Root growth varies seasonally in response to carbon fixation by leaves and demand by various parts of the tree. Deciduous species have wide range in photosynthetic capacity, while evergreen species maintain some photosynthetic capacity all year. Under these two scenarios we understand that an excess of carbohydrates would be available to deciduous species roots only after leaf-out in the spring, whereas evergreen root production would be bimodal, with excess carbohydrates produced in the early spring and autumn.

Root development is critical during seedling establishment. Establishment may be limited by site-specific properties (such as nitrogen or phosphorus availability, or aeration) or by process-limiting situations (such as establishment of a mycorrhizal hyphal network, production of absorbing root surface area, or allocation of resources between sources and sinks).

Exudates

Interest in the rhizosphere effect on microbial activity and plant health did not gain momentum until about 1955. Since that time, researchers have calculated that carbon released from roots growing in soil can amount to approximately 20% of the total plant dry matter. Exudates are produced from carbohydrates which are primarily synthesized in the shoot during photosynthesis and then translocated to the root system. A majority of total root exudates, approximately 60%, are cations and to a lesser extent anions. The carbon components of root exudates are typically composed of 66% organic acids, 29% carbohydrates, and 5% amino acids.

The presence of microorganisms in the rhizosphere increases root exudation, either through physical damage to the root tissues, or through release of metabolites from the microorganisms which affect root physiology. In this way, measuring microbial population in the rhizosphere in response to various factors indirectly assays exudation. Research has generally shown that change in any biological or physical factor that affects plant growth also affects the quantity of exudates released by roots. The principal factors affecting the type and quantity of substances released by roots into the rhizosphere include species and developmental stage of plant, soil physical stress factors, plant nutrition, mechanical or disease injury, microbial activities, and foliar-applied chemicals.

Decomposition

Decomposition of root systems provides a network of continuous root channels, and improves soil porosity. Roots are the principal source of organic matter in the deeper soil layers, and their decomposition directly and indirectly influences nutrient release. Studies of several tree species indicate that decomposition rate decreases as a function of increasing root diameter. Decomposition of large lateral roots and taproots can potentially impact nutrient release over several decades while decomposition of fine roots affects nutrient release on a seasonal basis.

Typically, a 'wet' forest has more living than dead roots, while a 'dry' forest has more dead than living roots. The major influence of increasing soil moisture is to improve decomposition and mineralization of dead roots and their nutrients. Because carbon dioxide, produced as a by-product of decomposition of organic material, equilibrates with the soil water, we can measure changes in respiration and link this to biological activity. Conversely, site disturbances including fire and clear-cuts will affect biological respiration presumably with little change in belowground biomass.

See also: **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Physiology**: Mycorrhizae; Nutritional Physiology of Trees; Root System Physiology.

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Soil Organic Matter Forms and Functions

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Introduction

Soil organic matter is important in determining both relatively stable soil properties as well as dynamics of soil systems. This article focuses on the contribution of organic matter to mineral soil horizons dominated by inorganic sand, silt, and clay-sized particles. The role of the organic forest floor is described elsewhere (*see* **Soil Development and Properties**: The Forest

Floor). Within mineral soil horizons, organic matter contributes to soil development through its role as food and nutrient sources for soil fauna and heterotrophic flora that give life to the soil, through production of organic acids and stabilization of structure, through its contribution to relatively stable characteristics such as color, water holding capacity and nutrient retention and release, and as the primary soil reservoir and sources of several plant nutrients. Soil organic matter consists both of relatively simple organic compounds as well as large complex and ill-defined molecules of high molecular weight classified based on chemical solubility or other characteristics. Elemental composition varies, but generally the least soluble and most complex organics have increased concentrations of nitrogen (N) and carbon (C) and decreased concentrations of oxygen (O). Functional groups of alcohol, carboxyl, enol, and phenol impart high capacity to adsorb and exchange nutrients and retain inorganic and organic contaminants. Human activities and forest management can alter the quantity and distribution of organic matter. This has ramifications both for forest productivity and ecosystem functions as well as for global carbon cycles.

Functions

Contributions to Soil Development (Pedogenesis)

Food source Organic matter created by binding of atmospheric C with water during photosynthesis and incorporated into leaves, roots, and wood is the base of a complex and still partly unknown universe of soil organisms. Beginning with large wood-boring beetles and other organisms that feed on freshly fallen logs or leaves, and ending with microbes that are involved in decomposition of the most recalcitrant organic compounds, organic matter sustains life within the soil. Between 10% and 20% of the CO_2 released from the soil during organic matter decomposition is associated with soil fauna. Fauna play an essential role in breaking down coarse debris with low surface area to weight ratio deposited on the surface soil as litter, or within the soil as roots, into finer particles and mixing these particles with mineral soil fractions where they can be further decomposed by the microbial community. It is through the activity of this microbial community that most of the C fixed through photosynthesis is returned to the atmosphere; however, the portion that remains in the soil is converted to complex, relatively stable compounds through a combination of biological and physiochemical processes.

Acid leaching Decomposition of organic matter in forests results in formation of soluble organic acids that, over time, have a major impact on soil formation. Acids produced during decomposition of litter on the surface move down through the soil with percolating water removing base cations such as calcium (Ca^{2+}), magnesium (Mg^{2+}), and potassium (K^+) weathered from minerals. Charge balance is maintained through accumulation of H^+ and concentration of acid forming aluminum (Al) in the process. This acid leaching creates soils that tend to be slightly (pH_w 6.5) to very acidic (pH_w 3.8) in the surface and contributes to development of distinct profile features associated with some forests. For instance, organic subsoil horizons resulting from leaching of organic acids from the surface and subsequent precipitation as organic–metal complexes deeper in the profile are characteristic of conifer stands grown on coarse textured soils throughout the world.

Stabilization of soil structure Organic matter is important to development of soil structure in two important ways. First, it serves as a food source for soil fauna. Through their movement, soil fauna create large pores that serve as major pathways for water and gas movement thereby increasing the depth of biological activity. Also, soil fauna that ingest organic and mineral material bring surfaces in close proximity where they can react with one another. Second, organic matter can directly bind soil particles together or combine with metals to create bridges that link individual soil particles. The size, shape, and stability of these aggregates are considered an important characteristic affecting water and gas flow, soil strength and suitability for root growth, ease with which the soil can be tilled, and the soil's resistance to erosion.

Contributions to Soil Properties

Color The dark surface colors of forest soils, particularly soils beneath productive hardwoods, are largely due to particulate organic matter and organic matter coatings of mineral surfaces. Even low concentrations of organic matter can create dark-colored soils, especially where dark colors are associated with organic coatings on mineral surfaces. For example, dark organic subsoil horizons resulting from accumulation of organic matter leached from surface organic layers can contain only 3–5% organic matter (2–3% organic carbon) on a mass basis. Color is important as characteristic for recognizing and describing soil profiles in all soil classification approaches. Additionally, color can affect thermal properties of soils. Dark surface soil colors promote soil warming and biological activity in cool climates.

Available water holding capacity Soils with high organic matter content generally have improved available water holding capacity. Water holding capacity is affected both directly and indirectly. Increases in organic matter content are associated with improved aggregation of soil particles into structural units. As a consequence of improved aggregation, the volume of large pores that drain under gravitational forces and provide air passages from the soil surface to deeper in the profile is increased. This is particularly important in fine textured (clay and clay–loam) soils. In coarser textured soils, organic matter can increase the volume of fine pores that retain water against gravitational drainage contributing to increased water holding capacity. General relationships between an increase in soil organic matter expressed as organic C and available water holding capacity have been developed and tested by several authors. Increases in available water holding capacity between 1% and 2% for each 1% increase in organic matter content (about 2–4% for each 1% increase in organic C content) are average for mineral soils.

Provision of reactive surfaces for nutrient and element retention In many soils, soil organic matter is responsible for the majority of charged sites that interact and hold nutrients and metals to soil surfaces. For each 1% increase in soil organic matter, there is between a 1–3 cmol kg^{-1} increase in cation exchange capacity (CEC). The charge of organic surfaces results from the presence of various functional groups such as carboxylic, phenolic, alcoholic, and amides (**Figure 1**) from which hydrogen can disassociate creating negative charges that serve as sorption sites. The degree to which disassociation occurs varies as a function of pH of the soil. When pH is low, the abundance of H^+ limits disassociation and positive charge can exceed negative charge. When pH is increased, and OH^- concentrations in solution are high relative to H^+, then H^+ disassociates from the surface creating negative charge than can hold cationic nutrients and metals. Under soil reaction (soil pH) typical of natural field conditions, the CEC of soil organic matter ranges from 60 to 3000 cmol kg^{-1}.

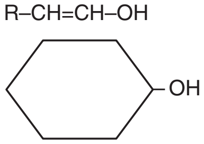
Alcoholic	$R–CH_2–OH$
Amides	R–C=O–NH–R
Amines	$R–CH_2–NH_2$
Carboxylic	R–COOH
Enolic	R–CH=CH–OH
Phenolic	

Figure 1 Important functional groups associated with soil organic matter.

Formation of complexes The variable physical structure and multiple functional groups in organic matter enables it to form complexes with inorganic compounds. These complexes have a number of important effects. Organic matter competes with P for sorption sites on minerals and can displace it from these sites rendering it available for plant uptake. Organic matter can increase availability of trace metals through formation of soluble organic–metal complexes. For example, organic matter forms soluble complexes with Fe that protect it from formation of insoluble inorganic precipitation products and increase its plant availability in near neutral pH soils. Conversely, formation of insoluble products that reduce plant availability can also occur. Formation of insoluble complexes limits copper (Cu) availability in many organic soils. Finally, organic matter plays a critical role in the contaminant retention (*see* **Soil Development and Properties**: Soil Contamination and Amelioration).

Nutrient source Organic matter is the chief reservoir and source of several key plant nutrients. Nitrogen, in particular, does not occur in appreciable quantities in primary minerals or on soil exchange sites. For instance, the surface soil beneath an upland forest may contain from 1500 to over 5000 kg ha^{-1} of total N. Less than 1% of this normally exists in inorganic forms retained on surfaces or in soil solution, a quantity much too small to support forest growth for extended periods. Sufficient supplies of N to support forest growth depend upon release of nutrients from bound organic forms into inorganic forms that are readily available for plant uptake during decomposition, a process termed mineralization. Organic sources of P and sulfur (S) are also important, particularly on sandy forested sites where both primary minerals and soil exchange is low.

Forest Productivity

Many of the soil properties affected by soil organic matter have direct bearing on rooting conditions, water retention and release, and nutrient availability. Thus, a relation between forest productivity and measures of total soil organic matter content or concentration should exist. Attempts to establish such relations have met with various degrees of success. On upland sites with good drainage, a positive relation often exists between soil organic matter in the surface soil or entire soil profile and measures of productivity such as site index (**Figure 2**).

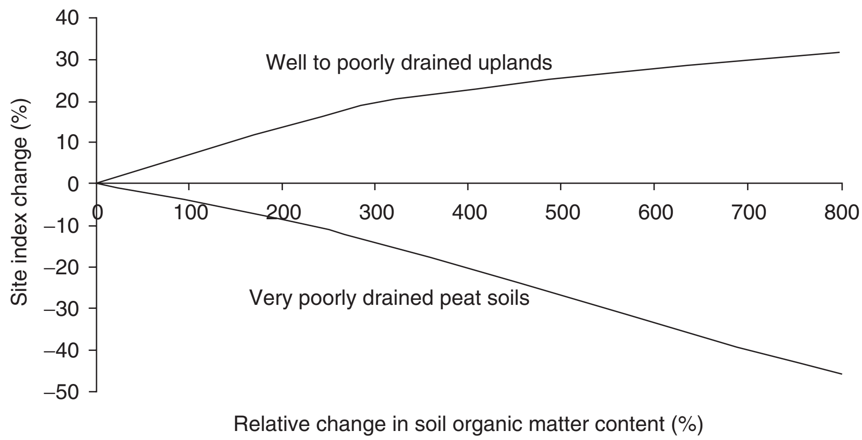


Figure 2 General relation between total soil organic matter content and forest productivity as measured by site index.

On these sites, increases in soil organic matter are associated with reductions in soil density and more favorable rooting conditions, improved moisture holding characteristics, and greater nutrient availability. Productivity increases associated with increased organic matter tend to be greater at low organic matter contents and are particularly important in sandy soils which have low water holding capacity and CEC in the mineral fraction. On very poorly drained bog or peat sites, a negative relation occurs between organic matter content and productivity. Under these very poorly drained conditions, increases in soil organic matter reflect increasingly unfavorable conditions for organic matter decomposition, nutrient mineralization, and root growth (**Figure 2**). For agricultural crops, specific fractions of organic matter (see following section) have been shown to be more closely related to productivity than total soil organic matter. Such relationships are being investigated for forests, but have not yet been established.

Characterization of Organic Matter

Soil organic matter consists of: (1) light fraction and particulate components that are largely recognizable as to chemical composition and consist of primary plant remains and (2) organic compounds called humus that have passed through one or more stages of decomposition and have been recombined into more complex molecules. Separation of the light fraction and particulate components can be accomplished by particle size sieving and density separation. These organics have a density less than 1.0 g cm^3. This fraction of organic matter is largely composed of identifiable organic polysaccharides such as cellulose and hemicelluloses, amino acids, chitin, waxes, and lignin. This organic fraction is extremely important in forest systems, particularly within the forest floor, because of its high energy content. It is an important source of mineralizable nutrients and is relatively sensitive to changes in the soil environment. In contrast, the humus fraction is less reactive and more important in development of stable characteristics of the mineral soil horizons. Traditional methods of classifying the humus fraction into constituent parts depend upon differences in solubility under alkaline and acidic conditions as illustrated in **Figure 3**. Three major components of soil humus are recognized in this classification approach: humin, which is the portion that is not soluble under alkaline (OH-rich) conditions, humic acid, which is the portion that is soluble under alkaline conditions but insoluble under acidic (H^+) conditions, and fulvic acid, which is soluble in both alkali and acid. Molecular weights, N and C concentrations decrease with humin > humic acid > fulvic acid. CEC, acidity and O concentrations decrease in the sequence: fulvic acid > humic acid > humin.

The chemical composition and structure of soil organic matter are not precisely known. Average element composition are about $C_{10}H_{12}O_5N$ and $C_{12}H_{12}O_9N$ for humic and fulvic acids, respectively. Structurally, they are largely comprised of aromatic rings heavily substituted with functional groups (carboxyl, hydroxyl, and carbonyl) and alkyl chains up to 20 C long that include bound proteins and carbohydrates. The molecules are randomly coiled and cross-linked. An example structure for a unit of fulvic acid is illustrated in **Figure 4**. There is a range in structure and the abundance of specific functional groups among humin, humic, and fulvic acids as well as within materials classified within any of these fractions from different locations.

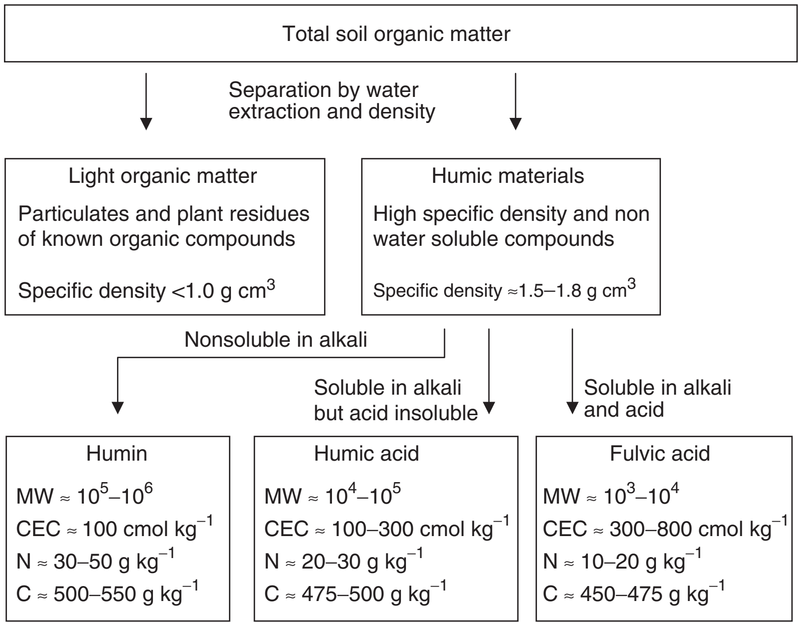


Figure 3 Major fractions of soil organic matter and approximate characteristics. CEC, cation exchange capacity; MW, molecular weight.

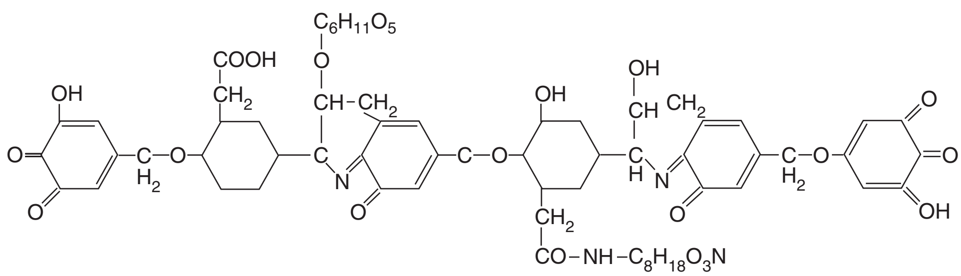


Figure 4 Possible structure of humic acid illustrating aromatic rings, peripheral chains, and functional units. Redrawn after Dragunov SS (1948) A comparative study of humic acids from soils and peats: Pochvovedenie 7. In: Kononova MM (1961) *Soil Organic Matter: Its Nature and Role in Soil Formation and in Soil Fertility*, p. 65. New York: Pergamon Press.

Quantity and Distribution

Comparisons among Forest Ecosystems

The quantity of soil organic matter within a given forest ecosystem reflects a balance between annual C inputs and loss through decomposition. In mature undisturbed forests, inputs and losses tend to approach an equilibrium condition determined by site factors such as overall forest productivity, species, soil and rooting depth, and soil physical and chemical properties. Increased precipitation is generally associated with increased soil organic matter, apparently because of its association with increased productivity. Under conditions of similar precipitation, organic matter tends to decline as temperatures are increased. Despite these general relationships, a clear pattern of differences in soil organic matter content does not exist among ecosystems from different climatic biomes (**Table 1**). Highly productive tropical soils may contain the same quantity of soil organic matter as some low productivity boreal forests. Production and incorporation of organic matter into boreal forest soils is slow, but so is decomposition. Additionally, several factors other than temperature and moisture affect soil organic matter content. Organic matter can adsorb to the surface of clay particles and this adsorption protects organic matter from decomposition; consequently, clay soils tend to have higher concentrations of organic matter than nearby coarser-textured sandy or loamy soils. Chemical composition plays an equally important role. High concentrations of multivalent cations (e.g., Ca^{2+}, Mg^{2+}, Fe^{3+}, or Al^{3+}) can potentially protect organic matter from decomposition in two ways. First, clays tend to

Table 1 Soil organic matter content as a proportion of total organic content (aboveground biomass, forest floor organic matter and soil organic matter to specified depth for several mature forest ecosystems)

Forest Ecosystem	*Aboveground biomass ($Mg\,ha^{-1}$)*	*Forest floor biomass ($Mg\,ha^{-1}$)*	*Soil organic matter[1] ($Mg\,ha^{-1}$)*
Boreal–*Picea mariana*, Alaska[2]	120	119	47
Boreal–*Picea abies*, Sweden[3]	289	19	207
Subalpine–*Picea nobili*[4]	606	53.5	244
Temperate–*Pseudotusuga menziesii* plantation[5]	158	10.9	56
Temperate–*P. taeda*[6]	247	70	192 (6 m)
Temperate–Mixed Hardwoods[7]	207	62	260
Temperate–*Liriodendron tulipifera*, USA[8]	134	6	159
Temperate–Mixed *Quercus*, Belgium[9]	322	5	300
Tropical–*Celtis-Triplochiton*[10]	334	27	106

[1] For rooting zone and exclusive of root mass.
[2] From Cole and Rapp, Stand No 3.
[3] From Cole and Rapp, Stand No 9.
[4] From Turner and Singer 1976, standing dead included with aboveground biomass.
[5] From Harmon *et al.* 1990.
[6] Estimated assuming carbon content of OM is $0.5\,Mg\,Mg^{-1}$ from Richter *et al.* 1995.
[7] Estimated assuming carbon content of OM is $0.5\,Mg\,Mg^{-1}$ from Johnson *et al.* 1995.
[8] From Cole and Rapp, Stand No 22.
[9] From Cole and Rapp, Stand No 28.
[10] Estimated from Greenland and Kowal (1960) and Sanchez (1976).

remain flocculated in soils with high concentrations of multivalent cations. The flocculation protects organic matter adsorbed to surfaces and within aggregates from microbial decomposition. Second, these multivalent cations form complexes with organic matter that, again, protect it from microbial attack.

Forestation and Afforestation

Changes in soil organic matter content resulting from forest removal and conversion to agricultural use are well documented, especially where old-growth forests are replaced by farming that includes regular tillage. Although the amount of reduction varies, the pattern is consistent from cool to tropical climates. Prior to forest removal, organic matter content is high and considered to be in near equilibrium with inputs and outputs. Following forest removal, organic matter content decreases rapidly reaching a new equilibrium determined by the inputs and outputs and the new management regime. On average, soil organic matter declines average from 25–30% of the predisturbance levels; however, on individual sites, declines can be much greater. This is particularly true on sites with coarse-textured (sandy) soils that afford little physical protection of organic matter from decomposition. Increases in soil organic matter similarly occur when areas formerly in agriculture or reclaimed mines are returned to forest; however, the processes of soil organic matter accumulation are much slower than loss and the period for a new equilibrium to be reached is decades or longer.

Harvesting and Management

Forest management affects the amount and composition of soil organic matter in two ways: by changing the quantity and composition of organic inputs and by altering decomposition rates. In the absence of other forest management activities, harvesting trees has only a small impact on soil organic matter content. Most data indicate that changes in soil carbon resulting from harvesting alone are less than 10% with almost an equal change of an increase as a decrease. It is likely that increases in soil organic matter content observed following harvest occur when large amounts of slash are left on site and allowed to decompose and become incorporated with the surface mineral soil. On sites that had initially low amounts of soil organic matter, such as reclaimed mines or degraded agricultural sites, long-term increases in soil organic matter can be expected when forests are managed with normal growth and removal cycles. In contrast, when forest harvest is followed by soil preparation treatments that displace or remove the forest floor and organic rich surface soil, then organic matter may be reduced from 20% to 50%.

Management activities other than harvest can affect soil organic matter. Fertilization can have either a positive or negative affect on organic matter contents depending upon the type of site. Where fertilization increases production without concomitant increases in decomposition rate, soil organic matter can be increased. In contrast, on sandy sites fertilization can decrease soil organic matter content even though forest production is increased. In this case, organic matter is poorly protected against decomposition by structural aggregates or clay–organic complexes and fertilization stimulates decomposition rates of organic matter by lowering the carbon-to-nitrogen ratios and/or carbon-to-phosphorus ratios. Although productivity is stimulated and overall site C content may be increased, the increase is in aboveground forest components and not in soil organic matter. Another management operation that can affect soil organic matter is understory vegetation control. In theory, removal of understory vegetation with a large proportion of production belowground can decrease inputs of soil organic matter. However, the limited research on this management activity tends to suggest it has a relatively small influence on soil C content.

Global Carbon Cycles

Conversion of forests into other land uses results in a release of CO_2 into the atmosphere both as a result of biomass burning or use and eventual decomposition and as a result of mineralization of soil organic matter and CO_2 evolution from the soil. In boreal and temperate regions of the world, little net deforestation is occurring. Most deforestation is occurring in tropical regions where about 17 million - ha of tropical forest are deforested annually and converted to other uses. As a result of this conversion, about 1.6 Pg C are contributed to the atmosphere annually. This represents about 20% of the annual input of CO_2 to the atmosphere from all sources. From 15% to 25% of this contribution can be directly attributed to loss of soil C.

Reforestation of former agricultural lands will increase soil C storage, the increase depending on how badly degraded the soil was prior to reforestation and the productivity of the forest. Projections of C storage potential in the worlds forests based on land availability suggest that between 1 and 2 Pg C could be stored in forests over the next 50 years with 20% of this storage attributable to increases in soil C.

See also: **Soil Development and Properties**: Nutrient Cycling; Soil Contamination and Amelioration; The Forest Floor.

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