FOREST ECOLOGY
Fourth Edition

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chapter 11

soil

forest trees, like all other terrestrial vegetation, require five primary resources for growth and development: radiant energy, carbon dioxide (CO2), water (H2O), mineral nutrients, and a porous medium for physical support. Although plants obtain energy from solar radiation and CO2 from the atmosphere, the remaining resources are provided by soil. Consequently, soil forms the “foundation” of forest ecosystems in more ways than one. As you will see, soil is critical to the cycling of nutrients (Chapter 19), a process that influences the growth of individual trees and the functioning of entire ecosystems. In this chapter, we provide an overview of the physical, chemical, and biological properties of soil that regulate the availability of soil resources to plants, particularly forest trees. We begin with a discussion of the soil forming process and explain how climate, geology, and biota influence the geographic distribution of forest soils.

there are many definitions of soil as it pertains to the growth of terrestrial plants. For our purpose, we define soil as a porous medium consisting of minerals, organic matter, water, and gases. The combined influences of climate, topography, biota, and time differentiate geologic materials into soil. As such, soils are as diverse as the climates in which they occur, the landforms on which they develop, and the plant life that grows upon and within them. One would expect soils supporting tropical rain forests to differ markedly in their physical, chemical, and biological properties from those beneath forests in temperate or boreal climates. In the pages that follow, we review the processes that give rise to such differences and focus on how they influence plant growth and ecosystem function.

parent material

the earth’s surface is blanketed by a wide array of geologic materials, differing in their chemical composition and degree of consolidation. the relatively-unweathered geologic
material from which a particular soil has developed is called parent material. It constitutes the basic substrate for soil formation and exerts a substantial influence on many soil properties. Parent materials, as you will read, are typically associated with characteristic kinds of landforms. Weathering is an important component of soil formation, because physical abrasion and chemical solution differentiate freshly-exposed geologic material (i.e., parent material) into soil. Living organisms play an integral role in this process too, wherein organic acids produced by plant roots and soil microorganisms solubilize minerals, allowing their constituents to be leached and deposited at depth. Additionally, the hydrolysis of CO₂ resulting from root and microbial respiration produces acidity, which further contributes to the dissolution of minerals and the weathering process.

Parent materials are broadly classified as consolidated and unconsolidated (Figure 11.1). Consolidated parent materials include igneous, sedimentary, and metamorphic rock. A description of them can be found in most introductory geology texts, and Fairbridge (1972) provides a particularly detailed discussion of their formation and chemical composition. Soil developing in consolidated geologic substrate is said to be formed in residual parent material (Figure 11.1). Forest soils derived from residual parent materials occur throughout North America, primarily in areas that have not been influenced by glaciation, moving water, or oceanic upland. Forests of the Piedmont Plateau and Appalachian uplands in the eastern United States occur on these materials, as do forests of the Sierra Nevada, Cascade, and Rocky Mountains in the western United States.

Rates of soil formation on residual parent material composed of hard minerals can be quite slow, and, in some situations, deep soils may never develop because erosion rates exceed those of soil formation. Such a situation commonly occurs in mountainous regions where steeply-sloping topography and exposed rock combine to form relatively thin soils. Nevertheless, not all consolidated parent materials weather at slow rates nor give rise to thin soils. The relative resistance of rock to physical and chemical weathering is as follows (Birkeland, 1974):

**Consolidated**
- Quartzite, chert > granite, basalt > sandstone, siltstone > dolomite, limestone

In general, rocks composed of insoluble minerals (i.e., quartzite, SiO₂) are relatively more resistant to weathering than those containing soluble minerals (i.e., calcite, CaCO₃ or dolomite, Ca₀.₅Mg₀.₅CO₃), which rapidly break down in warm, humid climates. Residual parent materials also yield very different chemical constituents as they are eroded and dissolved during the weathering process. For example, the average SiO₂ and Al₂O₃ contents of igneous and sedimentary rock are similar; however, their calcium (Ca) and sulfur (S) content can dramatically differ (Table 11.1).

There can be considerable differences in the chemical constituents among soils derived from residual parent material, with implications for tree growth. In the Ozark Mountains of Arkansas, for example, different forest ecosystems develop on two kinds of residual parent material: black and white oak are overstory dominants on soil derived from chert (SiO₂), whereas eastern redcedar and northern red oak are dominant on limestone-derived (CaCO₃) soil (Read, 1952). Although both of these parent materials are derived from sedimentary rock, differences in their chemical composition and weathering rate markedly influence the distribution of forest trees.

Unconsolidated parent materials are mineral particles that have been transported by water, ice, wind, or gravity (Figure 11.1). They are chemically similar to the rock from which they originate, but are distinguished from residual parent material by being moved from their point of geologic origin. The agent of transport has a substantial influence on the physical, chemical, and biological properties of soils formed from unconsolidated parent materials; differences that often influence forest composition and ecosystem productivity. In general, sediments deposited by water and wind have a narrow particle size distribution, whereas those deposited by ice contain fragments that range in size from microscopic clay particles to boulders several meters in diameter. A complete discussion of transported parent materials and the soils that they give rise to can be found in Baud et al. (1980).

One example of how unconsolidated parent materials influence forest composition and ecosystem productivity comes from the glaciated portions of eastern North America. In this region, the Wisconsinan Glaciation (14,000 years before present) left behind a landscape consisting almost exclusively of unconsolidated parent materials. Stratified materials were deposited near the margins of stagnant ice (ice contact), and unstratified materials were deposited directly by glacial ice (till). These parent materials differ markedly in their particle size distribution and their ability to supply water and nutrients for plant growth. In the northern portion of Michigan’s Lower Peninsula, for example, dry oak-dominated (northern pin, black and white oak) ecosystems consistently occur on sandy glacial outwash (72 percent coarse and medium sand). Mesic northern hardwood ecosystems occur

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**Table 11.1** Generalized Chemical Composition of Igneous, Metamorphic and Sedimentary Rock

<table>
<thead>
<tr>
<th></th>
<th>SiO₂</th>
<th>Al₂O₃</th>
<th>Fe₂O₃</th>
<th>FeO</th>
<th>MgO</th>
<th>CaO</th>
<th>K₂O</th>
<th>P₂O₅</th>
<th>S</th>
</tr>
</thead>
<tbody>
<tr>
<td>Igneous</td>
<td>69.9</td>
<td>15.2</td>
<td>2.0</td>
<td>2.0</td>
<td>4.0</td>
<td>3.3</td>
<td>0.20</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>Metamorphic</td>
<td>58.2</td>
<td>15.5</td>
<td>2.9</td>
<td>4.8</td>
<td>3.8</td>
<td>6.0</td>
<td>0.30</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>Sedimentary</td>
<td>49.9</td>
<td>13.0</td>
<td>3.0</td>
<td>2.8</td>
<td>3.1</td>
<td>11.7</td>
<td>2.0</td>
<td>0.16</td>
<td>0.18</td>
</tr>
</tbody>
</table>

Source: Modified from Raven and Yarnoski, 1972.
on till-derived soils with lower sand contents (55 percent coarse and medium sand; Host et al., 1988). In addition to differences in species composition, aboveground productivity varies by a factor of three between the dry oak ecosystems (1.3 Mg ha⁻¹ yr⁻¹) and the mesic northern hardwoods (3.4 Mg ha⁻¹ yr⁻¹). Similar relationships also have been observed among geology, soil, forest composition, and ecosystem productivity in the glaciated portions of Wisconsin (Pastor et al., 1984).

**SOIL FORMATION**

As parent material weathering and is occupied by plants and animals, it differentiates into more or less distinct horizontal zones, giving rise to a soil profile. The type of soil profile that develops depends upon the interaction of (1) climate, (2) parent material, (3) plants and animals occupying the soil, (4) relief of the land, and (5) the amount of time that has elapsed. Soil formation is in part a chemical process resulting from the weathering of geologic material exposed to air and water, and in part a biological process resulting from the activities of organisms growing on and in soil.

**Soil Profile Development**

Forests comprise the natural vegetation in many of the moistest parts of the earth regions where precipitation supplies more water than can be evaporated or transpired over the normal year. Under such conditions two factors dominate the soil-forming process: 1) precipitation in excess of evaporation and transpiration moves downward through the soil removing soluble minerals, and 2) tree roots remove both water and nutrients from the soil, transpiring most of the former and eventually returning most of the latter to the soil surface as leaves, twigs, fruits, cones, seeds, and fine roots. In temperate regions, the typical forest soil can be differentiated into five zones or horizons, so identified by the soil forming process occurring within them (Figure 11.2). A soil horizon is differentiated from the over- and underlying layers by attributes that can be easily identified in the field.

The accumulation of organic matter at the soil surface, or O horizon, is an attribute unique to forest soils. Material contained within this horizon consists almost entirely of leaves, twigs, flowers, fruits, cones, and seeds that have been deposited on the soil surface. The O horizon lies above the mineral soil and is distinguished from it by a high organic matter content (>20 percent organic matter if soil has no clay; >30 percent if soil is more than 50 percent clay). It can be divided into three subhorizons, each reflecting different stages of decomposition: 1) the A horizon contains relatively "fresh" organic matter whose origin is easily recognized, 2) the Oe horizon is composed of partially decomposed plant parts, and 3) the Oa horizon reflects the latter stages of decomposition and consists of well-decomposed organic matter of unrecognizable origin (i.e., humus).

The A horizon marks the surface of the mineral soil and is characterized by: 1) the leaching or eluviation of many soluble minerals that migrate in the downward flow of water, and 2) the accumulation of organic matter originating from the overlying O horizon. In many forest soils, the A horizon is dark in color and is well structured, owing to its relatively high organic matter content (4 to 12 percent). The majority of aggregates contained within this horizon are of crumb (<1 to 5 mm dia.) or granular (<1 to 10 mm dia.) size (see soil structure that follows). The A horizon also is characterized by a large number of fine roots which actively forage for nutrients released during organic matter decomposition. Because of the shallow distribution of fine roots and their decomposition products, most forest soils are characterized by a thin A horizon. In contrast, A horizons of grassland ecosystems support deeply rooted grasses that incorporate organic matter to depths of 50 cm.

![Figure 11.2](https://example.com/image.png)

*Figure 11.2. A theoretical mineral soil profile showing the major horizons that may be represented. Reprinted with permission of the Macmillan Publishing Co., Inc. from *The Nature and Properties of Soils*, 10th ed., by Nyle C. Brady. Copyright 01990 by Macmillan Publishing Co., Inc.*

In humid climates, the downward flux of water can remove humus, silicate clays, Fe oxides, and Al oxides from the surface soil, leaving behind light-colored, resistant minerals, especially quartz (SiO₂). The layer so formed is an E horizon, and it is distinguished from the overlying A horizon by its light color. In cool, humid climates, E horizons often develop under coniferous forest growing on course-textured (sand-to-sandy loam) parent material. The acidity of this horizon is typically higher than the over- or underlying horizons due to the loss of base cations and presence of manganic acids. Root densities within the E horizon are low because few plant nutrients reside within this highly leached horizon.

Materials leached from either the A or E horizon migrate downward and are deposited at depth to form the B horizon. The B horizon results from the process of illuviation (i.e., accumulation) and is distinguished from other soil horizons by this important soil-forming process. Materials that accumulate in the B horizon of temperate forest soils...
include silicate clays, humus, Fe and Al oxides—materials that can have a great impact on the physical, chemical and biological properties of the B horizon. In arid and semi-arid regions, CaCO₃, CaSO₄, and other salts can accumulate in the B horizon. The C horizon is the unconsolidated parent material underlying the A, E, and B horizons and is outside the influence of the processes giving rise to the horizons above it. The A, E, and B horizons can be derived from the same material contained within the C horizon. However, in areas where geologic activity has deposited a relatively thin layer of mineral material over a previously existing deposit, the A, E, or B horizon may be derived from a different parent material. This situation is common in the glaciated portions of North America where advancing ice has overridden preexisting deposits of glacial drift. In regions where soil forms in residual parent material, the C horizon is replaced by an R horizon that denotes the presence of the underlying consolidated rock.

Note that the A, B, and C horizons refer to zones that have been leached, enriched, and unaffected by soil forming processes, respectively. It does not necessarily follow that the upper mineral horizon is always the A horizon, or that all horizons are present in every soil. Following sheet erosion, the B or C horizon may be exposed on the surface. Likewise, very "young" or unweathered soils, like those forming on sand dunes, may lack a B horizon and consist only of an A and C horizon. In such cases, clay, humus, or Al- and Fe-oxides often have not accumulated to any great extent in the B horizon.

**Physical Properties of Soil**

As plant roots grow within the soil, they anchor the aboveground portion of the plant and supply it with water and nutrients. Plant roots also require oxygen for respiration, the supply of which is controlled by the rate at which oxygen diffuses through water and other gases in soil. The physical properties of the soil—liquid, and gaseous phases of soil have a substantial influence on the supply of water, nutrients, and oxygen for metabolism, and the availability of physical space to anchor aboveground plant structures. Providing physical support for aboveground tissues is of particular importance, because plants must properly orient themselves to capture the sun's energy for use in photosynthesis. In shallow and poorly-drained soils, windthrow is common because physical space is limited by the occurrence of shallow bedrock in the former and anoxic (without O₂) conditions in the latter. In the pages that follow, we discuss the physical properties of soil that are of particular relevance for the growth of forest plants and the functioning of forest ecosystems.

**Soil Texture**

Soils are composed of mineral particles with a wide array of sizes. These particles, or soil separates, are grouped into three size classes: sand, silt, and clay. Sand particles range in size from 2.00 to 0.02 mm in diameter, silt ranges from 0.02 to 0.002 mm in diameter, and the clay fraction is less than 0.002 mm. Soil texture refers to relative proportion of sand, silt, and clay-sized particles contained in a particular soil. This physical property plays an integral role in regulating the availability of water and mineral ions for plant use, and the rate at which gases (O₂ and CO₂) are exchanged between soil and the overlying atmosphere.

In addition to grouping mineral particles by size, soil separates in different size classes can be distinguished by their physical and chemical properties. For example, sand- and silt-sized particles are chemically identical to the rock from which they originate and are called primary minerals. They are round or irregular in shape, composed primarily of quartz (SiO₂) or other silicate minerals like orthoclase (KAlSi₃O₈) or plagioclase (CaAl₂[AlSi₃O₁₀]). As a consequence of their size and shape, sand particles have relatively low surface areas (1-2 m² g⁻¹) with large pores between individual particles. One grain of soil would form a mound in the palm of your hand equal to the size of a United States quarter coin. These attributes provide sandy soils with good aeration, but limit the amount of water available for plant use. Because silt-sized particles have higher surface areas (45 m² g⁻¹), they hold relatively larger quantities of water compared to a soil consisting primarily of sand.

The clay fraction of soil is comprised of secondary minerals, which result from the physical and chemical weathering of primary minerals. In temperate soils, clays consist primarily of aluminosilicate minerals that differ markedly from sand and silt in their shape and mineralogy. These minerals form plate-like structures or micelles that are referred to as phyllosilicate (leaf-like silicate) clays. Due to their shape, they have a high surface area (80 to 800 m² g⁻¹), enabling them to hold relatively large quantities of water for plant use. Phyllosilicate minerals differ widely in their physical and chemical properties from Al and Fe oxides, which compose the clay fraction of soils in the humid tropics. Differences in clay minerals found in temperate and tropical soils will be discussed in more detail later in this chapter (see Chemical Properties of Soil).

Soils are grouped into textural classes based on their sand, silt, and clay content. For example, a soil consisting of equal proportions of sand, silt, and clay is classified as a loam (Figure 11.3). For a soil to be classified as a clay, 60 percent of its particles must be...
Less than 0.002 mm in diameter. In contrast, sands are soils in which more than 90 percent of the mineral particles range from 0.02 to 2.00 mm in diameter. The textural classes illustrated in Figure 11.3 have been delineated with specific reference to plant growth. As you will read later in this chapter, water availability, nutrient supply, and aeration all are substantially influenced by this all-encompassing soil property.

Soil Structure

Primary soil particles (i.e., sand, silt, and clay) are arranged into secondary structures called aggregates or peds, which result from the combined activities of plants and soil microorganisms. Plant roots enmesh and compress mineral particles and bind primary particles to one another. Further pressure can be exerted during wetting and drying cycles, because clays expand as they hydrate and contract as they dry. Organic compounds (polysaccharides) excreted by plant roots, and produced during the microbial degradation of plant litter, function as cementing agents binding to the surface of one or more soil particles. In combination, these processes make soil aggregates highly-stable structures that often remain intact even when immersed in water.

Aggregates range from single-grain structure, in which soil particles are totally unattached, to massive structure, in which all soil particles adhere to one another in large clods. Beach sand is an example of the former, whereas the latter often occurs in poorly drained soils with a high clay content. The degree of aggregation most conducive to plant growth lies somewhere between these extremes. Within this mid range, aggregates vary in size from granules several millimeters in diameter to blocks, prisms, or columns several centimeters in size. Granular aggregates commonly occur in the surface horizons of many forest soils, whereas blocky aggregates often occur in subsurface horizons. Plant roots generally occupy the spaces between aggregates, rather than growing through or within them. These spaces, or micropores, have a substantial influence on the rate at which water and gases move into and through the rooting zone. As a result, a well-aggregated soil will typically hold more water and will have better aeration than an unstructured soil of the same texture.

Soil Color

Color provides insight into many physical and chemical properties of soil, particularly organic matter content and drainage (or aeration). The surface of mineral soils are generally dark in color, reflecting organic matter additions from leaf and root litter. A deep surface soil dark in color (e.g., black or dark brown) usually contains relatively greater amounts of organic matter than a thin, light-colored surface soil. The subsurface of sandy forest soils in northern climates can contain accumulations of organic matter and iron that have been leached from the surface soil. This subsurface accumulation is easily identified by its dark chocolate-brown color.

In addition to providing insight into organic matter content, soil color can provide qualitative information regarding soil drainage. Most soils contain large amounts of iron (Fe) which, in an oxidized state (FeOx), is bright orange or red. This condition occurs when soils are well aerated and O2 rapidly diffuses into the soil profile. However, during prolonged periods of water saturation, O2 in soil can be depleted if the demand by plant roots and soil microorganisms exceeds the diffusion rate of O2 in water. In these situations, Fe is reduced (FeOx) producing compounds blue-gray to gray in color. Zones of mottling, a patchwork of yellow-orange and blue-gray colors, indicate the presence of both oxidized and reduced conditions. This situation occurs where the level of the water table fluctuates within the soil profile, and color can be used to determine if it lies within the rooting zone of plants. High water tables in poorly-drained landscape positions greatly restrict the rooting depth of trees, making them prone to windthrow. Using soil color, one can easily identify soils with poor drainage that often restrict the growth of many forest trees.

Soil Water

Water availability controls the global, regional, and local distribution of vegetation on the Earth. For example, forests occur in regions where the annual amount of water supplied by precipitation exceeds that which is lost through evaporation. Although broad-scale patterns of precipitation control the total amount of water entering forest ecosystems, it is the interaction of water molecules with soil particles that largely influence the amount of water that can be used by an individual plant for growth.

Water flows along a continuum extending from the atmosphere, through the plant, and into soil. The force driving water movement along this continuum is transpiration; water is literally "pulled" from soil and through plants by this process. Transpiration at the leaf surface creates tensions that are translated down water columns extending through plants and into soil. Soils can be "dry" to plants but can still contain substantial amounts of water. This relationship may occur if the forces holding water in soil exceeds the force (i.e., tension) created by the transpiration of water at the leaf surface. Understanding the dynamics of water along the atmosphere-plant-soil continuum has clear relevance for the study of plant growth and ecosystem function, because these dynamics directly control the amount of water available for plant use.

Physical Properties of Water

The physical properties of water greatly influence its availability to plants. Water (H2O-H) molecules have a net positive charge on one side of the molecule and a net negative charge to the other. Mineral particles in soil also have charged surfaces that attract water molecules. The attraction of positively and negatively charged bodies is termed adhesion, a force in soil that greatly influences the amount of water available for plant use. Adsorbed water molecules, those attracted to charged surfaces in soil, are linked to others through hydrogen bonding, a chemical bond linking the oxygen atom (-O-) of one water molecule to a hydrogen atom (+H+) of another. Hydrogen bonding gives rise to the cohesive force, or cohesion, joining water molecules into chains or polymers that extend away from the surface of mineral particles.

Due to the strong attraction of water molecules to charged surfaces in soil, adsorbed water molecules are closely packed and exist in an energy state less than that of pure water. Although water in direct contact with mineral particles is strongly held to their surface by adhesion, that force diminishes as the distance to the solid surface increases, much like the attraction of a magnet for iron diminishes as the distance between them increases. When soils are saturated, some water molecules are only weakly attracted to the surface of mineral particles, because they lie at relatively large distances from any charged surface. Water draining from saturated soil does so because the Earth's gravitational pull exceeds the adhesive and cohesive forces holding a portion of soil water. As soil continues to dry, either through plant uptake or evaporation, the forces holding the remaining water molecules steadily increase. Adhesive and cohesive forces holding water in soil are ten-
sions that must be overcome if plants are to extract water from soil. Because the forces holding water in soil can exceed those imposed by plants, only a proportion of the water in soil is available for plant use.

In addition to being attracted to charged surfaces, water molecules also are attracted to ions with net positive (cations) or negative (anions) charges. Salts, like NaCl, dissolve in water because the attraction of water molecules for cations (Na⁺) and anions (Cl⁻) is much greater than the attraction between them. The strong attraction of water for positively or negatively-charged ions causes water molecules to lose energy as they hydrate either type of ion. Because water molecules lose energy as they associate with cations and anions, water in soil has a lower energy status than pure water.

The semi-permeable membrane surrounding plant cells (i.e., plasma membrane) functions as a "molecular sieve", allowing water to transverse while excluding larger, hydrous ions. The movement of water molecules across any semi-permeable membrane in response to differences in ion concentration (i.e., the energy status of water inside versus outside the cell) is osmosis. Water molecules moving across a semi-permeable membrane exerts a force known as osmotic pressure. Osmosis, and the energy it produces, is of particular relevance to plant growth because it influences the movement of water into and out of plant cells. For example, plants under salt stress suffer from a lack of available water, because dissolved ions in soil water lower its energy status to a point where it is less than that in the plant cell. Water flows from the plant into soil solution by osmosis. This can cause the water content of plant cells to decrease to such a low level that physiological processes are impaired and the plant is no longer able to maintain turgor.

SOIL WATER POTENTIAL

The movement of water in soil, its uptake by plant roots, and its loss to the atmosphere from the leaf surface are energy-related phenomena. In soil, adhesion, cohesion, the presence of dissolved ions, and the Earth's gravitational pull are the primary forces influencing the energy status of soil water, and hence the movement of soil water and the proportion of it available for plant use. Forces in soil acting upon water molecules can be pressures (gravities) or tensions (adhesion and cohesion), both of which are measured in megapascals (MPa; values less than 0 MPa are tensions and those greater than 0 MPa are pressures).

Soil water potential refers to the energy status of soil water; it also can be thought of as the effective concentration of water in soil. By definition, the potential of pure liquid water at 20 °C and at standard atmospheric pressure is 0 megapascals (MPa). Pure water is used as a standard reference point from which we measure the influence of adhesion, cohesion, dissolved ions, and gravity on the energy status of soil water.

Adhesion and cohesion, he forces holding water molecules to charged surfaces and to one another, give rise to the matric potential of soil water. Because adhesion and cohesion lower the energy status of soil water (i.e., relative to pure water) matric potentials are less than 0 MPa. As such, matric potentials represent tensions holding water molecules to one another and to the surfaces of charged particles in soil. The presence of dissolved ions, which also lower the energy status of soil relative to pure water, give rise to the osmotic potential of soil water. Gravitational potential results from the downward force of gravity and its ability to extract water from soil. Gravitational potentials are greater than zero (i.e., pressures), because the downward pull of gravity extracts water from soil. In combination, matric, osmotic, and gravitational potentials give rise to the total soil water potential, which represents the summed energy status of soil water. In most well-drained soils, matric potential is the most important factor regulating the supply of water to the root surface.

Because adsorption and dissolved ions lower the free energy status of soil water, plants must expend energy to remove water from soil. As such, the water potential (or energy status) of plants must be lower than that of soil, if water is to flow from soil into plant roots. Transpiration at the leaf surface drives the flow of water along the energy-related path from soil to the atmosphere. The atmospheric water potential, which greatly influences the transpiration rate of plants, is largely determined by relative humidity and air temperature. The concentration of water in the atmosphere is much less than the concentration of water in either plants or soils, and as a consequence, atmospheric water potentials are more negative (i.e., at a lower energy status) than those of plants or soil. It is not unusual for atmospheric water potentials to attain values of ~100 MPa, values 10 to 100 times more negative than those in soil (Bouiswell, 1974). Because water flows from a region of high potential (i.e., high energy state) to one of low potential (i.e., low energy state), water moves from soil into plant roots, through the vascular system of the plant, and into the atmosphere. Large negative atmospheric water potentials drive the process of transpiration and the flow of water from soil, through plants, and into the atmosphere.

Although large negative water potentials at the leaf surface are translated downward to the root surface, plants are generally unable to extract soil water held by potentials less than ~1.5 MPa (i.e., a tension of 1.5 MPa; Figure 11.4). Under these conditions plants will and are unable to regain turgor even following the addition of water. At a potential of ~1.5 MPa, soil water has attained the permanent wilting point, which defines the lower limit of plant available water (Figure 11.4). Field capacity represents the upper limit of plant available water and is the amount remaining in soil after it has freely drained due to the downward pull of gravity (a potential of ~0.01 MPa). The quantity of water bounded by field capacity and the permanent wilting point represents the available water content (ML cm⁻³) of soil. It differs substantially from the saturation water content, which is the total amount of water that can be stored within soil pores (Figure 11.4). The reader is referred to Kramer (1983) for a complete treatment of plant water relations and soil water dynamics.

Soil texture substantially influences the available water content of soil. Figure 11.5 illustrates the relationship between water content (ML of water per cm³ of soil) and soil water potential for a clay, loam, and sand. At field capacity (i.e., potential of ~0.01 MPa), the clay soil holds approximately 3.6 ML of water per cm³ of soil, almost 2.5 times more water than the sand (calculated from Figure 11.5). The adhesive properties of water, in combination with the large surface area of clay-sized particles, allow the clay to hold more water at any given potential than the sand. Notice that silt loam in Figure 11.5 contains the greatest quantities of plant available water. It does so because of the favorable distribution of macro- and micro pore spaces. The available water content of sand, calculated from Figure 11.5 is 0.15 ML cm⁻³, approximately 50% of that held by the silt loam (0.36 ML cm⁻³) and clay (0.33 ML cm⁻³).

CHEMICAL PROPERTIES OF SOIL

Plant life is constructed from a surprisingly small suite of elements, whether we consider the majestic redwoods of northern California or the single-cell algae growing on the soil surface. In Table 11.2, we summarize the chemical building blocks from which plant life is constructed and their source within terrestrial ecosystems. Each is required for plant growth and development, albeit in different quantities. Macro-nutrients are those ele-
ments required in relatively large amounts. They are commonly found as constituents of nucleic acids, proteins, carbohydrates, lipids, and chlorophyll (Table 11.3). Micro-nutrients (Fe, Mn, Mo, Cu, Zn, Cl, and Co), as their name implies, are required in relatively small amounts and occur as co-factors in enzymatic reactions. Although micro-nutrients are required in small amounts, they are nonetheless important in the biochemical functioning of plants and entire ecosystems; all are supplied to plants by chemical processes in soil. Further discussion regarding the biochemical and physiological function of plant nutrients can be found in Salisbury and Ross (1992).

Although plants assimilate carbon and oxygen from the atmosphere, the majority of macro- and micro-nutrients are supplied by ion exchange reactions, mineral weathering, or organic matter decomposition—processes all occurring within soil! The supply of nutrients often limits the growth of individual plants and entire ecosystems. Nitrogen (N) availability, for example, is known to limit the growth of many boreal and temperate forests (Flanagan and Van Cleve, 1983; Pastor et al., 1984), whereas phosphorus (P) has

Figure 11.4. Diagrams showing the relationship between the thickness of water films and the tension with which water is held by soil particles. Tensions are presented in megapascals in the upper illustration. The thickness of water films in relationship to matric potential is presented in the lower figure. Reprinted with permission of the Macmillan Publishing Co., Inc. from The Nature and Properties of Soils, 8th ed., by Nyle C. Brady. Copyright ©1974 by Macmillan Publishing Co., Inc.

Figure 11.5. The relationship between soil texture and the available water content of soil. Note that field capacity increases from the sand to the silt loam and then levels off as the proportion of clay increases. Because the permanent wilting point increases linearly as a function of soil texture, the largest amount of plant available water occurs in soil with a silt loam texture. Reprinted with permission of the Macmillan Publishing Co., Inc. from The Nature and Properties of Soils, 10th ed., by Nyle C. Brady. Copyright ©1990 by Macmillan Publishing Co., Inc.

Table 11.2 Macro-nutrient Elements Required by Plants and their Source within Terrestrial Ecosystems

<table>
<thead>
<tr>
<th>Element</th>
<th>Symbol</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon</td>
<td>C</td>
<td>Atmosphere</td>
</tr>
<tr>
<td>Hydrogen</td>
<td>H</td>
<td>Water</td>
</tr>
<tr>
<td>Oxygen</td>
<td>O</td>
<td>Atmosphere, water</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>N</td>
<td>Organic matter, atmosphere</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>P</td>
<td>Mineral soil, organic matter</td>
</tr>
<tr>
<td>Potassium</td>
<td>K</td>
<td>Mineral soil, organic matter</td>
</tr>
<tr>
<td>Sulfur</td>
<td>S</td>
<td>Mineral soil, organic matter, atmosphere</td>
</tr>
<tr>
<td>Magnesium</td>
<td>Mg</td>
<td>Mineral soil</td>
</tr>
<tr>
<td>Calcium</td>
<td>Ca</td>
<td>Mineral soil</td>
</tr>
</tbody>
</table>

Table 11.3 The Biochemical Function of Plant Macro-nutrients, their Form of Uptake, and Typical Leaf Concentrations in Plants

<table>
<thead>
<tr>
<th>Element</th>
<th>Biochemical Function(s)</th>
<th>Form Assimilated</th>
<th>Leaf Concentration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon (C)</td>
<td>Form the basic building blocks of all biologically-active compounds</td>
<td>CO₂, H₂O</td>
<td>90.98%</td>
</tr>
<tr>
<td>Hydrogen (H)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oxygen (O)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nitrogen (N)</td>
<td>Nucleic acids, amino acids, proteins, chlorophyll, asteroxymos, alkaloids</td>
<td>NH₄⁺, NO₃⁻</td>
<td>1.4%</td>
</tr>
<tr>
<td>Phosphorus (P)</td>
<td>Nucleic acids, nucleotides, sugar phosphates, phospholipids</td>
<td>H₂PO₄⁻</td>
<td>0.1-0.4%</td>
</tr>
<tr>
<td>Potassium (K)</td>
<td>Enzyme co-factor, osmotic regulation, cell ion balance</td>
<td>K⁺</td>
<td>1%</td>
</tr>
<tr>
<td>Calcium (Ca)</td>
<td>Peptin synthesis and cell wall formation, metabolism, formation of nucleus and mitochondria, enzyme activator</td>
<td>Ca²⁺</td>
<td>0.8%</td>
</tr>
<tr>
<td>Sulfur (S)</td>
<td>Amino acids, proteins, sulfatopilids</td>
<td>SO₄²⁻</td>
<td>0.2%</td>
</tr>
<tr>
<td>Magnesium (Mg)</td>
<td>Chlorophyll, enzyme co-factor</td>
<td>Mg²⁺</td>
<td>0.2%</td>
</tr>
</tbody>
</table>

Source: After Salisbury and Ross (1982).

been observed to constrain forest growth in the humid tropics (Vitousek, 1984; Vitousek and Sanford, 1986). In the following discussion, we explore some of the chemical processes in soil that regulate the supply of nutrients for plant growth in both temperate and tropical forest soils. These processes, in combination with plant uptake and litter decomposition, control the cycling of nutrients within forest ecosystems (Chapter 19).

Clay Mineralogy

In studying Table 11.3, note that many macro-nutrients exist as cations, the ionic form assimilated by plant roots. The mineralogy of clay particles, and the ion exchange reactions mediated by their negatively-charged surfaces, substantially influence the supply of cations for plant growth. Ion exchange reactions in soil also are an important mechanism influencing the retention and loss of nutrients from forest ecosystems, especially following disturbances like harvesting, large-scale windthrow, or fire.

Clay minerals form during the weathering process and, to some extent, chemically reflect the primary minerals from which they originate. Phyllosilicate minerals dominate the clay fraction of temperate soil and originate from a wide array of primary minerals including feldspar, orthoclase, and biotite. Although phyllosilicate clays may differ in mineralogy, they are all formed from the same chemical building blocks. The primary structures of these minerals are the silica tetrahedra (SiO₄) and the alumina-magnesia octahedra (AlO₆ or MgO₆; Figure 11.6). By sharing O atoms at their corners, these subunits can link to form tetrahedral [(AlO₄)₆] or octahedral sheets [(MgO₆)₆], secondary structures that confer many unique properties to phyllosilicate minerals.

Fine-grained mica, vermiculite, chlorite, montmorillonite, and kaolinite are common phyllosilicate minerals in temperate soil, and some of their physical and chemical properties are summarized in Table 11.4. The weathering process, which gives rise to clay minerals, substantially influences on the extent to which phyllosilicate clays attract and bind cation nutrients. As a consequence, unweathered soils and highly weathered soils differ markedly in clay mineralogy and their ability to supply nutrients for plant growth.

Isomorphic substitution conveys a permanent negative charge on phyllosilicate minerals enabling them to attract cations and supply them for plant growth. This process occurs as one type of clay mineral (i.e., montmorillonite) weathers and gives rise to another (i.e., kaolinite). During the formation of phyllosilicate minerals, atoms of the same size, but of lower charge, replace either Si in tetrahedral sheets or Al in the octahedral sheets. The extent to which a particular clay is substituted is influenced by the chemical structures of these minerals and the relative abundance of Si and Al within the clay mineral.

Figure 11.6. The structure of the silica tetrahedra and the alumina octahedra that form the basic building blocks of phyllosilicate minerals.

<table>
<thead>
<tr>
<th>Property</th>
<th>Fine-Grained Mica</th>
<th>Montmorillonite</th>
<th>Kaolinite</th>
<th>Chlorite</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ratio of Octahedral to Tetrahedral Sheets</td>
<td>2:1</td>
<td>2:1</td>
<td>1:1</td>
<td>2:1:1</td>
</tr>
<tr>
<td>Size (μm)</td>
<td>0.1-5.0</td>
<td>0.01-1.0</td>
<td>0.5-5.0</td>
<td>0.1-2.0</td>
</tr>
<tr>
<td>Shape</td>
<td>Plates</td>
<td>Flakes</td>
<td>Hexagonal</td>
<td>Variable</td>
</tr>
<tr>
<td>External Surface (m² g⁻¹)</td>
<td>50-100</td>
<td>70-120</td>
<td>10-30</td>
<td>70-100</td>
</tr>
<tr>
<td>Net Negative Charge (coul kg⁻¹)</td>
<td>100-180</td>
<td>80-120</td>
<td>2.5</td>
<td>15-40</td>
</tr>
</tbody>
</table>

*Ventimilios of negative charge per kilogram of dry soil
Source: After Hardy (1960).
constituents of the parent material and the degree to which it has weathered. This property is a permanent attribute of phyllosilicate minerals and is relatively unaffected by changes in soil acidity. As a consequence of a low degree of isomorphic substitution, kaolinite, a highly weathered clay mineral, has a low net negative charge that is balanced by a small number of cations adsorbed into its crystalline surface (Table 11.4). Montmorillonite, a clay mineral less weathered than kaolinite, is highly substituted in its octahedral sheets and has a relatively large net negative charge. The aforementioned examples illustrate how weathering directly controls the ability of phyllosilicate clays to absorb and exchange cations with soil solution, a factor that has a profound effect on the supply of nutrients for plant growth and the ability of ecosystems to retain nutrients against leaching.

Following long periods of intense weathering (i.e., 100,000 to 3,000,000 years), Si is lost from the structure of phyllosilicate minerals leaving behind oxides of Fe and Al, which constitute the clay fraction of some soils in the humid tropics. These oxides differ markedly in their chemical characteristics from the phyllosilicate minerals from which they originate. In contrast to the ordered crystalline structure of phyllosilicate minerals, oxides of Fe and Al are amorphous (without form) and exist in a less-ordered semi-crystalline state (Schwertmann and Taylor, 1977; Sposito, 1989). More importantly, these minerals exhibit a pH-dependent variable charge, in contrast to the stable, negative charge of phyllosilicate minerals. This property results from the large number of hydroxyl groups (–OH) contained within these minerals; the formulae for goethite (FeO(OH)) and gibbsite (Al(OH)₃) illustrate this point.

Soil acidity in highly-weathered tropical soils plays an important role in the functioning of clay minerals and their ability to supply plants with nutrients. In acidic soils, the hydroxyl groups of the Al and Fe oxides are protonated, conveying a net positive charge and the ability to adsorb and exchange anions. However, these minerals lose protons (H⁺) in relatively alkaline soil (e.g., Al(OH)₃ + H⁺), thus producing a net negative charge and the ability to adsorb and exchange cations. As a consequence, soils dominated by Al and Fe oxides have a pH-dependent point of zero charge at which neither cations nor anions are adsorbed; both cations and anions are susceptible to loss through leaching. Land management practices which alter soil pH clearly have the potential to alter the ability of tropical soils to adsorb and retain plant nutrients. For further elaboration on the dynamics of variable-charge soils and nutrient mobility within them, we refer readers to Solins et al. (1988) and Uehara and Gillman (1981).

**Cation Exchange and the Supply of Nutrients**

The cation exchange capacity of soil is a general measure of plant nutrient availability and represents the total amount of cations (centimoles of positive charge) that can be adsorbed by a kilogram of soil. Cations in soil solution exist in an equilibrium with those adsorbed to cation exchange sites on clay micelles. When cations in soil solution are assimilated by plants, those adsorbed to clay particles are released and a new equilibrium is established. As such, adsorbed cations can be thought of as a "reservoir" of plant nutrient in soil. Because cations vary in size and charge, they are adsorbed and exchanged in a predictable manner reflecting their affinity for exchange sites on clay micelles. In general, cations with a small hydrated radius and a large positive charge are most strongly held. We have listed the cations commonly found in soil solution in order of decreasing affinity: 

\[ \text{Al}^{3+} > \text{H}^+ > \text{Ca}^{2+} > \text{Mg}^{2+} > \text{K}^+ > \text{NH}_4^+ > \text{Na}^+ \]

Weaker adsorbed cations like K⁺ and NH₄⁺ are more available for plant growth; they also are more susceptible to leaching than others higher in the order.

---

**Table 11.5** The Relationship Among Soil Texture, Clay Mineralogy, and the Cation Exchange Capacity in Surface Forest Soils of the Eastern United States

<table>
<thead>
<tr>
<th>Vegetation/Physiography</th>
<th>Textures</th>
<th>Clay (%)</th>
<th>Mineralogy</th>
<th>Cation Exchange Capacity (cmol kg⁻¹)</th>
<th>Organic Matter (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Northeastern US</td>
<td>sand</td>
<td>2</td>
<td>mixed</td>
<td>13</td>
<td>6.4</td>
</tr>
<tr>
<td>Jack pine/</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>outwash plain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern pin oak-</td>
<td>sand</td>
<td>4</td>
<td>mixed</td>
<td>11</td>
<td>6.0</td>
</tr>
<tr>
<td>black oak-white pine/</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>outwash plain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sugar maple-</td>
<td>loamy sand</td>
<td>6</td>
<td>mixed</td>
<td>18</td>
<td>12.0</td>
</tr>
<tr>
<td>Basswood/moraine</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II. Southeastern US</td>
<td>silt loam</td>
<td>7</td>
<td>montmorillonite</td>
<td>11</td>
<td>3.9</td>
</tr>
<tr>
<td>lobolly pine/</td>
<td>silt loam</td>
<td>20</td>
<td>montmorillonite</td>
<td>20</td>
<td>3.7</td>
</tr>
<tr>
<td>coastal plain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loblolly pine/</td>
<td>silt loam</td>
<td>20</td>
<td>montmorillonite</td>
<td>28</td>
<td>2.3</td>
</tr>
<tr>
<td>coastal plain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>water oak-willow-</td>
<td>silty clay</td>
<td>37</td>
<td>montmorillonite</td>
<td>28</td>
<td>7.0</td>
</tr>
<tr>
<td>oak/coral/prairie region</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loblolly pine/</td>
<td>silty clay</td>
<td>39</td>
<td>montmorillonite</td>
<td>30</td>
<td>7.0</td>
</tr>
<tr>
<td>upper coastal plain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loblolly pine/</td>
<td>lomy sand</td>
<td>5</td>
<td>kaolinitic</td>
<td>4</td>
<td>0.9</td>
</tr>
<tr>
<td>upper coastal plain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loblolly pine/</td>
<td>sandy loam</td>
<td>11</td>
<td>kaolinitic</td>
<td>7</td>
<td>1.3</td>
</tr>
<tr>
<td>upper coastal plain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loblolly pine/</td>
<td>clay loam</td>
<td>28</td>
<td>kaolinitic</td>
<td>26</td>
<td>2.3</td>
</tr>
<tr>
<td>upper coastal plain</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

We summarize the cation exchange capacity for forest soils of different texture and mineralogy to illustrate the combined influence of weathering and parent material on supply of cations for plant growth (Table 11.5). Note that cation exchange capacity increases as the percentage of clay rises. Also note that soils dominated by kaolinite, a weakly-substituted and highly-weathered phyllosilicate mineral, generally have lower cation exchange capacities than those soils containing montmorillonite. The soils of mixed mineralogy contain a mixture of phyllosilicate clays and have relatively high cation exchange capacities even though clay contents are relatively low. As you will read later in this section, the high organic matter contents of these soils greatly contribute to their ability to supply plants with cation nutrients.
The proportion of cation exchange sites occupied by Ca\(^{2+}\), Mg\(^{2+}\), K\(^+\), and Na\(^+\) is the percent base saturation of soil. These cations are not technically bases, because they do not directly neutralize H\(^+\) in soil solution. Nonetheless, they reduce soil acidity when they are adsorbed in place of H\(^+\), a topic that we will further elaborate in the following section. Percent base saturation is a chemical property of particular relevance to plant growth, because it is both a general measure of cation nutrient availability and soil buffering capacity. In general, soils that have a high proportion of exchangeable bases have a high capacity to both supply plants with base cations and buffer acidic inputs.

### Soil Acidity

Soil pH is commonly used to quantify acidity and, by definition, is the negative log of the hydrogen ion concentration in soil solution (pH = -log [H\(^+\)]. In combination with adsorption and exchange reactions, soil acidity substantially influences the supply of nutrients for plant growth. It does so by controlling the solubility of soil minerals. Figure 11.7 illustrates the availability of plant nutrients along a pH gradient ranging from very acidic soils to those with high pH. Note that the availability of most nutrients is greatest at neutral pH values (Figure 11.7). By influencing mineral solubility, soil pH also affects the weathering rate of parent material, the formation of clay minerals, and soil development. Thus, the weathering process and soil acidification often go hand in hand. The activity of soil microorganisms also is influenced by soil acidity as we see in Figure 11.7.

There are several sources of H\(^+\) that contribute to the lowering of soil pH, the weathering of parent material, and the removal of base cations. Perhaps the most important source of H\(^+\) in soil results from the respiration of plant roots and soil microorganisms. Carbon dioxide produced during respiration dissolves in soil solution and forms carbonic acid (H\(_2\)CO\(_3\)). The prolonged exposure of soil minerals to this relatively weak acid results in their solubilization and the removal of base cations. Much stronger organic acids (e.g., fulvic and humic acids) are produced as by-products of the microbial decomposition of plant tissues. Plant roots also excrete organic acids that similarly act upon soil minerals. Over extended time periods (i.e., 10,000 to 1,000,000 years), these sources of acidity facilitate the weathering of soil minerals and lower pH.

The industrial activities of humans also have the potential to influence soil chemistry. Oxides of nitrogen (NO\(_x\)) and sulfur (SO\(_x\)) released during the burning of fossil fuels, can further oxidize in the atmosphere to produce nitric (HNO\(_3\)) and sulfuric (H\(_2\)SO\(_4\)) acids. The addition of these acids in precipitation has raised concerns in eastern North America and central Europe. Because the constituents of "acidic deposition" are relatively strong acids, they have the potential to act upon soil minerals in the same manner as the acids produced by the metabolism of plants and soil microorganisms. Some soils in eastern North America, particularly those with coarse textures where bedrock is shallow, are sensitive to acidic deposition because of their low cation exchange capacity, and low base saturation.

It is important to consider soil acidity, mineral weathering, and the removal of base cations simultaneously, because they are co-occurring processes in soil. As mentioned earlier, percent base saturation represents the ability of soil to buffer the input of H\(^+\) from chemical and biological sources. Base cations buffer the soil reaction when they weather from soil minerals and replace H\(^+\) adsorbed to exchange sites. The H\(^+\) so released initially enters soil solution; however, it is easily leached from the soil resulting in a decrease in acidity. Clearly, over long time periods, the ability of soil minerals to relinquish base cations to weathering can be exhausted. In such a situation, pH declines to the point where the soil reaction is dominated by Al. At a very low soil pH (< 4.0), Al exists as Al\(^{3+}\) and, along with H\(^+\), occupies the majority of cation exchange sites. In soil solution, Al\(^{3+}\) can react with water in the following manner:

$$\text{Adsozed-}\text{Al}^{3+} + \text{H}_2\text{O} \rightleftharpoons \text{Al(OH)}^2^+ + \text{H}^+$$

In studying this equation, note that the reaction of H\(^+\) with bases in soil solution will shift the equilibrium to the right, producing a "new" H\(^+\) during formation of Al(OH)\(^2^+\). This mechanism constitutes a buffering system that maintains acidic soils at a low pH. Furthermore, Al\(^{3+}\) released in the reaction is toxic to plants and can greatly restrict root growth (Rumme and Rode, 1991). High concentrations of Al\(^{3+}\) in soil solution are known to reduce root elongation, kill root meristems, and disrupt the functioning of the phloem sap across the above-ground tissues (Foy et al., 1978).

Most forest soils range from extremely acid (pH 4.0) to slightly acid (pH 6.5). Where a particular forest soil lies along this gradient is substantially influenced by organic matter additions (e.g., leaves, roots, twigs, reproductive structures) from overstory trees and the acids produced during microbial decomposition. The general trend is for conifers such as...
Soil Organic Matter

Although organic matter composes a relatively small fraction of most forest soils (e.g., <1 percent to 15 percent), it has a profound effect on a wide array of physical, chemical, and biological properties. As noted earlier, soil organic matter (i.e., plant litter) contributes to aggregation formation, which in turn influences the amount of soil water available to plants. It also functions as a "storehouse" of plant nutrients, supplying most of the nitrogen used in the annual growth of forest ecosystems. Finally, soil organic matter is the substrate used for the growth and maintenance of microbial populations in soil. It is through the metabolic activities of these organisms that nitrogen and other plant nutrients are released from soil organic matter. Because the nutrients so released can be re-assimilated by plants, soil organic matter represents an important "weatherting" in the cycling and storage of nutrients within forest ecosystems (see Chapter 19).

The organic matter entering the soil originates from above- and belowground sources of plant litter. Aboveground sources consist of leaves, reproductive structures, twigs and tree stems, whereas roots (fine and coarse) are the primary belowground source of litter. In most forests, belowground litter from fine roots equals or exceeds aboveground litter production (i.e., leaves, seeds, flowers). In general, plant litter contains approximately 15 to 60 percent cellulose, 10 to 30 percent hemicellulose, 5 to 30 percent lignin, and 2 to 5 percent protein (Paul and Clark, 1996). In soil, these compounds are metabolized by microorganisms, producing energy, CO₂, H₂O, and humus as end products. Humus, which composes the Oa horizon, is a complex and chemically-resistant material that gives surface soils their dark color and unique chemical properties. Due to its advanced state of decay, humus does not physically or chemically resemble the plant material from which it originated. Humus also is chemically resistant to further microbial degradation and can remain in soil for periods of 100 to 3,000 years (Paul and Clark, 1996). The surface of humus can have a net negative charge, resulting from the dissociation of H⁺ from hydroxy (-OH), carboxyl (-COOH), or phenolic (C₆H₅-OH) groups. At high pH values, the cation exchange capacity of humus (150 to 300 cmol kg⁻¹) can exceed that of many silicate clays. As such, cation or anion exchange reactions mediated by humus represent an important mechanism influencing nutrient availability in soil. In some soils, approximately 50 percent of the total cation exchange capacity of soil can be attributed to human activity. The relatively high cation exchange capacities of the sandy soils of mixed minerology in Table 11.4 result from high organic matter contents.

The organic matter content of soil reflects a balance between the addition of organic matter from plant production and its loss during microbial decomposition. Because forest harvesting can alter both rates of litter input and loss through decomposition, it also has the potential to alter the quantity of organic matter and associated plant nutrients stored in soil. In Chapter 19, we further consider the impact of forest harvesting on soil organic matter dynamics and the cycling of plant nutrients.

The organic matter content of soil exerts an important influence on the available water content of soil. Soil organic matter holds relatively large quantities of water at field capacity, but its permanent wilting point also is proportionally high, providing only small quantities of plant available water. However, organic matter content is the primary factor influencing aggregate formation. In turn, soil aggregation influences the proportion of micro- and macro pore space, which directly controls the water-holding characteristics of soil. Consequently, soil organic matter exerts its main influence on the water-holding characteristics of soil through its influence on soil structure. Well-aggregated, fine-textured soils with ample organic matter contents (5 to 10 percent) generally hold large quantities of available water, making them good substrates for plant growth.

SOIL CLASSIFICATION

A taxonomic system of soil classification, referred to as the Soil Taxonomy, is widely used throughout North America. It was developed by the soil survey staff of the United States Department of Agriculture to classify soils in regard to their potential for agricultural management (Soil Survey Staff, 1975). This system is based on measurable morphological characteristics present within a particular soil profile. The primary advantage of this approach is that the soil profile itself, rather than the soil-forming process, is classified. Soil taxonomy is modeled after the plant taxonomic system, with categories ranging from order (broad grouping) to series (narrowest category).

The main soil orders supporting forests in North America are Entisols, Inceptisols, Spodosols, Alfisols, Histic soils and Ultisols. Entisols (recent soils) are mineral soils without, or with only the beginnings, of horizon development. They often occur on talus slopes, flood plains, sand dunes, and where bedrock is close to the land surface. Inceptisols (from Latin inceptus) are moister than Entisols, and contain a weakly developed B horizon. These soils have a wide geographic distribution, and, with the exception of arid climates, can be found in most regions in North America. Inceptisols are common forest soils in the Pacific Northwest, Rocky Mountains, and the eastern United States. They often occur in well-drained, upland landscape positions, but also can be found along river corridors.

Alfisols (from the chemical abbreviation for aluminum and iron) typically form in cool to hot humid areas and are common under deciduous forests in the eastern United States. They are characterized by gray to brown surface horizons, medium to high base saturation, and the accumulation of silicate clay in the B horizon. Alfisols appear to be more strongly weathered than Inceptisols, but are less weathered than Spodosols.

In cold and temperate climates, the process of leaching can give rise to the formation of Spodosols (from Greek spados, wood ash). These soils are characterized by the presence of a strongly-developed E horizon and the accumulation of humus and oxides of Fe and Al in the B horizons. Spodosols often form beneath boreal forests occurring on course-textured parent materials. In general, these soils are best developed beneath spruce and fir, species whose litter generally acidify the surface soil, and are common in the northeastern United States, northern Lake States region, and the Pacific Northwest. It should be noted...
that Spodosols also can form beneath coniferous forest in warm climates. In Florida, Spodosols are often encountered in landscape positions in which coniferous forests are seasonally flooded.

Histosols form in poorly-drained landscape positions and are characterized by a high organic matter content (2-20 percent). These soils can form anywhere the land surface is continually saturated with water, and thus occur in all climates and have a global distribution. Forest vegetation occurring on these organically-derived soils include: black spruce bogs in the northern Lake States, black ash-red maple swamps in the northeastern United States, and the pocosin and cypress swamps of the southeastern United States. Large expanses of forested Histosols also can be found in Scandinavia, Siberia, and Canada.

Ultisols (from the Latin word ultimus) are a common forest soil on old land surfaces in warm, humid climates, such as those of the southeastern United States. These soils are characterized by an accumulation of silicate clay in the B horizon. However, Ultisols are distinguished from Alfisols by a low base saturation—the result of more intense weathering. These soils are widely distributed in the eastern US, extending southward from Maryland to Florida and westward from the east coast to the Mississippi River Valley. They also occur in portions of the Pacific Northwest and eastern California, and can be found on old land surfaces in Australia, Africa, India, southern China, and southern Brazil.

Oxisols (from the French oixide and the Latin word for soil, solum) support forest vegetation in the tropical and sub-tropical regions of Central and South America, south-east Asia, and Africa. The subsoil of these highly weathered soils contains an accumulation of kaolinite and oxides of Al and Fe. The old land surfaces on which these soils occur, in combination with the intense weathering of humid tropical climates, can give rise to profiles exceeding 15 meters in depth.

Forest and agricultural ecosystems differ in ways that limit the use of the soil taxonomy to classify forested landscapes. In the western United States, for example, a wide range of forest habitat types can be found on the same taxonomic unit of soil (Neiman, 1988), making it difficult to use soil classification to predict the occurrence of forest vegetation. The primary reason for such a disparity is that forest vegetation reflects a myriad of interacting factors like physiography, harvesting frequency and intensity, and prior land uses that are not considered by soil taxonomy. Nevertheless, soil factors that reflect moisture and nutrient regimes, like texture, aggregation, and coarse-fraction content, can be often related to the occurrence of some forest habitat types (Neiman, 1988). Because the relationship between forest communities and the soil developing beneath them is multifactorial and dynamic, it is likely that any single-factor classification, like the soil taxonomy, will be of limited use in predicting the distribution and growth of forest ecosystems. In Chapter 13, we further discuss the limitation of single-factor systems for classifying forested landscapes.

**LANDFORM, SOIL, AND FOREST VEGETATION: LANDSCAPE RELATIONSHIPS**

Changes in topography, vegetation, and parent material can give rise to marked differences in soil formation, even within a relatively small geographic area. In Michigan's Upper Peninsula, for example, forest ecosystems dominated by white pine, sugar maple, and red oak can occur in well-drained, upland landscape positions where a thin blanket of glacial drift overlies bedrock (Fig. 11.8). Soils forming in these landscape positions are Inceptisols, characterized by a shallow profile and the minimal development of a B horizon. The deeper deposits of glacial drift downslope give rise to Spodosols, which occur beneath a canopy of sugar maple and basswood. In lower slope positions also dominated by sugar maple, Inceptisols form in relatively recent deposits of colluvium. The formation of an Inceptisol in this landscape position is related to the relatively short duration over which the parent material has weathered. Swamp forest dominated by black ash and northern white-cedar occur in the poorly-drained bottom slope positions where the accumulation of organic matter has lead to the formation of Histosols (Fig. 11.8). The patterns of soil formation described above are repeatable features in the landscape, occurring in other locations with a similar set of soil-forming factors (i.e., parent material, vegetation, time).

In the southeastern United States, topography exerts a similar influence on the soil developing beneath the flatwood vegetation of the lower coastal plain (Fig. 11.9). In this region, relatively small elevational differences differentiate well-drained from poorly-drained landscape positions. This land surface is relatively old compared to the relatively recent (ca. 10,000 years before present) deposition of glacial materials in Michigan's Upper Peninsula. As a consequence, the parent material giving rise to this soil has been affected by climate, biota, and topography for a longer duration.

In uplands dominated by longleaf pine, relatively-dry conditions give rise to Inceptisols—poorly-developed soils with minimal horizon formation. The warm, humid climate of this region, in combination sandy parent material and coniferous vegetation, give rise to Spodosols in somewhat poorly-drained landscape positions. Histosols also form in very poorly drained landscape position in the southeast United States, similar to the landscape distribution of these soils in other regions.
Figure 11.8. The relationship among topography, vegetation, and soil development in the coastal plain flatwoods of the southeastern US. Organic matter accumulation in the surface horizon dramatically increases as one moves from the well-drained upland positions to the poorly-drained bottom slope positions. In this region of the United States, relatively small changes in elevation elicit large changes in soil drainage, profile development, and overstory composition. Adapted from Pritchett and Smith (1970)

Suggested Readings


Fire has affected a substantial portion of the forests of the world at one time or another. In North America, virtually all of the upland forests in the South, the Lake States and adjacent Canada, the West, and most of those in the Northeast, Appalachian Mountain Region, and Central States have been burned more or less frequently. In the boreal forests of Alaska and the Canadian Nort, fire has been a powerful natural factor affecting vegetation and wildlife. Wetlands, such as swamps (Cysak, 1973; Ewel, 1990), bogs, marshes, and even moist tropical forests (Goldammer, 1990b) also have been burned, although less frequently, and their vegetation markedly affected. In addition, fire was extensively used by Native Americans prior to European settlement. Natural fire has patterned the forests and savannas of the Mediterranean Region (Navas, 1974; Gill, 1977), South America (Contino, 1990; Soares, 1990), much of Africa (Koma-ek, 1972, Phillips, 1974; Boosen and Tainton, 1984), and of Europe, Australia (Gill et al., 1981, 1990; Pyne, 1991), and Asia (Goldammer and Penafiel, 1990; Stout et al., 1990). In addition, humans have introduced fire into the wet tropics during deforestation for economic development (Kaufman, et al., 1990; Levine, 1991). Books by Kozlowski and Ahlgren (1974), Pyne (1982, 1991), Wein and MacLean (1983), Goldammer (1990a), Levine (1991), Johnson (1992), Agee (1993), Whelan (1995), and Bond and van Wilgen (1996) provide an entry into the voluminous literature on fire.

Fire has always been a natural and extremely important process shaping the evolution of species and the functioning of ecosystems in which they reside. Fire in prehistory and the remarkable interactions of fire with humans and wildlife is considered by Schiele (1990). Its frequency, intensity, extent, and time of occurrence are characteristic of different regional and local landscape ecosystems. It is a principal influence on plant traits and life cycles as well as ecosystem processes: carbon, nutrient, and water cycling; biomass accumulation; succession; and diversity. Specifically, fire plays many major roles in land-