

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.

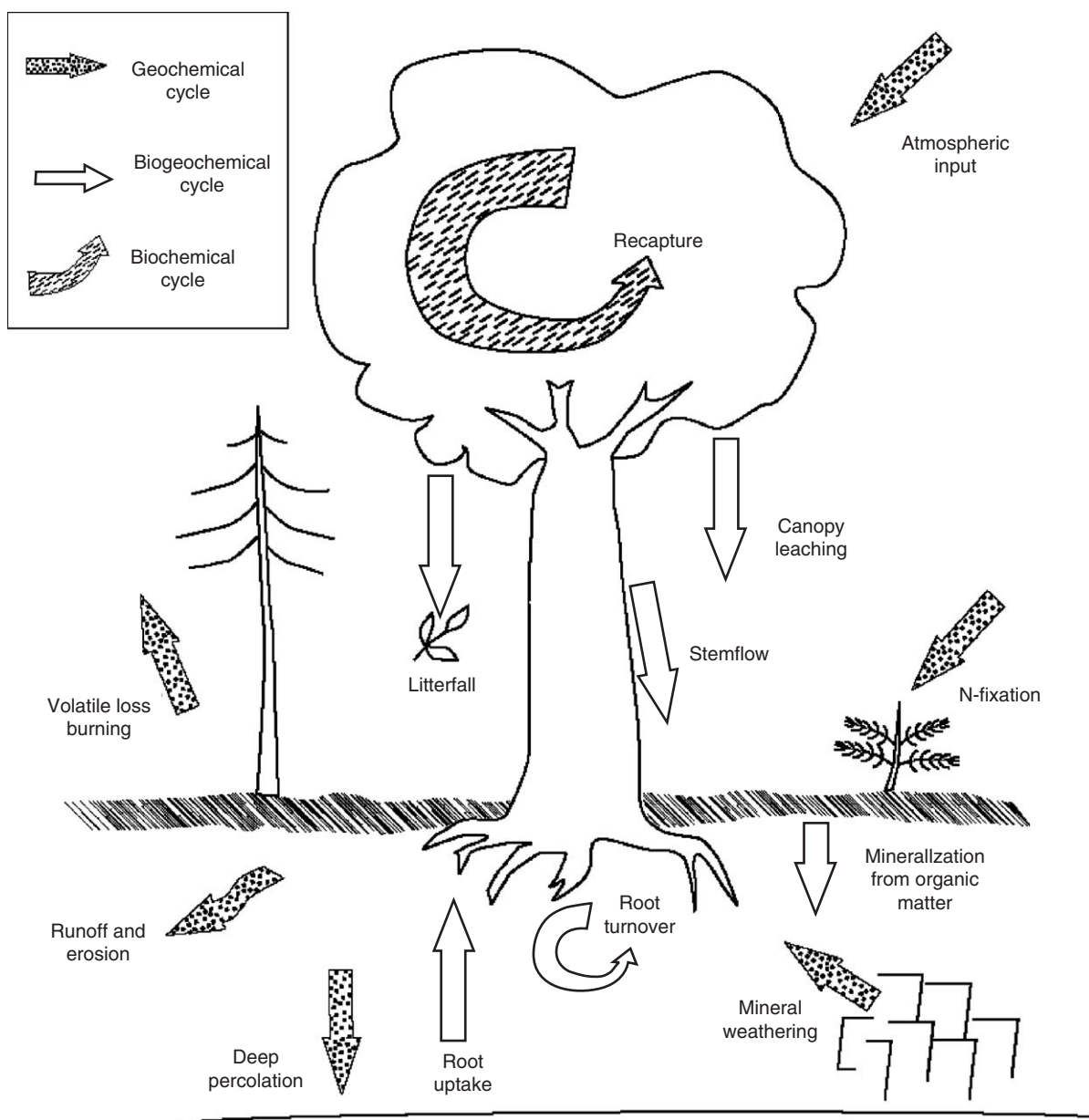


Figure 1 Potential pathways of nutrient flux within the geochemical, biogeochemical, and biochemical nutrient cycles.

The Biochemical Cycle

The biochemical cycle involves the process of transfer and retention of nutrients within an individual plant. In particular, trees can withdraw some nutrients from leaves prior to abscission and store these nutrients within woody tissue where they can be mobilized to supply a portion of the nutrient requirements for subsequent growing seasons.

Contribution of Nutrient Cycles to Nutrient Requirements for Growth

A major portion of the annual nutrient requirements of a forest for growth is supplied by recycling and

reuse of nutrients. An example annual nutrient cycle is presented for a hypothetical *Pinus elliottii* forest in the southeastern USA in Table 1. On an annual basis, fluxes of nutrients through the geochemical cycle are small in comparison to fluxes through the biogeochemical and biochemical cycles. While the balance of nutrients in the geochemical cycle is important from a long-term forest productivity standpoint, the biogeochemical and biochemical cycles play a much more important role in supplying the annual nutrient requirements for foliage production and annual growth increment.

Major differences exist among individual nutrients in the predominant pathways of transfer within

Table 1 Annual fluxes (in $\text{kg ha}^{-1} \text{ year}^{-1}$) of nutrients through three components of the nutrient cycle for a mature *Pinus elliotii* forest in the Coastal Plain of the southeastern USA

Cycle and pathway	Nitrogen	Phosphorus	Potassium	Calcium
Geochemical				
Inputs to ecosystem (+)				
Atmospheric	7.8	0.2	6.0	15.0
N-fixation	2.0			
Weathering	0	0	0	0
Export from ecosystem (–)				
Watershed runoff	6.0	0.13	2.3	5.8
Leaching	0.1	0.03	0.1	1.1
Forest ecosystem balance	+ 3.7	+ 0.04	+ 3.6	+ 8.1
Biogeochemical				
Mineralization of forest floor (0)	10.2	0.3	3.2	22.8
Inputs to trees (+)				
Root uptake	56.0	3.4	21.0	50.0
Losses from trees (–)				
Litterfall return to forest floor	23.2	0.8	2.7	19.1
Root mortality (turnover)	23.5	1.7	8.5	9.6
Canopy leaching	4.4	0.35	7.3	14.5
Stemflow	0.1	0.01	0.1	0.4
Net tree balance	+ 4.8	+ 0.5	+ 2.4	+ 6.4
Biochemical				
Retention by trees (+)	28.3	1.5	8.1	0

Based on data of Riekerk H, Jones SA, Morris LA, and Pratt DA (1979) Hydrology and water quality of three small Lower Coastal Plain forested Watersheds. *Soil Crop Science Society of Florida Proceedings* 38: 105–111. Burger JA (1979) *The Effects of Harvest and Site Preparation on the Nutrient Budgets of an Intensively Managed Southern Pine Forest*. PhD thesis, University of Florida, Gainesville. Shan J (2000) *Accumulation, Allocation and Dynamics of Carbon in Slash Pine along a Management Intensity Gradient*. PhD thesis, University of Georgia, Athens and others.

biogeochemical and biochemical pathways. Nitrogen is the nutrient most often limiting growth of forests. It is recycled through the pathway of leaf fall, root mortality, and biochemical retention in almost equal amounts. Canopy leaching and stemflow play a relatively small role in the cycling of nitrogen. This pattern can be contrasted with the patterns of cycling for calcium (Ca) and potassium (K). Calcium is structurally bound with the cell wall of foliage and woody tissue and there is little retention of Ca through the biochemical cycle or return of Ca to the soil in canopy leaching and stemflow. In contrast, K is not structurally bound within the cell and can be leached from plant tissue. The result is that stemflow, in particular, plays an important role in return of K to the soil where it can be recycled through root uptake. Biochemical cycling plays a particularly important role in phosphorus (P) nutrition. Soils of the southeastern USA where the *Pinus elliotii* forest is found contain low amounts of P and are also acidic. Because of high acidity in these soils, and fixation of P by oxides of aluminum and iron, concentrations of P in soil solution where it is available for plant uptake are low. Pine forests growing on these sites have adapted to ensure adequate quantities of P for future growth by translocating a major portion of the

P contained in foliage (up to 60%) into permanent woody tissue prior to leaf abscission at the end of the growing season. This P is then available to be recycled back to the foliage at the start of the subsequent growing season.

Species differences, age and differences in inherent site fertility all influence nutrient cycling patterns. For example, differences in geochemical cycling occur for forests located within industrialized areas of the world such as in the northeastern USA and central Europe. These forests receive greater atmospheric inputs of nutrients, particularly N. In some places, high N inputs threaten long-term productivity of the forests. Forests containing N-fixing species as a significant component of the stand have much greater geochemical inputs and outputs of N. For instance, N inputs in red alder stands of the northwestern USA can exceed $100 \text{ kg ha}^{-1} \text{ year}^{-1}$. Biogeochemical and biochemical fluxes also vary as a function of species and site characteristics. Forests located on young soils with high concentrations of easily weathered primary minerals often export quantities of K, Ca, and other nutrients in runoff that greatly exceed the amounts entering the forest in atmospheric inputs. Hardwood species generally have higher Ca demands and uptake than do pine

species. Consequently, uptake and return of Ca is much greater in hardwood stands than in conifer stands grown on similar sites. Species differences in the capacity for biochemical withdrawal of P from senescing foliage occur and these differences produce differences in nutrient cycling for different species grown on the same site. Thus, while nutrient cycling plays a role in the growth of all forests, the role varies depending on specific conditions of the forest and nutrient of interest.

Nutrient Accumulation in Forests

The accumulation of specific nutrient elements varies widely among forest ecosystems. Large differences occur among climatic regions due to factors that control overall biologic activity such as temperature and moisture, but other differences are associated with species, age, and overall site fertility. Table 2 provides examples of accumulation of macronutrients in some forest ecosystems. Observe that each nutrient element has a unique distribution pattern within the forest ecosystem and that this distribution pattern varies among forests. For example, forest ecosystems on young soils in fertile regions contain large amounts of nutrients such as P, K, and Ca found in minerals of parent rocks (e.g., mixed *Quercus*). In contrast, forests growing on quartz sands of marine origin contain low amounts of these nutrients in soil and relatively greater amounts of storage is associated with biomass of the vegetation and the forest floor (organic soil horizon) (e.g., *Pinus elliotii*–*P. palustris*). Accumulations of these nutrients in mineral soils also appear to be particularly low in tropical regions (*Celtis*–*Triplochiton*). It is important to note that the soil accumulations presented in Table 2 represent different analytical techniques and different soil depths. Depth of rooting is great in many tropical soils and, thus, the content of nutrients available to trees is greater than is represented by the shallow depth of soil included in the contents presented in this table.

A number of other general differences in nutrient accumulation exist among forest ecosystems. Relatively greater accumulations of nutrients occur in the forest floor of boreal forest ecosystems than in either temperate ecosystems or in the tropics. This is due both to the low temperature and reduced biological activity in boreal ecosystems and the relatively low decomposability of foliage of coniferous tree species characteristic of boreal forests. These accumulations can be contrasted with the low accumulations of nutrients in forest floors of tropical systems. Although nutrient inputs in litter of tropical systems are much greater, rates of decomposition and

Table 2 Nutrient content (in kg ha^{-1}) and distribution in aboveground biomass, forest floor, and mineral soils of several forest ecosystems

Forest type, location	Vegetation			Forest floor and organic debris						Mineral soil ^a			Reference
	N	P	K	Ca	N	P	K	Ca	N	P	K	Ca	
<i>Abies procera</i> , subalpine, USA	347	54	843	1025	675	57	312	568	15855	3212	85780	180960	Turner and Singer (1976)
<i>Picea</i> – <i>Abies</i> , boreal, Canada	387	52	159	413	1465	100	1052	253	559	114	9383	766	Weetman and Webber (1972)
<i>Pinus banksiana</i> , boreal, USA	346	29	146	294	544	40	37	254	5554	495	500	1727	Green and Grigal (1980)
<i>Pseudotsuga menziesii</i> – <i>Tsuga</i> temperate, USA	566	86	189	687	445	62	80	619	4560	660	2040	34	Cole and Rapp (1981)
Mixed <i>Quercus</i> , temperate, USA	415	29	185	1250	150	12	20	160	3725	1041	23205	6270	Johnson and Todd (1987)
<i>Fagus sylvatica</i> , temperate, Europe	285	39	187	152	180	11	20	51	6640	42	254	365	Ovington (1962)
<i>Pinus taeda</i> , temperate, USA	320	48	225	ND	306	30	28	ND	1752	270	403	ND	Wells and Jorgensen (1975)
<i>Pinus elliotii</i> – <i>P. palustris</i> , subtropical, USA	140	12	43	150	271	10	9	96	2959	24	82	396	Morris and Pritchett (1982)
<i>Celtis</i> – <i>Triplochiton</i> , tropical, Nigeria	1530	103	702	2140	514	34	204	530	4592	13	650	2576	Greenland and Kowal (1960)

ND, not determined.

^a To approximate rooting depth using a variety of extraction procedures. Refer to original citation for information on soil depth and method utilized.

mineralization of nutrients are also much greater; consequently, storage is low. Except in the tropics, accumulations of nutrients in the forest floor are relatively large and, in many systems, exceed accumulation in tree biomass.

Forest age also has a major influence on nutrient accumulation in biomass. A typical pattern of nutrient accumulation for a developing forest is illustrated in **Figure 2**. Accumulations of nutrients over time reflect both tree demands and the physiological use of the nutrient. Nitrogen and Ca are both used in large quantities and for the example illustrated are accumulated more than other nutrients. Nitrogen accumulation is much more rapid early in stand development as it is concentrated in foliage, which develops rapidly. In contrast, Ca is accumulated more slowly, but because it is an integral part of the cell wall of woody tissue, it tends to continue to accumulate as long as the forest is continuing to increase biomass.

Mineralization of Nutrients Accumulated in Biomass

Nutrients contained in organic matter returned to the forest floor or soil are not available for plant use until they are released from the structures in which they are

chemically bound. The processes of release of nutrients into inorganic plant available forms is termed mineralization. As organic matter is decomposed, CO₂ is released through respiration and bonds between elements and organic molecules are broken. Mineralization rates are, thus, closely associated with overall decomposition rates. Both characteristics of the substrate being decomposed and environmental conditions affect the rate of decomposition and mineralization. Organic materials that contain a relatively high concentration of compounds easily used by microorganisms involved in decomposition, such as sugar and cellulose, are more rapidly decomposed than compounds that have complex bonds that are not easily broken and used by this decomposer community. Examples of such compounds are polyphenols and lignin. Differences in the decomposition rate among substrates under the same environmental conditions are expressed in terms of a substrate decomposition rate constant. Decomposition rate constants are based on the observation that decomposition of most organic materials tends to follow the pattern of a negative exponential curve:

$$C_t = C_i e^{-kt}$$

where C_i is initial carbon (or organic matter) mass, C_t is carbon (or organic matter) remaining at time t , k is the decay rate constant, and t is time (usually expressed in days or years).

For comparison among species, decay rate constants are usually developed for leaves or ground materials and, thus, are not limited by physical characteristics of the material. Foliage of coniferous species tends to have lower decay rates than species of deciduous angiosperms. Wood and branches have lower decay rates than leaves due to chemical differences. In addition, few surfaces available for microbial colonization exist in branch and stemwood falling to the forest floor. Decomposition of these materials is greatly accelerated by the activity of soil fauna that bore into, create galleries in, or otherwise expose internal surfaces to microbial colonization.

Nutrient mineralization can also be modeled using an exponential decay model, but the actual process is more complicated. Before nutrients will be released into the soil where they are available for plant uptake, the nutrient requirements of decomposing organisms must be satisfied. When a large amount of C, the energy source of heterotrophic decomposers, is available, nutrients released from broken chemical bounds of organic molecules are immediately re-incorporated into the bodies of the decomposing community, a process termed immobilization. This

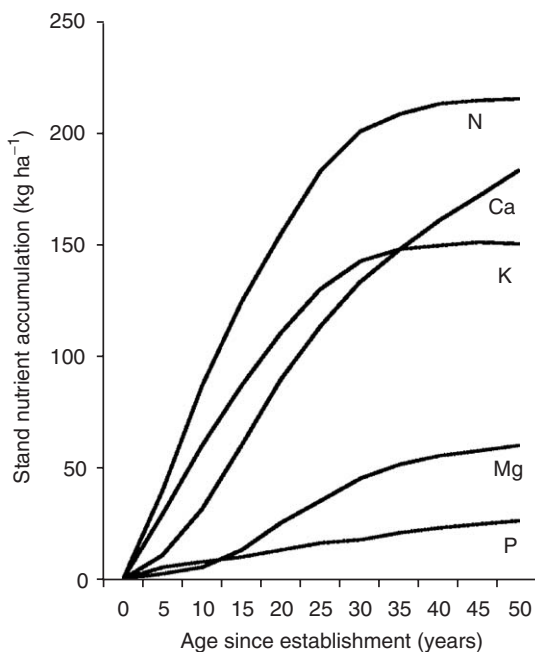


Figure 2 Accumulation of nutrients in biomass of a pine forest in the southern USA. Note the differences in total accumulation among nutrients as well as the difference in pattern. Based on Switzer GL and Nelson LE (1972) Nutrient accumulation and cycling in loblolly pine (*Pinus taeda* L.) plantation ecosystems: the first twenty years. *Proceedings of the Soil Science Society of America* 36: 143–147.

occurs because under this condition, nutrients are in low supply relative to C. Only after a balance is achieved between C availability and nutrient availability does net mineralization of nutrients occur.

The chief environmental variables affecting mineralization of nutrients are temperature, moisture, and oxygen availability. The rate of decomposition, expressed as the decay rate, approximately doubles for each 10°C increase in temperature between 5°C (biological zero) and 35°C. Decomposition and mineralization rates in subpolar regions are so slow that despite large storage of nutrients in the forest floor, forest growth is constrained by low nutrient availability. In contrast, many tropical forests with relatively low nutrient storage have high growth due to rapid decomposition and mineralization of nutrients in organic debris falling to the forest floor. Moisture limits decomposition under either extremely wet or extremely dry conditions. Oxygen does not diffuse rapidly through water. When soils are saturated and all pores filled with water, oxygen will be, essentially, unavailable below the water surface and decomposition and mineralization will not proceed. Bog forests of subpolar regions and swamp forests throughout the world contain large amounts of nutrients but growth is slow because of nutrient limitations. Decomposition also ceases under very dry conditions because water remaining in soil is held so tightly by particle surfaces that microbes cannot incorporate it into their bodies to support their growth. Decomposition is most rapid under moist soil conditions when water is available and soils contain air-filled pores to facilitate oxygen transport.

Forest Management Impacts on Nutrient Cycles

Forest management affects nutrient cycling in a variety of ways. Selection of species for rapid growth increases the demand for, and accumulation of, nutrients in the forest. Harvesting of wood, branches, and/or foliage removes nutrients from the system. Losses of nutrients may be accelerated due to more rapid mineralization and leaching loss or through increased erosion following harvest. Slash reduction and preparation of the site for planting also accelerate leaching and erosion losses. Finally, efforts to reduce competing vegetation regrowth through herbicide application or mechanical removal can contribute to this accelerated leaching and erosion. On the other hand, fertilization or use of N-fixing species has the opposite effect and can greatly increase both the storage and rate of nutrient cycling within forest ecosystems. A summary of the

effects that forest management can have on nutrient cycling is presented in Table 3.

In undisturbed forests, atmospheric inputs of most nutrients, or inputs from weathering, exceed losses and these systems accumulate nutrients. Over time, forests tend to become more productive as their storage of nutrients increases and the potential for nutrient cycling increases. Removal of wood, branches, and leaves for fuel, timber, or pulp can remove nutrients more rapidly than they are naturally replaced. Over the long term, this can lead to declines in forest growth.

The greatest concentrations of plant nutrients are found in needles and leaves. Wood and branches contain relatively low concentrations of nutrients. Since foliage contains a disproportionate amount of nutrients, harvesting foliage will increase nutrient removal and, in the absence of fertilization or other inputs, can lead to a reduction in nutrient storage and, eventually, loss of productivity. The significance of this tends to be greatest with genera that retain many years of needles (e.g., *Picea*, *Abies*) than in genera that retain only a few years' worth of leaves or needles. Also, because forests tend to accumulate nutrients most rapidly when they are young, shortening the period between harvests can also increase nutrient removal (Table 4). Generally, periodic removal of just the wood does not remove an unsustainable amount of nutrients from a forest site. However, frequent harvests especially when coupled with foliage removal will likely lead to unsustainable reductions of nutrient storage in forest ecosystems.

In intensively managed industrial forests, it is common practice to reduce slash from harvest prior to soil preparation and planting. Burning is one common method of slash reduction that can result in volatile losses of nitrogen. Volatile loss of N during burning tends to be very site-specific. Losses during site preparation can be large because large amounts of logging slash are often on the ground and fires are hot. Nitrogen volatilization during site preparation burns following harvest of forests in the northwestern USA may exceed 800 kg ha⁻¹. In contrast, cooler fires associated with understory control beneath an established forest canopy may volatilize only 20–50 kg ha⁻¹ N. A second method of slash reduction involves pushing slash and soil into long rows or piles. Such operations have been shown to displace large quantities of nutrients from the majority of the soil surface, concentrating them in a small area where they cannot be efficiently used. In some cases, two or three times more nutrients can be displaced from the soil surface during these operations than are removed from the site in harvest.

Table 3 Potential effects of selected forest management activities on nutrient cycling

<i>Activity</i>	<i>Geochemical cycling</i>	<i>Biogeochemical and Biochemical cycles</i>
Conversion of natural mixed forests to conifer plantation	Differences are small except where N-fixing species are used	Reduced uptake of base cations, decreased forest floor mineralization, lower overall biogeochemical cycling rates
Shortening length of time between harvests	Increase nutrient removal and slight increase in runoff and leaching losses due to accelerated erosion and increased mineralization	Young forests are building crown and biomass so uptake from soil and accumulation of nutrients predominates; biochemical transfer is less important than in mature forests
Increased utilization of branches and foliage	Foliage and small branches contain a disproportionate quantity of nutrients; utilization of foliage and branches can double the average annual nutrient removal by harvest	Short-term effects will be minor; long-term effects may be to reduce mineralization of nutrients from forest floor
Burning for slash reduction	Increase N losses from forest; amount varies from a low of 25 kg ha ⁻¹ to more than 800 kg ha ⁻¹	More rapid mineralization due to warmer soil temperatures and the absence of carbon-rich woody debris
Piling of slash for improved access	Displaces nutrients from planting surface; N displacement from 200 to 600 kg ha ⁻¹ observed; small increase in actual loss from system due to accelerated leaching and erosion	More rapid mineralization due to mixing of mineral soil, forest floor and organic debris during operation
Soil tillage (disking or mounding)	Can be associated with small increase in nutrient loss in runoff and erosion	More rapid mineralization due to mixing of mineral soil, forest floor, and organic debris
Herbicide use to control competition	Operational herbicide application has little impact on geochemical cycle; repeated control of regrowth will increase nutrient losses and erosion	Reduced uptake and accumulation in vegetation early in the rotation
Use of N-fixing species	Potential to increase N inputs to forest by 50–150 kg ha ⁻¹ year ⁻¹	Annual uptake and cycling of N will be increased
Fertilization	Can increase ecosystem storage of applied nutrients and compensate for harvest removals; small increases in runoff losses of applied nutrients can occur	Uptake of applied nutrients is increased; quantities of nutrients transferred in the biogeochemical cycle are often increased; absolute quantities of nutrients retained by biochemical cycling may be increased

Accelerated erosion losses are another impact on nutrient cycles. Losses associated with erosion can be considered either displaced productivity or as site loss. Generally, a strong relationship exists between bare mineral soil and erosion loss. Losses are often greatest during first year following harvest and planting and decrease as vegetation regrowth occurs on the site. Increased soluble losses of nutrients can also occur following forest operations due to improved conditions for decomposition. These losses are generally ephemeral and low in comparison to geochemical inputs over a rotation for many forests.

Fertilization is an important silvicultural technique for adding nutrients to forest ecosystems and balancing losses of nutrients in the industrialized world where the value of wood production provides economic justification. Nitrogen-fixing species also provide a way to add nitrogen to managed forests. Planting or seeding of N-fixing species at the time of

forest establishment can add from 50 to 150 kg ha⁻¹ N to the forest in the years prior to crown closure, sufficient N to more than balance losses associated with harvest and site preparation.

Summary

Nutrient cycling plays an important role in the nutrition of forest stands. The balance between inputs and exports of nutrients from the forest ecosystem included within the geochemical cycle has implications for long-term sustainability. Fluxes of nutrients through the biogeochemical and biochemical cycles are larger than through the geochemical cycle and supply a major portion of the annual nutrient requirements of the forest. These cycles provide a framework within which forest management activities can be evaluated. Activities that result in nutrient exports in excess of nutrient

Table 4 Comparison of nutrient removals and annualized removal rate with different levels of biomass utilization and rotation length for two commercial forest species

Forest type	Harvest utilization	Rotation length (age)	Nitrogen		Phosphorus		Potassium		Calcium	
			kg ha ⁻¹	kg ha ⁻¹ year ⁻¹	kg ha ⁻¹	kg ha ⁻¹ year ⁻¹	kg ha ⁻¹	kg ha ⁻¹ year ⁻¹	kg ha ⁻¹	kg ha ⁻¹ year ⁻¹
<i>Pinus taeda</i>	Stem only	20	293	14.6	17	0.8	169	8.4	178	8.9
	Whole tree	40	464	11.6	28	0.7	293	7.3	304	7.6
<i>Picea</i>	Whole tree	20	385	19.2	27	1.4	212	10.6	205	10.2
		40	570	14.2	40	1.0	346	8.6	348	8.7
	Stem only	50	217	4.3	20	0.4	248	5.0	278	5.6
	Whole tree	85	328	3.1	23	0.3	161	1.9	390	4.6
		50	842	16.8	80	1.6	442	8.8	463	9.2
		85	722	8.5	78	0.9	330	3.9	521	6.2

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inputs are unlikely to be sustainable without nutrient amelioration through fertilization or use of N-fixing species.

See also: **Environment:** Carbon Cycle; Environmental Impacts. **Hydrology:** Impacts of Forest Management on Water Quality; Soil Erosion Control. **Soil Biology and Tree Growth:** Soil and its Relationship to Forest Productivity and Health; Soil Organic Matter Forms and Functions. **Soil Development and Properties:** Nutrient Limitations and Fertilization; The Forest Floor.

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Nutrient Limitations and Fertilization

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Historical Background

While the benefits of applying manure to land has long been appreciated the idea of a plant nutrients probably only dates from 1727 when Stephen Hale noted that ‘we find by chemical analysis of vegetables, that their substance is composed of sulphur, volatile salt, water and earth.’ Despite observed growth responses of plants to compounds such as saltpetre (a nitrate salt), Epsom salts (magnesium sulfate), and phosphates, further advance in the understanding of plant nutrition was stymied by the widespread acceptance of the idea of Wallerins that humus itself was the fundamental source not only of nutrients but also of carbon. Progressively this came to be questioned and in 1845 Liebig, on the basis of calculations of the yield of carbon as wood and agricultural produce from nonmanured land, concluded that ‘it is not denied that manure exercises an influence upon the development of plants; but it may be affirmed with positive certainty, that it neither serves for the production of carbon, nor has any influence on it.’

Building upon the work of Liebig, chemists such as Bossingault in France and Lawes and Gilbert in Britain weighed and analyzed manure and plants to construct early nutrient input–output balance sheets for a range of agricultural crops. Bossingault’s data were used by Ebermayer in 1882 to compare nutrient accumulation in forest stands with that in agricultural crops. Earlier Ebermayer had been the first to diagnose nitrogen (N) deficiency in trees in Bavaria on sites that had been degraded by long histories of

litter removal for animal bedding and other agricultural purposes. Despite this new understanding, foresters of a century ago seldom showed much interest in tree nutrition, being able to turn to the work of Dengler who had demonstrated that the nutrient requirements of a closed-canopy forest stand were on average only about one-twelfth of that of agricultural crops. Indeed, in his silvicultural textbook of 1904 Schlich enunciated the orthodoxy of his time when he stated that ‘almost any soil can furnish a sufficient quantity of mineral substances for the production of a crop of trees, provided the leaf mould is not removed.’ This sentiment was echoed by Baker in his book of 1934, for long one of the standard silvicultural texts.

Despite this complacency, at the start of the twentieth century foresters in Belgium, and later in Ireland and Scotland, were finding that trees newly planted on poor soils could show dramatic growth responses by application of the phosphate-containing basic slag (thomasphosphat) and some responses to wood ash application were reported from the Nordic countries (probably a response to potassium (K)). Similarly, in both Australia and New Zealand growth of the new forest plantation were found to be dependent on the application of phosphorus (P). In South Australia trees sometimes failed even where P had been applied until it was noted that those grown adjacent to galvanized wire fences were better than those distant from them, and so zinc deficiency was identified. In the decades that followed, forest scientists from many of the countries with large afforestation programs have identified deficiencies of one or more of nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), iron (Fe), zinc (Zn), copper (Cu), molybdenum (Mo), and boron (B) in young plantation trees. Calcium (Ca) deficiency has been confirmed in the nursery but the few reports of deficiencies of this element in the forest remain rather unconvincing. Additionally, by the middle of the twentieth century reports were also coming in of nitrogen deficiency in older coniferous forests in the boreal regions of Europe and North America.

Nutrient Cycles and Fertilizer Need

The study of nutrient cycling in forests of various ages has provided the explanations to a number of the conundrums posed by early work on fertilizer responses. The cycles within a well-established forest are characteristically very tight, that is there is efficient reuse of nutrients, largely through recovery (retranslocation) of nutrients from dying organs, notably leaves before they are shed, and through the efficient capture by roots and mycorrhizae of