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THE SOIL HABITAT

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At first sight nothing seems more obvious than that everything has a beginning and an end and that everything can be subdivided into smaller parts. Nevertheless, for entirely speculative reasons the philosophers of Antiquity, especially the Stoics, concluded this concept to be quite unnecessary. The prodigious development of physics has now reached the same conclusion as those philosophers, Empedocles and Democritus in particular, who lived around 500 BCE and for whom even ancient man had a lively admiration. (Svante Arrhenius, Nobel Lecture, 1903)

INTRODUCTION

Soil is the naturally occurring, unconsolidated mineral and organic material at the earth's surface that provides an environment for living organisms. Recently, it has been referred to as the earth's "critical zone" and as deserving special status, because of its role in controlling the earth's environment and thus affecting the sustainability of life on the planet. This concept, that the earth's physicochemical properties are tightly coupled to the activity of the living organisms it supports, was proposed in the early 1970s by James Lovelock as the Gaia hypothesis. He theorized that the Earth behaved as a superorganism, with an intrinsic ability to control its own climate and chemistry and thus maintain an environment favorable for life. However, it is only microorganisms that have proven they can sustain the biosphere and can do so even without larger organisms.

The soil is where living organisms, or the biosphere, interact with rocks and minerals (geosphere), water (hydrosphere), atmosphere, and dead organic matter (detritosphere). Scientists study soil because of the fundamental need to understand the dynamics of geochemical–biochemical–biophysical interactions at the earth’s surface, especially in light of recent and ongoing changes in global climate. What complicates this study is that while geochemical fluxes between the hydrosphere, atmosphere, and geosphere may take place over the time span of hundreds to millions of years, biologically induced fluxes between the geosphere, atmosphere, biosphere, and detritosphere take place over a much shorter time frame, hours and days to months.

The soil habitat is defined as the totality of living organisms inhabiting soil, including plants, animals, and microorganisms, and their abiotic environment. The exact nature of the habitat in which the community of organisms is living is determined by a complex interplay of geology, climate, and plant vegetation. This interaction of rock and parent material with temperature, rainfall, elevation, latitude, exposure to sun and wind, and many more factors, over broad geographical regions with similar environmental conditions and characteristic plant communities, has evolved into the current terrestrial biomes with their associated soils (Fig. 2.1).

Because soils provide such a tremendous range of habitats, they support an enormous biomass, with an estimated 2.6×10^{29} prokaryotic cells alone, and harbor much of the earth’s genetic diversity—a single gram of soil contains kilometers of fungal hyphae and more than 10^9 bacterial cells, organisms belonging to tens of thousands of different species. Micro-zones of good aeration may be only millimeters from areas poorly aerated. Areas near the soil surface may be enriched with decaying organic matter and other nutrients, whereas the subsoil may be nutrient poor; the soil solution in some pores may be highly acidic, others more basic, depending on soil mineralogy and biological activity. Temperature and water contents of surface soil can vary widely from that of subsoils; and the microenvironment of the surfaces of soil particles, where nutrients are concentrated and water films vary in thickness, is very different from that of soil pores.

SOIL GENESIS AND FORMATION OF THE SOIL HABITAT

By definition, soils are greater than 10 cm thick if formed from minerals and extend from the earth’s surface into the underlying parent material from which they are formed. Soil may even be covered with water to a depth of up to 0.5 m as in coastal tidal marshes or inland water areas where bodies of periodically submerged soils merge into bodies of water in the natural landscape.

When plant residues are submerged in water for prolonged periods of the year and availability of O_2 is limited, biological decay is slowed and organic matter in various stages of decomposition accumulates. Deposits containing >30% organic matter and extending to depths of ~ 0.5 m or more form organic soils, and they include peatland, muck or bog, and fen soils.

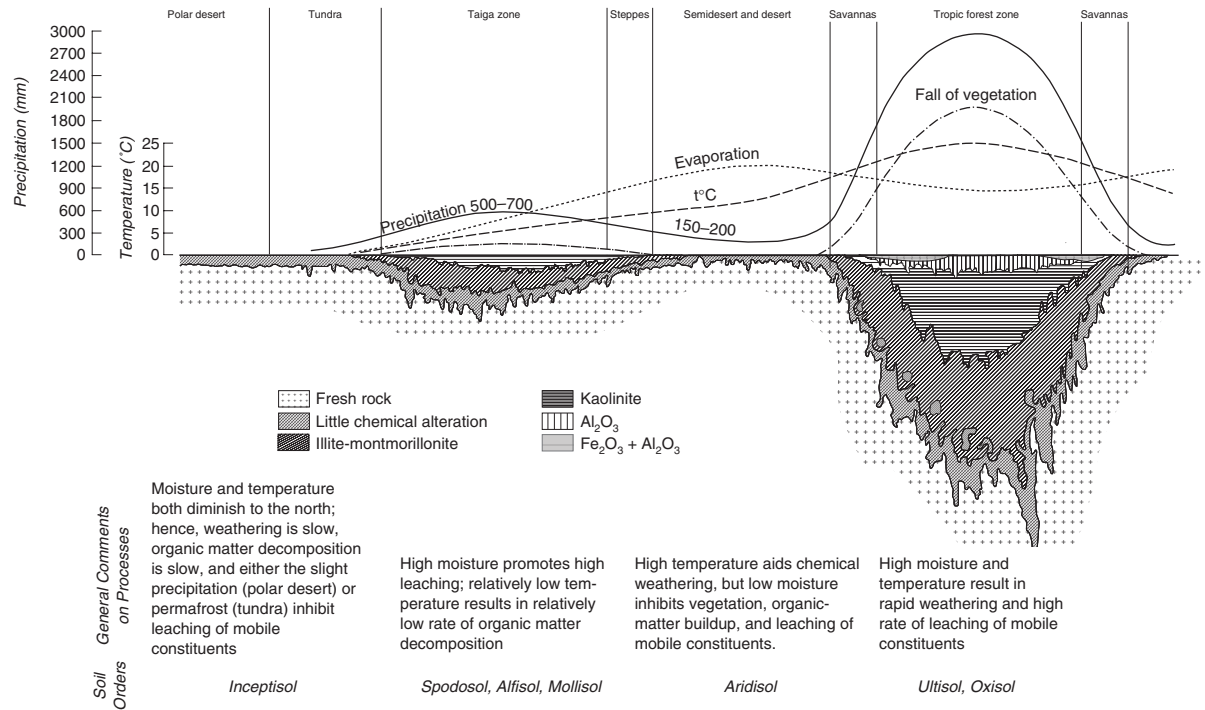


FIGURE 2.1 Environmental factors affecting the distribution of terrestrial biomes and formation of soils along a transect from the equator to the north polar region (with permission from Birkeland, 1999).

Mineral soils are formed by the physical and chemical weathering of the rocks and minerals brought to the earth's surface by geological processes. The parent material of mineral soils can be the residual material weathered from solid rock masses or the loose, unconsolidated materials that often have been transported from one location and deposited at another. The disintegration of rocks into smaller mineral particles is a physical process brought about by heating and cooling, freezing and thawing, and abrasion from wind, water, and ice masses. Chemical and biochemical weathering processes are enhanced by the presence of water, oxygen, and the organic compounds resulting from biological activity. These reactions convert primary minerals such as feldspars and micas to secondary minerals such as silicate clays, and they promote the release of constituent elements in soluble forms available to soil organisms and plants.

Physical and chemical weathering of rocks to fine particles with large surface areas and the accompanying release of plant nutrients initiate the soil-forming process (Fig. 2.2).

The initial colonizers of soil parent material are usually organisms capable of both photosynthesis and N_2 fixation. Early plant vegetation has intimate root-bacterial/fungal/actinomycetal associations with soil organisms to assist with supplying nutrients and water.

Soil organisms together with plants constitute one of the five interactive factors responsible for soil formation. By 1870, Russian soil scientists had developed the concept of soils as independent natural bodies each possessing unique properties resulting from parent material, climate, topography, and living matter, interacting

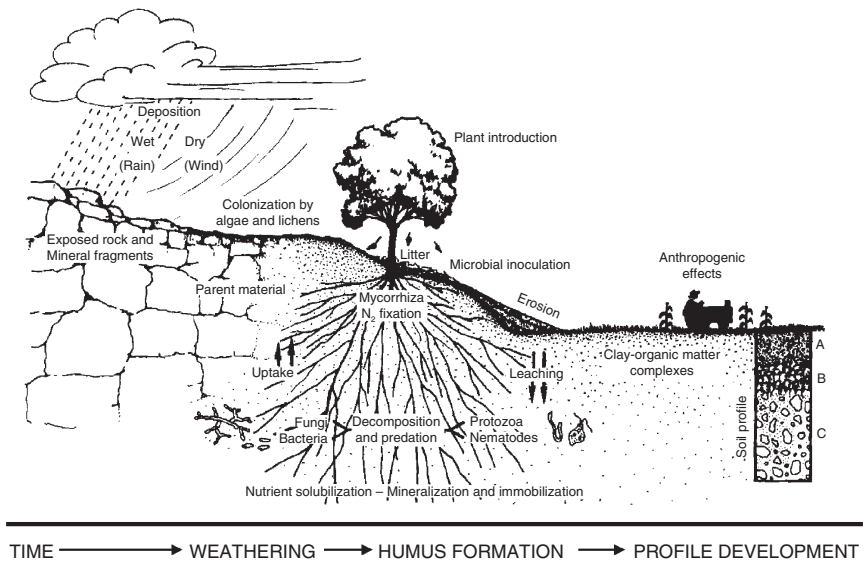


FIGURE 2.2 Interrelationships of organisms, organic matter, and parent materials in soil development.

over time. The approach to describing soil genesis as a biochemical product of organisms participating in their own genesis was quantified by Hans Jenny in his now classic equation of soil-forming factors:

$$\text{Soil} = f[\text{parent material, climate, living organisms, topography, time}].$$

SOIL PROFILE

During formation soils develop horizontal layers, or horizons, that look different from one another (Fig. 2.3).

The horizons within a soil profile vary in thickness depending on the intensity of the soil-forming factors, though their boundaries are not always easy to distinguish. Uppermost layers of mineral soils are most altered during soil formation, whereas the deeper layers are most similar to the original parent material. Horizon differences in the solum, the parent material most altered during soil formation, involve: (i) organic matter from plant residues and roots in the surface mineral horizons decaying and forming humus, which gives these horizons a dark color—the organic-matter-enriched horizons nearest the soil surface are called A horizons; (ii) movement of soluble and colloidal inorganic and organic constituents from surface layers; and (iii) accumulation of varying amounts of inorganic and organic precipitates. These underlying, enriched layers in mineral soils are referred to as B horizons. The C horizons are the least weathered part of the mineral soil profile. Organic soils are commonly saturated with water and consist mainly of mosses, sedges, or other hydrophytic vegetation; the upper material is referred to as the O layer. In upland areas where drainage is better and forest vegetation supported, follic-derived organic materials accumulate to form the L–F–H layer. In both types of organic soils, it is the residual organic matter in the surface layer that most resembles the vegetation from which it is derived.

The vadose zone is the underlying, unsaturated, parent material extending (from the soil surface) downward to where it reaches the water table and the soil becomes saturated. Below the solum, this zone contains relatively unweathered parent material, low in organic matter and nutrients and often deficient in O_2 . The thickness of the vadose zone can fluctuate considerably during the season, depending on soil texture, soil water content, and height of the soil water table. When the water table is near the surface, for example as in wetlands, it may be narrow or nonexistent. But in arid or semiarid areas where soils are well drained, the vadose zone can extend for several meters and even be hundreds of meters deep.

PHYSICAL ASPECTS OF SOIL

Dimensions of physical features commonly encountered when considering the soil habitat range from meters (pedon, soil landscape, and watershed), down through a few millimeters (the fine-earth fraction), to a few micrometers (microorganisms and clay minerals) and nanometers (humic molecules) (Table 2.1).

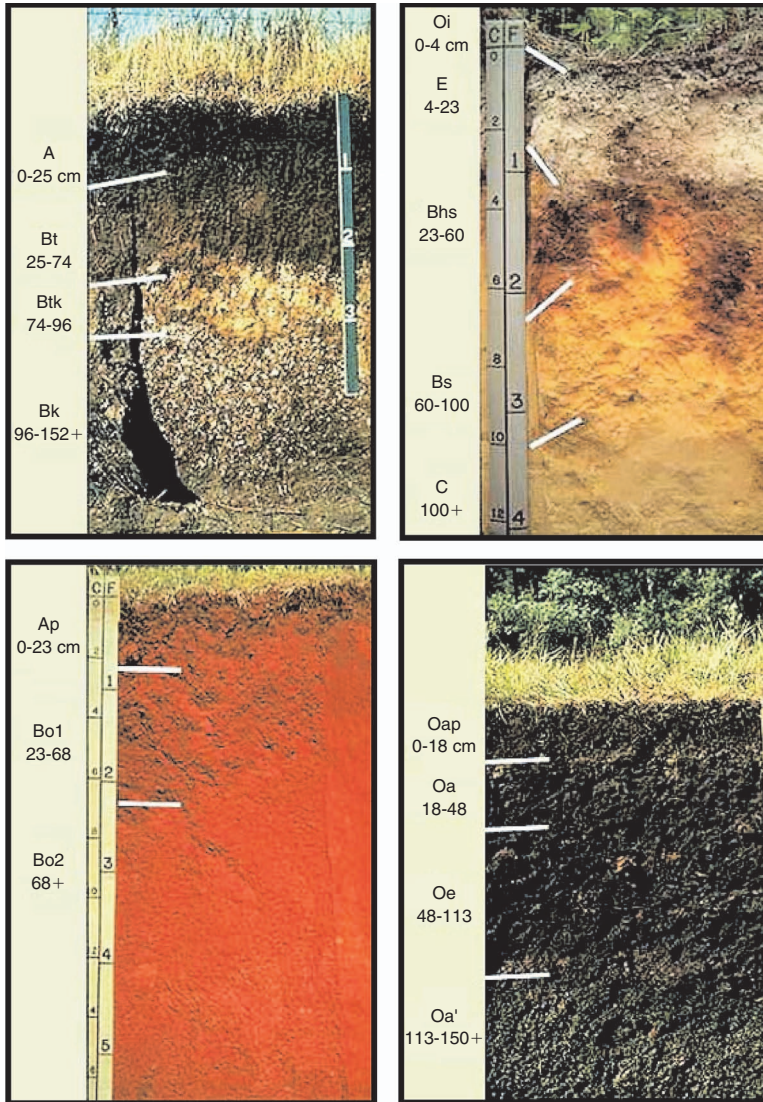


FIGURE 2.3 Natural (undisturbed) mineral and organic soils showing the soil profile: mollisol (top left), spodosol (top right), oxisol (bottom left), and histosol (bottom right). (Soil profiles reproduced with permission: spodosol and oxisol from University of Nebraska Press, mollisol from American Society of Agronomy; histosol from University of Idaho.)

SOIL TEXTURE

The larger mineral particles include stones, gravels, sands, and coarse silts that are generally derived from ground-up rock and mineral fragments. While particles >2 mm in diameter may affect the physical attributes of a soil, they are excluded

TABLE 2.1 Spatial Dimensions of Features Commonly Encountered in Describing the Soil Habitat

Scale (m)	Particles	Aggregations	Pore (functions)	Biota	Scale (m)
10 ⁻¹⁰	Atoms				10 ⁻¹⁰
10 ⁻⁹	Molecules	Amorphous minerals	MICROPORES	Organic molecules	10 ⁻⁹
10 ⁻⁸	Macromolecules		(Adsorbed and intercrystalline water)	Poly-saccharides	10 ⁻⁸
10 ⁻⁷	Colloids	Clay micro-structure		Humic substances	10 ⁻⁷
10 ⁻⁶	Clay particles	Quasicrystals	$\psi > -1500$ kPa	Viruses	10 ⁻⁶
10 ⁻⁵	Silt	Domains	MESOPORES	Bacteria	10 ⁻⁵
10 ⁻⁴	Sand	Assemblages	(Plant available water)	Fungal hyphae	10 ⁻⁴
10 ⁻³		Micro-aggregates	$\psi < -10$ kPa	Root hairs	10 ⁻³
10 ⁻²	Gravel	Macro-aggregates	MACROPORES AND CRACKS	Roots-Mesofauna	10 ⁻²
10 ⁻¹	Rocks	Clods	(Aeration)	Worms	10 ⁻¹
10 ⁰			(Fast drainage)	Moles	10 ⁰

from the definition of soil. The fine-earth fraction of soil particles ranges in size over four orders of magnitude: from 2.0 mm to smaller than 0.002 mm in diameter. Sand-sized particles are individually large enough (2.0 to 0.05 mm) to be seen by the naked eye and feel gritty when rubbed between the fingers in a moist state. Somewhat

smaller, silt-sized particles (0.05 to 0.002 mm) are microscopic and feel smooth and slippery even when wet. Clay-sized particles are the smallest of the mineral particles (<0.002 mm), seen only with the aid of an electron microscope, and when wet form a sticky mass. The proportion of these different size classes in soil is referred to as soil texture, and terms such as sandy loam, silty clay, and clay loam are textural classes used to identify the soil's texture. When investigating a field site, considerable insights into the behavior and properties of the soil can be inferred from its texture, so it is often one of the first properties to be measured.

The surface of mineral soils contains an accumulation of living biomass, dead and decomposing organic material, and humus. This soil organic matter (SOM) typically accounts for 1–10% of the total soil mass, but because it is intimately associated with the mineral fraction it is difficult to isolate from the soil. The larger, recognizable remains of plant, animal, and soil organisms that can be separated from soils by hand picking and sieving techniques are referred to as particulate organic matter. These tissues undergo continuous decay, and over periods of years to decades, brown to black-colored, colloidal humus is synthesized and accumulates. Soil humic substances can account for 50–60% of the total SOM, and together with the nonhumic material provide a nutrient reservoir to sustain the soil microbial biomass.

SOIL STRUCTURE

Typically, the individual mineral particles in surface soils are coated and glued together with colloidal organic matter and encrusted with inorganic cements forming spatial clusters within the matrix known as aggregates or peds. In 1982, two Australian soil scientists, Drs. Judy Tisdall and Malcolm Oades, presented a conceptual model of the aggregated, hierarchical nature of the soil system and described the linkages between the architecture of the soil habitat and the role of microbial activity in its genesis. If soil was but a single ped, scientists could describe its physical and chemical properties in sufficient detail to understand how the nature and activity of soil organisms are controlled. But soils are composed of highly variable peds, derived from a wide range of parent materials that exist within innumerable landscapes, and exposed to diverse climates. And they have formed in concert with the development of the complex communities of living organisms that make up the biosphere.

Overall, the shape, size, and arrangement of the aggregates within the soil profile describe soil structure. Three assemblages of aggregates are recognized with diameter classes of 0.002–0.020, 0.020–0.250, and >0.250 mm and are referred to as microaggregates, mesoaggregates, and macroaggregates, respectively.

Microaggregates are formed by flocculation of fine silt and clay particles, amorphous minerals (composed of oxides and hydroxides of aluminum, silicon, iron, and manganese and silicates of aluminum and iron), and nonhumic and humic substances, largely dominated by electrostatic and van der Waal forces. Polyvalent cations such as Al^{3+} , Fe^{3+} , Ca^{2+} , and Mg^{2+} adsorbing onto their surfaces and

reacting with exposed functional groups promote these flocculation reactions. Sticky polysaccharides and proteins derived from plant and animal tissues, microbial cells, and exudates from roots, hyphae, and bacteria further enhance these stabilization reactions. In particular, soil microorganisms produce extensive exopolysaccharides, which they use to adhere to individual soil particles.

The core of mesoaggregates is usually the residual debris left from the decay of plant and microbial tissues. Bits of decaying particulate organic matter and their colonizing microbial biofilms become encrusted with fine mineral particles and they act as nuclei for the formation of aggregates and contribute to their resilience. Microaggregates can form throughout the surface soil matrix wherever intense microbial activity associated with organic matter decomposition occurs. The larger macroaggregates are formed only where a network of living and decaying plant roots, fungal hyphae, and microbial filaments physically enmesh clusters of micro- and mesoaggregates for a period sufficient for them to be chemically linked.

In the rhizosphere, hyphae of arbuscular mycorrhizal fungi contribute to the aggregation effect as they grow into small pores and bind soil particles together. Although macroaggregates comprise microaggregates, not all soil microaggregates exist as macroaggregates. Macroaggregates can contain soil primary particles that may eventually go on to form microaggregates. This hierarchical organization of soil structure and aggregation, i.e., large aggregates being composed of smaller aggregates, which in turn are composed of even smaller aggregates, is characteristic of most soils (Fig. 2.4).

Micro- and mesoaggregates tend to be especially resistant to mechanical breakdown, for example, from the impact of rainfall or from slaking—rapid rewetting of dry soil—or from freezing and thawing. The restricted size of the pores within these aggregates (<0.01 mm diameter), also referred to as intra-aggregate pore space, can limit the interactions of soil organisms. The pore space surrounding microaggregates and contained within macroaggregates is collectively referred to as the soil interaggregate pore space. It contains plant roots and is usually rich in fresh inputs of particulate macroorganic matter (>0.05 mm diameter). Macroaggregates usually remain intact as long as the soil is not disturbed, for example, by earthworm and other faunal activity or by disturbance such as heavy rains. Macroaggregation is important for controlling microbial activity and soil organic matter turnover in surface soils because it gives fine-textured, clayey and loamy-textured soils pore space characteristics similar to those of sandy soils. The physical properties affected by macroaggregation include pore size distribution, pore continuity and tortuosity (irregular, twisted pores), aeration, drainage, and tilth.

SOIL HABITAT SCALE AND OBSERVATION

SCALE OF SOIL HABITAT

The soil habitat is characterized by heterogeneities across all measured scales, from nanometers to kilometers, which differ in chemical, physical, and biological

interactions, and survival of other organisms found in it. Together these characteristics define the range of habitats available for organisms and their enzymes to occupy. They vary vertically, through the soil vadose zone, and horizontally across the landscape.

For higher organisms, such as animals that range over wide territories, the habitat may be on the scale of a landscape or watershed and even beyond. At the other extreme, microorganisms, the habitat occurs on a microscale and therefore has been referred to as microhabitat. The spatial characteristics of the general habitat, as well as the fine features of the microhabitats, must be considered in describing the activity of soil microorganisms. Microregions within soil aggregates control the nature and availability of nutrient resources, directly impacting population dynamics. Metabolically similar groups of microorganisms, referred to as guilds, occupy a unique ecological niche that encompasses their life strategy. Sets of guilds, which carry out interdependent physiological processes, form microbial communities. While ecological theory has proposed that no two species ever occupy exactly the same ecological niche for long, in soils it is the rule that different species share aspects of their niche with others. Soil habitat spatial heterogeneity is an important contributor to the coexistence of species in soil microbial communities, enhancing overall soil biodiversity by promoting the persistence of individual populations.

Studies have confirmed that soil organisms are usually not randomly distributed but exhibit predictable spatial patterns over wide spatial scales (Fig. 2.5).

Spatial patterns of soil biota also affect the spatial patterns of microbial activity and processes they carry out. Accumulations of inorganic N may not be observed where sites of plant residue decay are adjacent and closely linked to those where ammonification of SOM is occurring. Inorganic N can accumulate and nitrification can occur where these microbial processes are physically separated in soil space. Recent studies of “trigger molecules” have identified substrates that appear to promote metabolic linkages over spatially diverse soil microbial communities (De Nobili *et al.*, 2001).

Although the main factors influencing the gross behavior of soil organisms are known, their relative importance and influence on spatial distribution have not been studied in detail. For soil microorganisms, there are few methods currently available that enable the study of their detailed activity *in situ* at the level of the soil microhabitat. In fact, when collecting samples in the field from a soil profile, it is common practice for soil scientists to homogenize the samples before analysis, after removal of the plant debris and macrofauna, by passing the soil through a 2-mm sieve.

PORE SPACE

Between the solid (mineral and organic) components of soil is space forming pores that vary in size. On a volume basis, mineral soils are about 35–55% pore space, whereas organic soils are 80–90% pore space. But total soil pore space can

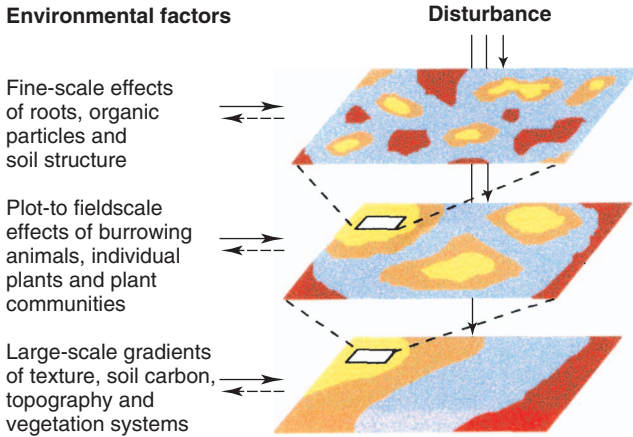


FIGURE 2.5 Determinants of spatial heterogeneity of soil organisms. Spatial heterogeneity in soil organism distributions occurs on nested scales and is shaped by a spatial hierarchy of environmental factors, intrinsic population processes, and disturbance. Disturbance operates at all spatial scales and can be a key driver of spatial heterogeneity, for example, through biomass reduction of dominant organisms or alteration of the physical structure of the soil substrate. Feedback between spatial patterns of soil biotic activity and heterogeneity of environmental factors adds further complexity (dotted arrows) (from Ettema and Wardle, 2002, with permission from Elsevier).

vary widely for a variety of reasons, including soil mineralogy, bulk density, organic matter content, and disturbance. Pore space can range from as low as 25% for compacted subsoils in the lower vadose zone to more than 60% in well-aggregated clay-textured surface soils. Sandy-textured soils, though having a higher mean pore size, tend to have less total pore space than do clay soils.

Soil pore space is defined as the percentage of the total soil volume occupied by soil pores:

$$\% \text{ pore space} = (\text{pore volume}/\text{soil volume}) \times 100. \quad (2.1)$$

Direct measurement of the soil pore volume is somewhat tedious to carry out; it is usually estimated from data on soil bulk density and soil particle density using the following formulas:

$$\text{soil bulk density—}D_b \text{ (Mg/m}^3\text{)} = \text{soil mass (Mg)}/\text{soil bulk volume (m}^3\text{)}, \quad (2.2)$$

$$\text{soil particle density—}D_p \text{ (Mg/m}^3\text{)} = \text{soil mass (Mg)}/\text{soil particle volume (m}^3\text{)} \quad (2.3)$$

(usually assumed to be 2.65 Mg/m^3 for silicate minerals, but can be as high as 3.25 Mg/m^3 for iron-rich tropical soils and as low as 1.3 Mg/m^3 for volcanic soils and organic soils),

$$\% \text{ pore space} = 100 - [(D_b/D_p) \times 100]. \quad (2.4)$$

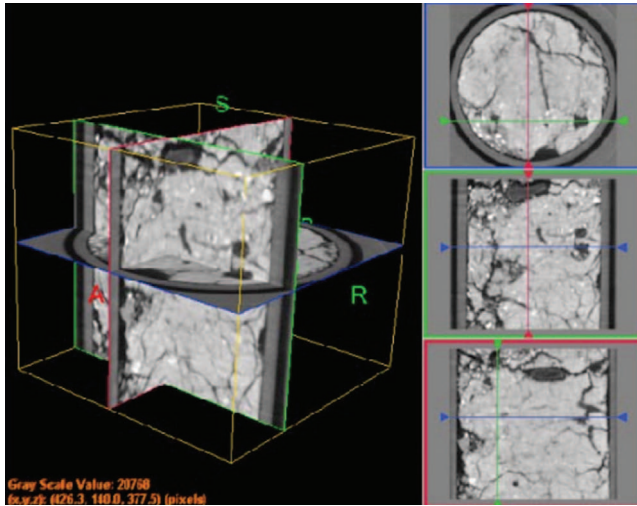


FIGURE 2.6 A 3-D CT X-ray scan of a soil core 6.4 cm in diameter \times 10 cm in length, with a resolution of 10 μm , showing pore space distribution. (Courtesy of R. Heck, University of Guelph.)

Though total pore space is important, fundamentally it is the size, shape, and interconnection of soil pores that are the key in determining the habitability of the soil, for they directly control soil aeration and water relationships; this is largely a function of soil texture and structure (Fig. 2.6).

Total pore space is usually divided into two size classes, macropores and micropores, based on their ability to retain water after water drainage under the influence of gravity (Table 2.2). Macropores are those pores larger than $\sim 10 \mu\text{m}$ in diameter that allow rapid diffusion of air and rapid water infiltration and drainage. They can occur as the spaces between individual sand and coarse silt grains in coarser-textured soils and in the interaggregate pore space of well-structured loam- and clay-textured soils. Macropores can also be created by roots, earthworms, and other soil organisms, forming an important type of pore termed “biopore.” Biopores are typically lined with cutans rich in organic matter and clay and are ideal habitats for soil microorganisms. They provide continuous channels extending throughout the soil, often for lengths of a meter or more.

Soil pores less than 10 μm in diameter are referred to as micropores. Though important for retention of water available for plants and providing an aqueous habitat for microorganisms, the restricted size of micropores can limit interactions of soil organisms and their access to potential substrates.

While the larger micropores together with the smaller macropores can accommodate plant root hairs and microorganisms, pores smaller than $\sim 5 \mu\text{m}$ in diameter are not habitable by most microorganisms and may even be too small to permit entrance of their exoenzymes.

structure. These systems have resolution capabilities down to 10 μm , which allow differentiation of solids, and are able to quantify the distribution of organic and mineral materials. The technology is also able to readily distinguish air-filled and water-filled pore space. Distinguishing microbes from soil particles with this technology, however, is still not possible. A CT image of a soil core in three orthogonal planes is shown in Fig. 2.6. Highly attenuating features like iron oxide nodules appear bright in the imagery, while features with low attenuation capability such as pore space appear dark.

SOIL SOLUTION CHEMISTRY

An understanding of the chemistry of the soil solution providing an environment for soil organisms needs to take account of the nature and quantity of its major components: water, dissolved organic matter and inorganic constituents, and O_2 and CO_2 . The biogeochemistry of the soil solution is mainly determined by acid–base and redox reactions. Consequently the thermodynamic activities of protons and electrons in soil solution define the chemical environment that controls microbial activity. Both can be considered as flowing from regions of high concentration to regions of low concentration, and soil microbial activity has a profound effect on regulating this flow.

The most reduced material in the biosphere is the organic matter contained in living biomass. Organic matter in soils ranges from total dominance, as in peatlands, to the minor amounts found in young soils or at depth in the vadose zone. Soil organisms generate electrons during the metabolic oxidation of organic matter, and these electrons must be transferred to an electron acceptor, the largest of which is atmospheric O_2 in freely drained, aerobic soils. The O_2 trapped in the soil or present in the water can be consumed within hours by soil microbes and is replenished by O_2 diffusion. If O_2 diffusion into the soil is impeded, for reasons of waterlogging, restricted pore sizes due to clay texture or to soil compaction, the resultant soil becomes practically devoid of O_2 . When microbial activity uses up all of the available dissolved O_2 , the soil solution as a whole changes from aerobic (oxic) to anaerobic (anoxic). Microbial activity will then be controlled by the movement of electrons to alternative electron acceptors.

Development of anaerobic conditions results in a shift in the activity of the soil microbial populations, with the activity of aerobic and facultative organisms, which dominate well-drained soils, decreasing and the activity of obligate anaerobic and fermentative organisms increasing. This switch in electron acceptors promotes the reduction of several important elements in soil, including nitrogen, manganese, iron, and sulfur, in a process known as anaerobic respiration and carbon dioxide by methanogenesis.

Redox potential (E_H) measurements provide an indication of the soil aeration status. They are a measure of electron availability occurring as a result of electron transfer between oxidized (chemical species that have lost electrons) and reduced (chemical species that have gained electrons) chemical species. The measurements

SOIL pH

Acidic protons supplied to the soil from atmospheric and organic sources react with bases represented by aluminosilicates, carbonates, and other mineralogical and humic constituents. In a humid climate with excess precipitation, and given sufficient time, basic cations (Na^+ , K^+ , Ca^{2+} , Mg^{2+}) will be exchanged from mineral and organic constituents by H^+ and leached from the surface soil. The presence of clay minerals such as smectites, which are saturated with basic cations, retards the progress of acidification, and calcite buffers the soil between pH 7 and 8 until it is completely dissolved. Continued hydrolysis results in the formation of a residuum made up of such minerals as kaolinite, gibbsite, and goethite, together with resistant minerals, of which quartz is common, that are buffered between pH 3.5 and 5. Semiarid and arid conditions lead to an opposite trend, a soil solution buffered at an alkaline pH and in the presence of sodium.

Soil pH influences a number of factors affecting microbial activity, like solubility and ionization of inorganic and organic soil solution constituents, and these will in turn affect soil enzyme activity. There are a large number of both organic and inorganic acids found in soils; the majority of these acids are relatively weak. Traditionally soil pH is measured in a soil paste prepared by the addition of a dilute CaCl_2 solution with an appropriate electrode. While achieving a pH measurement of the soil is relatively easy, interpretation of its affect on microbial processes is difficult. This is because concentrations of cations sorbed to the surfaces of the negatively charged soil colloids are 10–100 times higher than those of the soil solution. The pH at the colloid surface will be much more acidic than that of the measured pH of the bulk soil solution. For soil exoenzymes sorbed to colloid surfaces, their apparent pH optimum would be 1–2 pH units higher than if measured free in solution. An example of this is soil urease activity, which has an apparent pH optimum of 8.5–9.0 that is about 2 pH units greater than optimal urease activity measured in solution.

SOIL TEMPERATURE

Many physical, chemical, and biological processes that occur in soil are influenced by temperature. Increasing temperature enhances mineralization of SOM or decomposition of plant residues by increasing rates of physiological reactions and by accelerating diffusion of soluble substrates in soil. An increase in temperature can also induce a shift in the composition of the microbial community. Whereas rates of molecular diffusion always increase with increasing temperature, solubility of gases in soil solution do not, and can even decrease, thereby slowing microbial activity (Table 2.4).

The relation between a chemical reaction rate and temperature was first proposed by Arrhenius:

$$k = A e^{-E_a/RT}. \quad (2.5)$$

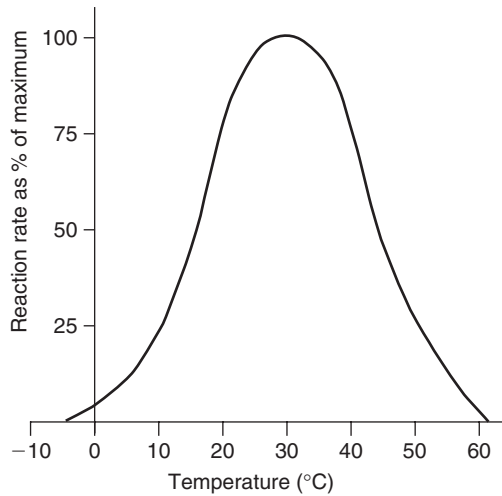


FIGURE 2.8 Generalized soil microbial activity response curve to soil temperature, assuming soil moisture and aeration are not limiting.

soils are less subject to large diurnal temperature fluctuations than are dry soils. Among factors affecting the rate of soil warming, the intensity and reflectance of solar irradiation are critical. The soil's aspect (south- versus north-facing slopes), steepness of slope, degree of shading, and surface cover (vegetation, litter, mulches) determine effective solar irradiation. Given the importance of soil temperature in controlling soil processes, models of energy movement into the surface soil profile have been developed. They are based on physical laws of soil heat transport and thermal diffusivity and include empirical parameters related to the temporal (seasonal) and sinusoidal variations in the diurnal pattern of near-surface air temperatures. The amplitude of the diurnal soil temperature variation is greatly dampened with profile depth.

SOIL WATER CONTENT

Soil water affects the moisture available to organisms as well as soil aeration status, the nature and amount of soluble materials, the osmotic pressure, and the pH of the soil solution. Water acts physically as an agent of transport by mass flow and as a medium through which reactants diffuse to and from sites of reaction. It acts chemically as a solvent, as a reactant in important chemical and biological reactions, and as a chemical buffer fixing the activity of water in soil solution at about 1. Of special significance in the soil system and to microbial cells in particular is the fact that water adsorbs strongly to itself and to surfaces of soil particles by hydrogen bonding and dipole interactions. The thin layer of adsorbed water remains unfrozen even at temperatures $<0^{\circ}\text{C}$.

Soil water content can be measured on a mass or volume basis. Gravimetric soil water content is the mass of water in the soil, measured as the mass loss in a soil dried at 105°C (oven-dry weight) and is expressed per unit mass of oven-dry soil. Volumetric soil water content is the volume of water per unit volume of soil. Soil water is also described in terms of its potential free energy, based on the concept of matric, osmotic, and gravitational forces affecting water potential. Soil water potential is expressed in units of pascals (Pa) or, more commonly, kilopascals (kPa). Matric forces are attributed to the adhesive or adsorption forces of water attraction to surfaces of mineral and organic particles and to cohesive forces or attraction to itself. Since these forces reduce the free energy status of the water, matric forces reduce the water potential to values less than 0; that is, matric forces result in negative water potentials. Solutes dissolved in soil solution also contribute to a reduction in the free energy of water and give rise to an osmotic potential that too is negative. Combined, the matric and osmotic forces are responsible for the retention of water in soils. They act against gravitational forces tending to draw water downward and out of the soil. Gravitational forces are usually positive.

When the gravitational forces draining water downward are exactly counterbalanced by the matric and osmotic forces holding onto the water, the soil is said to be at field capacity or at its water holding capacity. This will occur after irrigation, after a heavy rainfall, or after spring thaw, which leave the soil saturated and having a soil water potential of 0 kPa. Gravitational forces begin immediately to drain away water in excess of that which can be retained by matric + osmotic forces, leaving the soil after 1–2 days at field capacity. By definition the field capacity for loam and clay loam soils is a soil water potential of –33 kPa, and for sandy soils –10 kPa.

Water retention or soil water content at a given soil water potential is a function of the size of pores present in the soil, or pore size distribution. Soils of different textures have very different water contents even though they have the same water potential (Table 2.2). An important property of water influencing its behavior in soil pores is surface tension. Because of the strong cohesive forces, water has a high surface tension. Based on matric forces and properties of surface tension, the maximum diameter of pores filled with water at a given soil water potential can be estimated using the Young–Laplace equation:

$$\begin{aligned} \text{Maximum pore diameter retaining water } (\mu\text{m}) \\ = -300/(\text{soil water potential (kPa)}). \end{aligned} \quad (2.7)$$

Those soil pores greater than about 10 μm diameter drain under the influence of gravitation forces, given that the soil water potential at field capacity is –33 kPa.

Soil water potential determines the energy that an organism must expend to obtain water from the soil solution. Generally aerobic microbial activity in soil is optimal at a soil water potential of about –50 kPa and decreases as the soil either becomes wetter and saturated, i.e., waterlogged, or dries (Fig. 2.9).

While plants are at their wilting point when the soil water potential reaches –1500 kPa, relative rates of soil microbial activity can still be quite high.

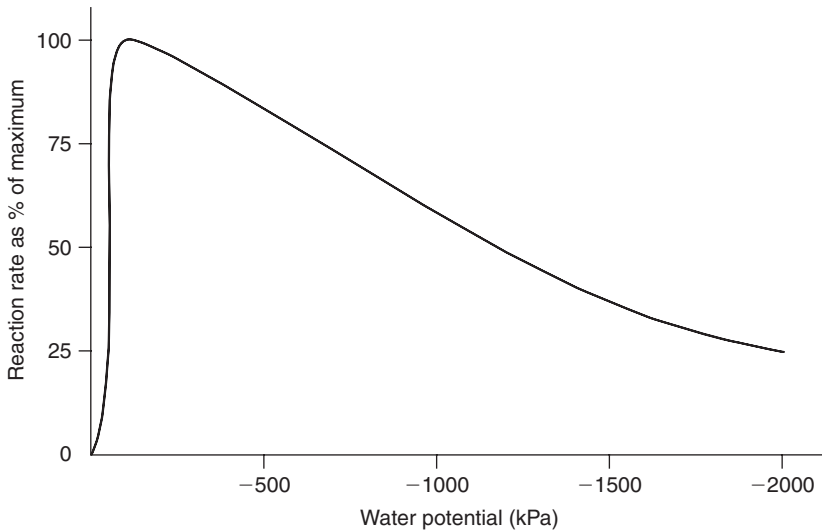


FIGURE 2.9 Generalized aerobic microbial activity response to soil water potential, assuming soil temperature is not limiting.

TABLE 2.5 Ability of Different Organisms to Tolerate Water Stress (from Paul and Clark, 1996)

kPa	A_w	Organism
-1500	0.99	<i>Rhizobium</i> , <i>Nitrosomonas</i>
-1000	0.93	<i>Clostridium</i> , <i>Mucor</i>
-2500	0.83	<i>Micrococcus</i> , <i>Penicillium</i>
-6500	0.62	<i>Xeromyces</i> , <i>Saccharomyces</i>

Diffusion of substrates to microorganisms is greatly slowed by drying; however, the relative humidity in the soil remains high. Rapid changes in soil water potential associated with rewetting cause microbes to undergo osmotic shock and induce cell lysis. A flush of activity by the remaining microbes, known as the Birch effect, results from mineralizing the labile cell constituents.

Different microbial communities are likely to be active over the range of water potentials commonly found in soils. A decline in microbial activity at low soil moisture levels can be explained as resulting from limited diffusion of soluble substrates to microbes or to reduced microbial mobility. Fungi are generally considered to be more tolerant of lower soil water potentials, i.e., drier soils, than are bacteria, presumably because soil bacteria are relatively immobile and rely more on diffusion processes for nutrition. Table 2.5 shows differences in the ability of different organisms to tolerate water stress. The nitrifiers, for example, typified by

Nitrosomonas, are less tolerant of stress than are the ammonifiers, typified by *Clostridium* and *Penicillium*. Ammonium may accumulate in a droughty soil because the nitrifiers do not have access to ammonium generated at water potentials at which the ammonifiers are still active.

ENVIRONMENTAL FACTORS, TEMPERATURE AND MOISTURE INTERACTIONS

Soil moisture and temperature are the critical climatic factors regulating soil biological activity. This control is affected by changes in the underlying rates of enzyme-catalyzed reactions. Where water is nonlimiting, biological activity may depend primarily on temperature, and standard Arrhenius theory can be used to predict temperature effects. But as soils dry, moisture is more controlling of biological processes than is temperature. These two environmental influences do not affect microbial activity in linear fashion but display complex, nonlinear, interrelated effects that likely reflect the individual responses of the various microorganisms and their associated enzyme systems.

The interaction of temperature, moisture, and organisms is exemplified by the current discussions about climate change. A hundred years ago, Swedish scientist Svante Arrhenius asked the important question “Is the mean temperature of the ground in any way influenced by the presence of the heat-absorbing gases in the atmosphere?” He went on to become the first person to investigate the effect that doubling atmospheric carbon dioxide would have on global climate. The globe is warming because of increased CO₂ in the atmosphere from man’s burning of past SOM depositions (fossil fuels) and from management changes such as cultivation of forested soils as in the Amazon. This in turn is causing the extensive organic deposits in frozen tundra to thaw. The melting allows the vegetation to change as the former tundra becomes boreal in nature. In turn, the trees will result in less light reflection and further increase warming and primary productivity. Will the generally warmer globe result in less overall organic matter as decomposition is increased? Theory such as the Arrhenius equation suggests that the more resistant organic matter compounds with high activation energy should be more decomposable at higher temperatures (Davidson and Janssens, 2006). But as always in soils there are interactions. What is the effect of physical protection by aggregates? Will there be more or fewer soil aggregates in a warmer climate with different vegetation–decomposer interactions, given that aggregates are formed by microorganisms and roots? Many of the environmental constraints affect decomposition reactions by altering organic matter (substrate) concentrations at the site at which all decomposition occurs, that of the enzyme reaction site. We must also consider decomposition rates at the enzyme affinity level; Michaelis–Menten models of enzyme kinetics are covered in Chap. 16 and energy yield in Chap. 9. Changes in microbial community structure (Chap. 8) also will have profound influences. The goal of this chapter is to provide an environmental boundary of the soil habitat and a description of its fundamental physical and chemical properties.