with other soil components is accepted, their role in decomposition is largely unknown. We know that earthworms ingest and move organic material but the extent of direct decomposition by soil animals is relatively unknown.

Energy Sources and Modes of Nutrition of Soil Biota

Soil microorganisms in forest ecosystems function through control of decomposition and the release of materials from organic substrates. In particular, they mediate carbon (C), phosphorus (P), nitrogen (N) and sulfur (S) biogeochemical cycling. The way in which soil microorganisms satisfy their demands for energy and nutrients is a guide to their particular role in the flow of energy and nutrients in forests and, more broadly, to their role in ecosystem function. A useful functional classification of these organisms is based on the nature of their principal carbon sources and energy. On the basis of principal carbon source organisms are classified as either autotrophic (inorganic C source; mostly CO_2; also referred to as lithotrophic) or heterotrophic (organic C source; diverse range of compounds; also referred to as organotrophic). In a similar way, organisms are classified based on their energy source; those using radiant energy (phototrophs) and those dependent on energy released during chemical oxidation (chemotrophs) (**Table 4**). Microorganisms regulate a wide range of processes critical to forest ecosystem function including denitrification, sulfate reduction, methanogenesis, and manganese reduction (see **Table 5** for a comprehensive listing of chemoautotrophic transformations).

Heterotrophs and Autotrophs

The vast majority (>90% biomass) of bacteria and fungi in forest soils are chemoheterotrophic (derive

Table 4 Energy and carbon sources for classes of soil organisms

Class of soil organism	*Energy source for generating ATP*	*Source of carbon for the cell*	*Example of organisms*
Photoautotroph	Light	CO_2	Cyanobacteria, plants
Chemoautotroph	Inorganic compounds	CO_2	Non-purple sulfur bacteria
Photoheterotroph	Light	CO_2, organic matter	Bacteria
Chemoheterotroph	Organic matter	Organic matter	Most bacteria, fungi

Table 5 Physiological groups of soil chemoautotrophs

Physiological group	*Life form*	*Energy source*	*Oxidized end product*	*Organism*
Hydrogen bacteria	Bacteria	H_2	H_2O	*Alcaligenes, Pseudomonas*
Methanogens	Archaea	H_2	H_2O	*Methanococcus*
Carboxydobacteria	Bacteria	CO	CO_2	*Rhodospirillum, Azotobacter*
Ammonium oxidizing bacteria	Bacteria	NH_3	NO_2^-	*Nitrosomonas*
Nitrite oxidizing bacteria	Bacteria	NO_2^-	NO_3^-	*Nitrobacter*
Sulfur oxidizers	Bacteria	H_2S or S	SO_4^{2-}	*Thiobacillus*
	Archaea	H_2S or S		*Sulfolobus*
Iron bacteria	Bacteria	Fe^{2+}	Fe^{3+}	*Gallionella, Thiobacillus*

both energy and materials for cell growth from an organic substrate). Because of the dominance of this group in most soil conditions they are often simply referred to as the heterotrophs. In well-aerated forest soils, aerobic heterotrophic respiration dominates, but fermentation and anaerobic respiration take over as soils become waterlogged. Among the bacteria two groups of heterotrophic nitrifiers exist, one oxidizing ammonium and the other the various organic forms of N including hydroxylamine, amino acids, peptones, oximes, and some aromatic compounds. Autotrophic microflora carry out a wide range of transformations and also play a critical role in ecosystem functioning. **Table 5** summarizes the major groups and end products of these organisms. Foremost in forest soils are the chemoautotrophic nitrifying bacteria that are responsible for the transformation of ammonium (NH_4^+) into nitrite (NO_2^-) and nitrate (NO_3^-). Autotrophs grow more slowly and are less abundant in soil than heterotrophs, due to their lower energy yield. Despite this there is good evidence to show that chemoautotrophic bacteria are the main nitrifying agents in most acid forest soils.

Activities and Impacts of Soil Biota in Forest Ecosystems

Forest floor litter type provides evidence of differences in composition and activity of forest soil biota. The activity of soil biota is directly related to the three humus forms generally recognized in forests (see **Table 6**). A mull humus results from the rapid disappearance of leaf litter under the influence of a wide range of faunal groups (macro-, meso-, and microfauna). Mull is typical of grasslands and deciduous forests and is associated with rapid litter decomposition and relatively nutrient-rich soils. A mor humus is characterized by the accumulation of undecomposed plant remains that form a distinct organic horizon overlying the mineral soil. Compared with mull humus, biological activity is low in a mor with minimal animal and lignin-decomposing fungal activity. This humus type is associated with acidic surface soils, cool to cold climates and relatively nutrient-poor soils. Typically, mor humus is associated with coniferous forests where decomposition of the acidic litter is dominated by saprophytic fungi; and the 'ecosystem engineer' functional group is dominated by ants rather than deep-burrowing earthworms, which tend to be acid-sensitive. Moder humus is intermediate between mull and mor, with reduced macrofaunal activity compared with a mull and a microflora dominated by fungi due to the predominantly acid conditions. Moder humus forms are mainly found in deciduous and coniferous forests.

Functional Groups Among Forest Soil Biota

Each group of soil organisms contributes either directly or indirectly to the breakdown of organic matter, decomposition and the release of nutrients back into the soil environment for plant growth (**Table 7**). The following section outlines the roles of microbial and faunal organisms in the process of decomposition. In forest ecosystems only about 1.5–5% of primary production is consumed by herbivores. A very large portion of primary production is consumed by the soil organisms. The microbial component of the soil biota is the main consumer of this organic matter in forest soils, being responsible for over 90% of decomposition and mineralization. The soil fauna play an important role in the physical breakdown or comminution of litter that a exposes a surface area for subsequent microbial attack.

The Decomposers

Bacteria and fungi drive the decomposition and release of nutrient ions from organic substrates; they are central to the functioning of forest ecosystems and more broadly to the functioning of the biosphere. Soil microorganisms are unable directly to ingest the often large and complex range of

Table 6 Summary of biological features associated with the three main humus forms found in forests

Characteristic	*Mull*	*Moder*	*Mor*
Biodiversity and productivity	High	Medium	Low
Phenolic content of litter	Low	Medium	High
Humification rate	Rapid	Slow	Very slow
Mycorrhizal partners	Zygomycetes	Basidiomycetes	Ascomycetes
Faunal group dominant in biomass	Earthworms	Enchytraeids	None
Microbial group dominant in biomass	Bacteria	Fungi	None

Reproduced with permission from Ponge J-F (2003) Humus forms in terrestrial ecosystems: a framework to biodiversity. *Soil Biology and Biochemistry* 35: 935–945.

Table 7 Influences of soil biota on soil processes in forest ecosystems

Group	*Nutrient cycling*	*Soil structure*
Microflora (fungi, bacteria, actinomycetes)	Catabolize organic matter; mineralize and immobilize nutrients	Produce organic compounds that bind aggregates; hyphae entangle particles into aggregates
Microfauna (e.g., protozoa, nematodes)	Regulate bacterial and fungal populations; alter nutrient turnover	May affect aggregate structure through interactions with microflora
Mesofauna (e.g., Acarina, Collembola, enchytraeids)	Regulate fungal and microfaunal populations; alter nutrient turnover; fragment plant residues	Produce fecal pellets; create biopores; promote humification
Macrofauna (e.g., isopods, centipedes, millipedes, earthworms)	Fragment plant residues; stimulate microbial activity	Mix organic and mineral particles; redistribute organic matter and microorganisms; create biopores; promote humification; produce fecal pellets

Adapted from Hendrix PF, Crossley DA Jr, Blair JM, and Coleman DC (1990) Soil biota as components of sustainable ecosystems. In: Edwards CA *et al.* (eds) *Sustainable Agricultural Systems*, pp. 637–654. IA: Soil and Water Conservation Society.

molecules that comprise soil organic matter; instead they secrete enzymes that digest organic matter outside the cell and they accumulate nutrients – either from the decomposing substrate or the surrounding soil solution – against a concentration gradient; most are aerobic. Overall, fungi are a crucial link in terrestrial nutrient cycling as they are involved in decomposition, in mycorrhizal associations, and in predatory and pathogenic activities. The activity and abundance of fungi in forest soils can be assessed by a number of means including analysis for ergosterol (a major sterol found in most fungi but not in higher plants) that can be used to measure fungal penetration of plant material. Another relatively recent and promising line of investigation is analysis for C and N stable isotope abundance in fungal sporocarps, a technique that can differentiate between ectomycorrhizal and saprotrophic forest fungi. For example, forest basidiomycetes become enriched in ^{13}C relative to their bulk C source, and either enriched or depleted in ^{15}N relative to atmospheric N. The coupling of molecular marker methods with stable isotope abundance in biomarkers offers considerable promise in linking bacterial identity with function in the environment. These molecular and isotope techniques are likely to become important diagnostic tools and will help elucidate ecological roles of various fungi and bacteria in the field.

The Ecosystem Engineers

Soil fauna play an indirect role in decomposition and mineralization through regulation and stimulation of microbial populations, fragmentation of plant residue and alteration of the physical soil environment. From a functional perspective, organisms that regulate the availability of resources to other species by physically rearranging biotic materials – to modify, maintain and/or create habitats – have become known as ecosystem engineers. Foremost among ecosystem engineers in forest soils are earthworms and termites. The natural tilling effect of earthworms in soils has been long known; they may pass up to 30 tonnes ha^{-1} of soil through their bodies, some of which is excreted as casts which may be enriched in nutrients relative to bulk soil.

Climate Change, Forest Management, and Soil Biota

Impact on Soil Processes

There is considerable interest in fluxes of CO_2, N_2O, and CH_4 from forest soils because of the potential for climate change to alter emission rates of these greenhouse gases. Soil organic matter (SOM) is a major pool of carbon and its magnitude and dynamics are largely controlled by soil microbial activity. For this reason, there is interest in improving our understanding of humus formation and degradation as controlled by soil microorganisms; however, research into the direct effects of increased atmospheric CO_2 on the soil microbial community is not sufficient to predict outcomes. Where nitrogen deposition or inputs to forests are high there is concern for increased N_2O emissions through either heterotrophic denitrification or, possibly, through leakage from autotrophic nitrification. For example, N_2O emissions of the order of 1–4 kg N ha^{-1} $year^{-1}$ occur from spruce forests in southern Germany, where N deposition is around 30 kg N ha^{-1} $year^{-1}$. These N_2O emissions are thought to result mainly from the activities of facultative anaerobic heterotrophs, such as *Pseudomonas*, that switch to NO_3^- as

Table 8 Denitrifying bacteria in soil, and their metabolism and energy source – an example of the diverse range of organisms potentially involved in converting nitrate to gaseous N in forest soils

Denitrifying organism	*Metabolism*	*Energy source*
Pseudomonas	Chemoheterotroph	Soil organic matter
Paracoccus denitrificans	Chemoautotroph	H_2
Thiobacillus denitrificans	Chemoautotroph	Reduced S
Rhodopseudomonas	Photoautotroph	Light

a terminal electron acceptor when O_2 diffusion is limited by high soil moisture. There is also some evidence of N_2O production in woodland soils by heterotrophic fungi, where NO_3^- is used as an alternative for O_2 in respiration, and denitrification occurs simultaneously. Because of the broad range of processes with potential to produce N_2O in forest soils (summarized in **Table 8**), further studies are required to determine the impacts of forest management and climate change on N_2O emissions. There has been considerable interest in the impacts of forest management on methane (CH_4)-oxidizing bacteria because temperate forests are major sinks for atmospheric CH_4. For example, forest clear-cutting can reduce the activity of methane-oxidizing bacteria and therefore the net CH_4 consumption in forest soils; changes that apparently result from the inhibition of CH_4 oxidation by elevated soil inorganic N. Less invasive forms of management such as thinning have been associated with increased CH_4 consumption.

Impact on Species Composition and Abundance

Determining the impact of climate change and forest management on soil biota and the critical processes they mediate in forest soils remains a significant challenge for the future. For example, the current literature indicates that there is not enough information to predict the impact of increased atmospheric CO_2 on the soil microbial community. Progress towards this task will rely on linking, through empirical testing, functional groups and key species among the soil biota with key processes maintaining ecosystem stability, such as decomposition and nitrogen fixation. In this way the contributions of the huge diversity of soil biota may be simplified to allow a better understanding of changes in the soil environment on ecosystem processes and stability.

Further Reading

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Soil and its Relationship to Forest Productivity and Health

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Forest Soil and its Functions

Soil is a mixture of mineral materials, organic matter, water, air, and plant and animal life. It varies in depth from a few centimeters to several meters across most of the earth's terrestrial surface. Its rock, sand, silt, clay, and organic matter physical composition varies in texture and structure, which controls the infiltration, percolation, and storage of water and the balance between water and air in its pore space. The amount and nature of clay and organic matter and the influence of parent material and vegetation largely control its chemistry and level of fertility. Soil also contains and is made up of myriad macro-, meso-, and microorganisms, both plant and animal, essential for organic matter decomposition, nutrient cycling, energy conversion, and soil formation processes. Soils vary greatly across the landscape