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The Forest Floor

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Introduction

One of the most striking features of forests is the canopy, which consists of leaves and branches forming a noticeable layer that shades the ground and provides habitat for numerous birds, mammals, and insects. In addition to providing habitat, the canopy provides a substantial input of organic litter to the soil surface as the trees cyclically shed foliage, flowers, fruit, twigs, and bark. Over time as forests grow and develop, organic remains of plants and animals accumulate on the soil surface. The accumulation of foliage and branches is collectively referred to as the forest floor. The forest floor, along with tree roots, is an integral component of the forest soil system that distinguishes forest soils from agricultural soils.

The forest floor has a tremendous impact on the soil environment. One of the most important factors affecting tree growth is the capacity of the soil to transfer energy, water, and gases from the soil surface to organisms and roots living deeper in the soil. One of the fundamental soil physical properties influencing this transfer is soil structure, which refers to the aggregation of primary soil particles (sand, silt, clay) into secondary units. Well-developed granular structure occurs in the surface mineral soil horizons creating pores that are large enough for water to flow freely through. Soil structure is described by shape (i.e., granular refers to small spheres, and blocky refers to larger aggregates). There is no quantitative expression currently available to describe soil structure.

Bulk density is a commonly used soil physical property that is influenced by soil structure. Bulk density is a measure of dry mass per unit volume of undisturbed soil. The undisturbed volume includes both the solid particles as well as pore space. For a given type of soil particle (organic vs. mineral), increased pore space results in lower values of bulk density. The particle density of organic matter is approximately half that of mineral soil, which averages $2.65\,\mathrm{Mg\,m^{-3}}$. The combination of low particle density and a relatively high volume of pores impart a low bulk density to the forest floor, which ranges from less than 0.1 to $0.30\,\mathrm{Mg\,m^{-3}}$. Contrast that figure with the range for typical surface mineral soil horizons of $1.0–1.3\,\mathrm{Mg\,m^{-3}}$. For purposes of comparison, the density of water is $1.0\,\mathrm{Mg\,m^{-3}}$.

The large pore space volume associated with the forest floor has several important consequences. Air filled pores of forest floors act as an insulator, buffering soil temperature by reducing daily high and increasing daily low temperatures. Water infiltration, the movement of water into the soil, and water storage capacity are high because of the large volume of pore space. Consequently, overland water flow in forest soils is rare. The forest floor provides a physically favorable environment for plant roots and soil fauna. Low bulk density does not restrict root growth or organism movement, while high pore space and water holding capacity ensure adequate moisture and aeration required by aerobic organisms. These favorable physical properties promote a high level of biological activity which decreases with depth below the soil surface.

Characterization of Organic Horizons

The forest floor is differentiated from mineral soil on the basis of organic matter expressed as carbon (C) concentration. The organic material comprising the forest floor exists in a decay continuum, ranging from relatively undecayed plant material on the surface to black, highly decomposed organic material referred to as humus. The US soil classification system divides the decay continuum into three discrete layers or horizons (**Figure 1**): (1) Oi, fibric material, relatively undecomposed; (2) Oe, hemic material, moderately decomposed; and (3) Oa, sapric

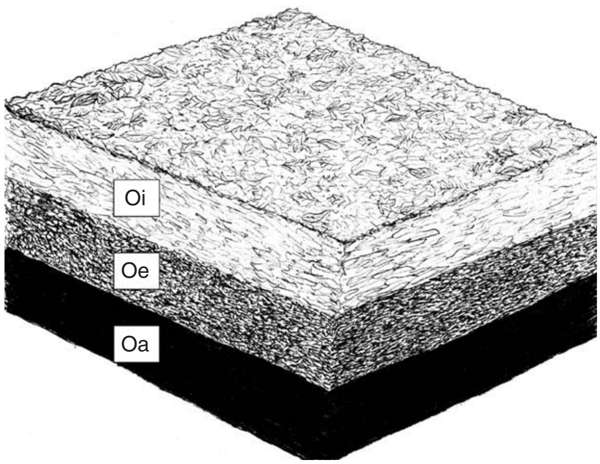

Figure 1 Idealized schematic of forest floor organic horizons. Proceeding downward from the fibrous Oi to the highly decomposed Oa horizon, litter identity is lost and the C : N ratio becomes smaller. *In situ* boundaries among organic horizons often are indistinct along the decay continuum and are not easily differentiated. Illustration by Rachael Briggs.

material, highly decomposed amorphous humus. Comparison with other classification systems is provided in **Table 1**. The letter O signifies the organic master horizon. The accompanying lowercase letters indicate the relative degree of decomposition. All three horizons may not always be present in the forest floor. The presence or absence and degree of development of each horizon depends on a variety of factors including amount and type of organic inputs, decomposition rate, and the activity of soil fauna.

Degree of decomposition is quantitatively defined on the basis of rubbed fiber content. Rubbed fiber content is the proportion of sample volume comprised of fibers that remain after rubbing between the fingers under a stream of water. Highly decomposed material is removed by this simple process, leaving only fibers. The Oi horizon, which consists of relatively undecomposed material that can be identified as to original plant component, has a rubbed fiber content exceeding 75%. At the other extreme, the highly decomposed Oa horizon has a rubbed fiber content less than 17%. The Oe horizon has a rubbed fiber content between 17% and 75%.

The use of quantitative criteria has improved field identification of the boundaries among organic horizons as well as the boundary between the Oa and the mineral soil. Mineral soil horizons contain less than 18% organic carbon on a weight basis. Laboratory analysis is often used to confirm field determinations. Prior to the use of rubbed fiber content to classify organic horizons, they were designated qualitatively as L (litter), F (fermentation), and H (humus) layers. Those classes approximately correspond to the current Oi, Oe, and Oa horizons, respectively. Differentiation among L, F, and H horizons in the absence of quantitative criteria often proved difficult; there was considerable inconsistency among forest soil scientists. Inconsistency was also noted for individual scientists over time.

Table 1 Comparison of organic horizon designations for three soil classification systems

US	*Canada*	*FAO*[a]
Oi (L)	Of	O
Oe (F)	Om	O
Oa (H)	Oh	O

[a] The Food and Agriculture Organization (FAO) system does not differentiate on the basis of degree of decomposition among organic horizons. Organic horizons that are saturated are designated as H.

Forest Humus Types

The concept of humus type, which is the classification of forest floors on the basis of morphology and arrangement of organic horizons, originated in Denmark in the late nineteenth century. The concept has evolved to generate detailed hierarchical classification systems with numerous subcategories. One of the most comprehensive was published in 1993 as a monograph. Three general categories associated with productivity and the rate of nutrient cycling described in this early work continue as the foundation for all of these systems: mor, duff mull (also referred to as moder), and mull.

The mor forest humus type is sometimes referred to as acid humus. It is associated with coniferous species that produce recalcitrant, nutrient poor litter. In this humus type, there is an abrupt boundary between the Oe or Oa and the mineral soil horizon. This abrupt boundary indicates that there is very little if any incorporation of organic matter with the underlying mineral soil, reflecting a relatively low level of biological activity. In addition, incomplete decomposition of the nutrient poor organic material generates large quantities of organic acids. As the organic acids are washed down the profile by percolating water, they strip organic matter and sesquioxides from mineral soil particle surfaces, carrying them downward and depositing them in an underlying horizon.

The mull forest humus type, associated with fertile systems and high rates of nutrient cycling, represents the other extreme of the spectrum. The mull is characterized by highly decomposed, amorphous organic matter intimately incorporated into the mineral soil (A horizon). Thick organic horizons do not accumulate; Oe and Oa horizons are absent due to the high rate of biological activity. Decomposition is relatively rapid, releasing nutrients and preventing immobilization in organic residues. The mull forest humus type is associated with fertile sites supporting nutrient demanding species such as sugar maple (*Acer saccharum*), basswood (*Tilia americana*), and white ash (*Fraxinus americana*).

The duff mull forest humus type is intermediate between the mor and mull types described above. There is greater incorporation of organic matter in the mineral soil than for the mor forest humus type but less than the complete incorporation associated with mulls. The rate of nutrient cycling and decomposition is intermediate.

Decomposition and Nutrient Cycling

The forest floor serves an important role in cycling of nutrients and organic matter. Organic matter chemical composition reflects that of the material from which it originated; approximately 90% of plant dry weight consists of carbon, hydrogen, and oxygen. Nitrogen comprises 1–2% and the remainder is comprised of plant nutrients such as phosphorus, potassium, calcium, magnesium, etc. The organic horizons provide habitat for a diverse biota. In addition, organic matter is a substrate, serving as a source of energy and nutrition for a multitude of organisms. Ultimately, aerobic organisms convert organic matter to carbon dioxide and water. In the process, essential plant nutrients are converted from organically bound to soluble plant available forms, a process known as mineralization. Biological activity is greatest for mull and least for mor forest humus types.

A host of organisms ranging in size from moles and gophers down to microscopic bacteria and fungi participate in mineralization. Macrofauna that tunnel and burrow generate large pores that facilitate removal of excess moisture and transfer of oxygen from the atmosphere to the soil atmosphere. These macrofauna indirectly affect decomposition by improving soil aeration. The role of earthworms in improving soil physical properties, as well as soil chemical properties, is well documented. A variety of organisms physically reduce particle size, a process known as comminution. Reduced surface area: volume ratio facilitates microbial attack, biochemical decomposition and synthesis of new compounds.

Organic matter decomposition rates can be estimated by successively measuring mass loss of confined organic residues (i.e., foliage, fine roots) in nylon mesh bags over time. The mesh is small enough to contain decaying material and large enough to permit mesofauna entry. Numerous such studies have found that the negative exponential function can be used to model the loss of mass over time:

$$y = e^{kt}$$

where y is the proportion of mass remaining at time t, k is the decomposition constant, and t is time (years). This model is convenient because the proportion of mass remaining over time can be described by a single variable, k. The model is a monotonically decreasing function bounded by 1 and 0 (**Figure 2**).

Environmental Variables Constraining Decomposition

Numerous studies in forest systems have demonstrated the degree to which organic matter decomposition rates are constrained by aeration, temperature, precipitation, and litter quality. Decomposition is promoted by a plentiful supply of oxygen for aerobic organisms. In the absence of oxygen, organic matter decomposition is very slow and organic matter builds up. Organic soils, which form in saturated conditions, illustrate what happens in the absence of oxygen. Saturated conditions prevent aerobic organism activity, effectively stopping the decomposition process. When organic soils are drained, they are very productive for both agriculture and forestry because of their desirable physical and chemical properties. One of the problems associated with drainage of organic soils is subsidence. Organic matter exposed to atmospheric oxygen decomposes and the organic soil depth decreases rapidly.

Given adequate oxygen, temperature and moisture constrain decomposition. In the absence of adequate

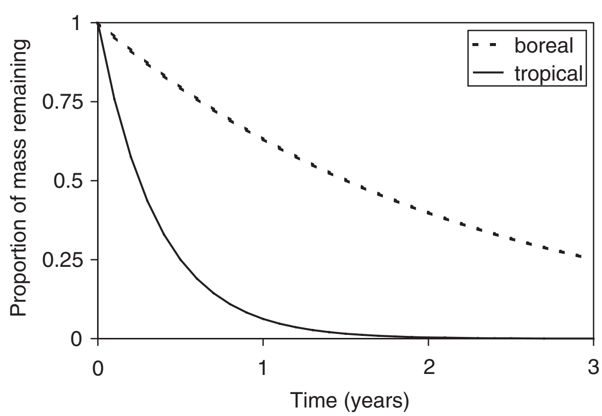

Figure 2 Mass of deciduous leaves over time modeled for deciduous leaves using the model $y = e^{kt}$, with $k = -0.46$ for *Betula papyrifera* in the boreal forest and $k = -2.77$ for *Pentaclethra macrolobal* in the tropical forest. Values of k were obtained from published literature.

moisture, biologic activity is limited and decomposition proceeds slowly even at warm temperatures. Decomposition rates are notably reduced in arid environments. When moisture is not limiting, decomposition rates increase with increasing temperature and litter disappears more rapidly. The minimum temperature for appreciable biological activity (5°C) is often referred to as biological zero. Comparison of the rate of mass loss for deciduous leaves in boreal and tropical rainforests illustrates the influence of temperature on decomposition (**Figure 2**). Organic matter builds up in cold, wet conditions characteristic of the boreal forest and the tundra.

Within a given climatic regime, decomposition rate increases with increasing litter quality. Generally, high quality litters have narrow C:N ratios and relatively low proportions of recalcitrant constituents such as complex fats and waxes. Nitrogen is required by the bacteria and fungi that decompose plant tissue. When adequate quantities of nitrogen are available to those organisms, decomposition proceeds more rapidly. As decomposition proceeds, the C:N ratio decreases. Consequently, the C:N ratio is higher for the Oi than the Oa horizon.

Decomposition Influences Productivity

Rates of organic matter decomposition, which are reflected in the forest humus type classification, are related to forest productivity. During the process of decomposition, carbon bound in the forest floor is converted to carbon dioxide. Plant essential nutrients undergo mineralization, which is the conversion from organic to a readily soluble plant available form. Higher rates of decomposition result in a more rapid cycling of essential plant nutrients and higher productivity.

The thick forest floors of boreal forests accumulate and immobilize large quantities of nutrients. In some boreal forests, the average time litter resides in the forest floor before it is completely decomposed, or its mean residence time, is 350 years. Thus, in spite of the large amount of nitrogen contained in the forest floors, trees in the boreal forest may exhibit nitrogen deficiency because the nitrogen is bound in an organic form that is unavailable to plants. This situation also may occur in upland conifer forests where litter quality is low. Rates of nutrient cycling in the humid tropical forests, in contrast, are much more rapid. Mean residence time for organic matter in tropical rainforests is on the order of 4 years. Consequently, forest floors generally do not build up except where saturated conditions prevent aerobic organism activity.

Forest Floor Mass: Accumulation – Decomposition

Forest floor mass is the difference between litter accumulation and decomposition. Global patterns for litterfall reflect the effects of climate on production. Although there are wide ranges within latitudinal zones, annual litterfall generally increases with decreasing latitude from boreal (2–4 $Mg\,ha^{-1}$) to tropical (5–13 $Mg\,ha^{-1}$) forests. Rates of organic matter decomposition also vary with latitude, increase with increasing temperature from the boreal forests to the tropics when moisture is not limiting.

Published values for forest floor mass range from a few to more than 100 $Mg\,ha^{-1}$. Although accumulation and decomposition vary with latitude, it is not possible to make generalizations regarding forest floor mass because of additional factors that operate at a more local scale. Disturbances such as fire, tornadoes, hurricanes, and timber harvesting are common features of all forest ecosystems. The cyclical nature of disturbance in a variety of ecosystems has a profound effect on density and species composition. Large-scale disturbances that remove portions of the canopy reduce litter inputs for a given time period. In addition, the exposure of the forest floor to increased light and moisture levels due to reduction of the canopy and in plant transpiration, increases the rate of decomposition. At some point in stand development, accumulation rate may equal decomposition rate and the forest floor mass remains relatively constant. Steady state is the term used to describe this condition.

Forest Management and the Forest Floor

An important goal of forest management is to minimize disturbance to the forest floor, in order to preserve the integrity and function of this vital component of the forest ecosystem. The intact forest floor has a high infiltration capacity and absorbs the kinetic energy of falling raindrops. The combined effects of the highly absorbent forest floor and the presence of numerous large pores from roots and organism activity eliminates overland flow of water and prevents soil erosion. Soil loss from forested systems, the result of streams cutting through their banks, is the benchmark rate of natural erosion, against which rates of accelerated erosion are compared.

It is clear that the forest floor is a dynamic entity having a profound impact on the functioning of forest ecosystems. The forest floor modifies the forest soil environment, increasing the capacity for exchange of water, energy, and gases between the atmosphere and the soil system. Decomposition of the forest floor over time provides a continual source of nutrients for vegetation preventing excessive losses through leaching and insuring high levels of forest productivity. In addition, the forest floor provides favorable habitat and substrate for a diversity of organisms that contribute to cycling of nutrients through the forest ecosystem.

See also: **Ecology**: Forest Canopies; Natural Disturbance in Forest Environments. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health; Soil Biology. **Soil Development and Properties**: Forests and Soil Development; Water Storage and Movement. **Tree Physiology**: Physiology and Silviculture; Root System Physiology.

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Nutrient Cycling

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Introduction

Worldwide, healthy, productive forests grow on a variety of sites that are of low fertility such as mountains, coastal plain deposits, old highly weathered tropical soils, abandoned agricultural lands, and lands reclaimed after mining. The ability of forests to grow and prosper on such sites is due to the ability of forests to accumulate essential plant nutrients, to utilize these nutrients in production of foliage, and to return these nutrients to the soil or recapture them internally for reuse in subsequent year's growth. This is the process of nutrient cycling.

Geochemical, Biogeochemical, and Biochemical Nutrient Cycles

Nutrient cycling in forests can be divided into three individual but interconnected cycles (**Figure 1**).

The Geochemical Cycle

The geochemical cycle is associated with transfers of elements into or out of the ecosystem. Inputs to the forest from the geochemical cycle include nutrients added to the forest as solutes in precipitation, associated with fine particulates or as aerosols. Additionally, nitrogen (N) can be removed from the atmosphere and added to the forest ecosystem through symbiotic associations of nitrogen-fixing rhizobium or actinorrhiza or through free-living nitrogen fixing organisms. Weathering and release of nutrient elements from parent rock is also considered an addition in the geochemical cycle because of long time factors involved in this process and the conversion of nutrient elements from non plant available to plant available forms. Losses of nutrients from the forest occur as ions dissolved in runoff water and associated with soil particles eroded from the site and moved as suspended sediment or bed load in streams. Nutrients can also be leached below the rooting zone. Fires can play an important role in the geochemical cycle of forests. Large quantities of N and sulfur (S) can be volatilized by fire and returned to the atmosphere. Ash produced during forest fire can be transported long distances and be a significant loss of nutrients from the forest.

The Biogeochemical Cycle

The biogeochemical cycle involves external transfers of elements among different components of a forest system. Uptake of nutrients from the soil and return of these nutrients in leaf fall, branch shedding, root growth and death, or through tree mortality is a major component of the biogeochemical nutrient cycle. Nutrients returned to the soil in this way are not available for plant reuse until decomposition occurs and nutrients are converted from organic to mineral forms, a process termed mineralization. Mineralization of nutrients from organic matter of the forest floor plays an important role in the supply of nutrients available for forest growth. Also included with the biogeochemical cycle is the washing of nutrients from leaves and stem tissue and its return to the soil in precipitation falling through the canopy or flowing down the stem as stemflow.