

Fundamentals of Tree Nutrition

DALE W. COLE and STANLEY P. GESSEL

ABSTRACT. Trees differ significantly from agronomic crops in their nutritional needs and the way these needs are met. As a perennial system that usually lives for many decades, a tree has a number of mechanisms that minimize nutritional requirements by allowing for less annual use of nutrients in biomass production than is typically found in agronomic crops. Uptake, recycling, and internal translocation of nutrients are discussed as examples of the mechanisms by which nutrients are added to and conserved by forest ecosystems. Although trees are efficient in the use and conservation of nutrients, many forest sites in the Pacific Northwest are still deficient in certain elements, resulting in depressed rates of forest growth.

With few exceptions, the same nutrients are required to support the growth and nutrition of all organisms within the plant kingdom. These nutrients serve basically the same functions in carrying out physiological processes and providing biological structures, whatever the species. Consequently, one might ask why we should discuss the fundamentals of tree nutrition. Why not address the nutrition of plants in general?

Although trees require the same essential elements as other plants, they differ in how they secure and process the elements. In this chapter we discuss these differences, paying particular attention to the nutrition of trees of the Pacific Northwest, a subject recently addressed by Walker and Gessel (1991). We treat the nutrition of our northwestern forest species within the context of other ecosystem processes, especially sources of nutrient input, mechanisms by which nutritional needs of the trees are met, including uptake, recycling, and internal translocation of nutrients, and processes of nutrient conservation and loss.

Nutrition of Forests Compared with Annual Plants

The overall nutritional requirements of a tree are similar in concept to those of other plants—with nitrogen, phosphorus, calcium, magnesium, potassium, and sulfur required in the greatest amounts. Of these

elements, nitrogen is the only one that is consistently deficient in the forests of the Northwest. This is somewhat surprising in that the soils of the region are very young, with relatively low base exchange capacities, and have thin surface organic layers and generally low nutrient status. In part, the ability of trees to produce reasonable growth under these low nutrient regimes is explained by the special adaptive characteristics of forest trees:

- All tree species are perennial. This provides the tree with a series of significant advantages over annual species in meeting nutritional requirements: (1) Uptake can take place year around. (2) The immediate nutritional needs of the tree are not met exclusively through uptake but can be met partly through the internal translocation of essential elements. (3) The annual growth increment of a tree is additive to an existing structure, including well-established branch, bole, and root systems. Although there is clearly a turnover and systematic renewing of parts of these structures, entirely new stem, branch, and root systems are not produced each year. (4) The retention of foliage for more than one year by evergreen trees results in a further decrease in the nutrients needed for foliage production. This point takes on added significance in that foliage is high in nutrients compared with the other tree components (Table 1). (5) Elements are withdrawn from foliage before leaf fall and translocated to other parts of the tree for storage or use. (6) Nutrient losses from harvesting are significantly less in forests compared with agricultural crops because of the long harvest cycle and the low elemental level of components removed.

D.W. Cole is Professor and Associate Dean, and S.P. Gessel is Professor Emeritus, College of Forest Resources, University of Washington, Seattle.

Table 1—Nutrient content of various components of Douglas-fir. Adapted from Walker and Gessel (1991).

Tree Component	Nutrient Content (%)				
	N	P	K	Ca	Mg
Foliage	1.40	0.21	0.85	0.45	0.11
Bark	0.29	0.07	0.31	0.42	0.13
Cones	0.65	0.13	1.26	0.06	0.10
Branches	0.36	0.07	0.21	0.51	0.05
Bole	0.08	0.01	0.05	0.10	0.05

Table 2—Annual use of nitrogen by various ecosystems in the production of biomass. From Cole (1981).

Ecosystem Type	Production per Unit of N Uptake (kg/ha)
Forest	168 ± 49
Tundra	55
Mediterranean shrub	100 - 115
Corn	25 - 60
Bermuda grass	61 ± 30

- A tree uses less nutrients than most plants to produce a given quantity of biomass (Table 2). While there are several reasons for this, as will be discussed later, the principal one is that much of a tree's biomass is in the form of structural members such as the stem, branches, and roots which are high in cellulose and thus low in their nutrient-to-carbon ratio (Table 1).

- A tree is a part of an ecosystem in which cycling of nutrients between the soil and the tree is an important process by which the nutritional requirements of the tree are met. Nutrients are also temporarily accumulated in, or on, the soil during the cycle. However, in some forest ecosystems excess storage can take place in the form of undecomposed material. In these cases the cycling is interrupted, leading to nutritional problems.

One must consider the total nutritional needs of the ecosystem when evaluating the nutritional needs of the tree. For example, if a tree is under nutritional stress, it is more than likely that the rest of the higher plants in the ecosystem are under similar stress. This nutritional relationship between a tree and the forest ecosystem is illustrated in Figure 1.

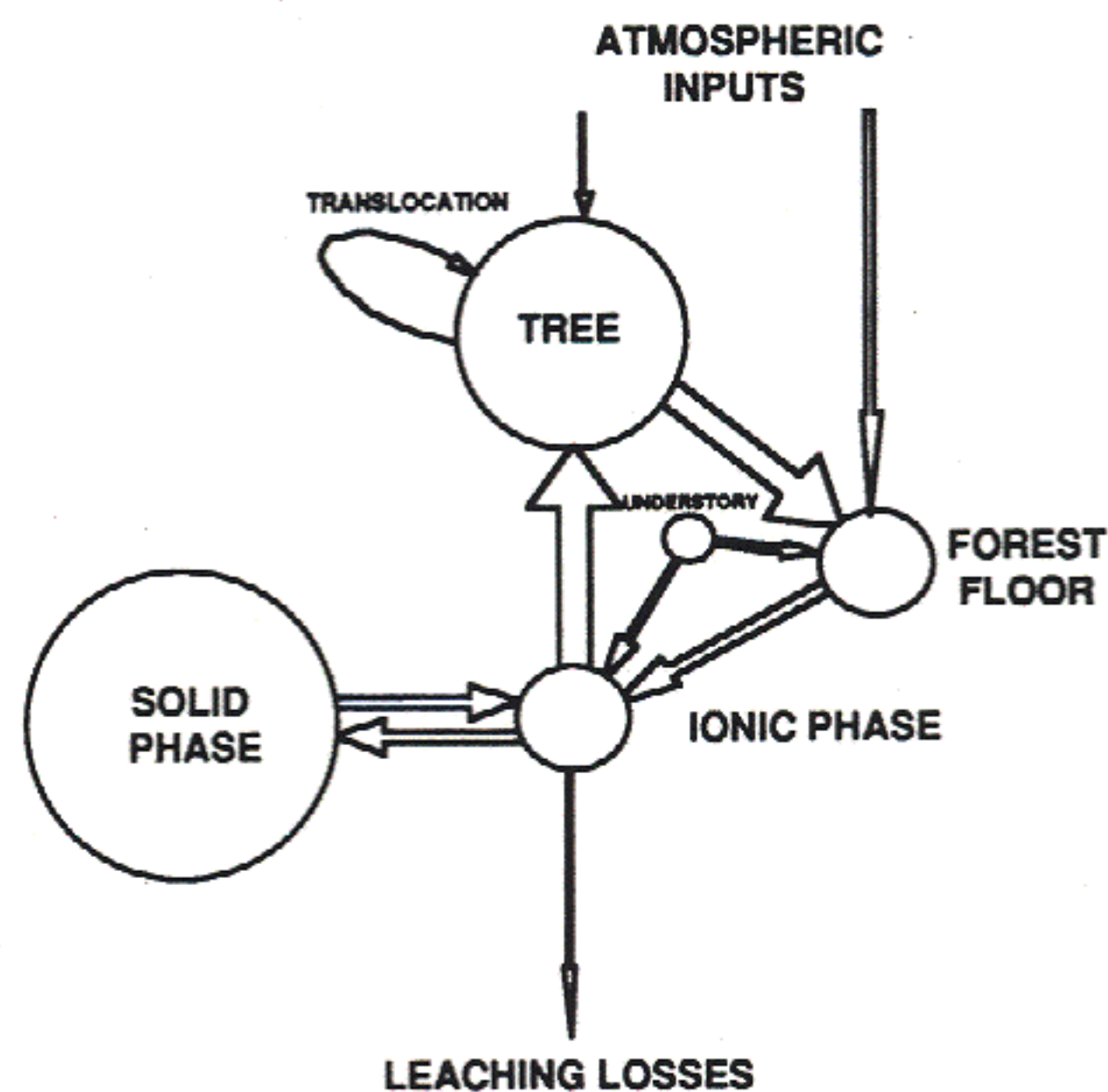


Figure 1. Cycling of nutrients within a forest ecosystem.

Nutritional Needs of Trees

Diagnostic Indicators of Deficiency Symptoms

Several tools are available to evaluate the nutritional status of a forest stand. These are discussed in some detail by Carter (this volume) and also by Walker and Gessel (1991). While reduced growth is a clear indicator that a tree is under some form of environmental stress, the source of the stress is not always obvious. Environmental conditions other than nutritional stress could be responsible for reduced growth, including moisture stresses and root diseases. Techniques available to diagnose deficiency problems and determine nutritional needs include evaluation of visual foliage deficiency symptoms and foliage and soil analysis.

Foliage Deficiency Symptoms. Nutritional stress can potentially be diagnosed by evaluating foliage deficiency symptoms. Through their studies of seedlings grown in sand and solution cultures, Walker and Gessel (1991) have described deficiency symptoms for Northwest conifers: Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). However, abnormal appearance of foliage can also be caused by disease, insect attack, pesticide application, atmospheric pollutants such as ozone, temperature extremes, and moisture deficits. In the Pacific Northwest, visual nutrient deficiency symptoms, other than those for nitrogen, have not been substantiated under field conditions, although incidences of sulfur (Blake et al.

1990; Turner et al. 1977), magnesium (Harrison et al., this volume), and phosphorus (Steinbrenner 1968; Heilman 1971) deficiencies have been reported.

Foliage and Soil Analysis. Another method for detecting nutritional deficiencies and sufficiencies is through foliar and soil analysis. But such analysis is not an exact science because the elemental concentrations of the foliage are not exclusively regulated by nutrient availability in the soil (Ingestad 1979; Kimmins 1987:81-90). As discussed above, foliar concentrations can also be affected by other environment factors. Tree age, crown position, and season of the year are additional variables. Despite these shortcomings, foliage nutrient concentration levels can still be an important indicator for establishing nutrient deficiency problems. Table 3 illustrates critical concentrations of foliage nutrients for Northwest conifer seedlings grown under sand and solution culture conditions. It should be recognized, however, that concentration levels where deficiency symptoms appear are somewhat lower for field grown plants, especially mature trees, than for seedlings grown under controlled environmental conditions such as those reported in Table 3. Van den Driessche has published a number of papers on foliar nutrient levels for Pacific Northwest conifer seedlings (1969, 1989) and treats the subject in more depth in a book published recently (1991).

Soil analysis can also play a role in diagnosing forest nutritional deficiencies, but results have to be interpreted carefully. Strong statistical relationships between yield and specific soil nutrient levels have not been as successfully applied to forestry as they have in agriculture. The reasons for this are several: (1) greater soil and plant cover variability in forestry results in high variability between soil samples, (2) the rate of nutrient removal by trees from the soil is slower, (3) trees realize a part of their nutrient requirements through internal

redistribution of nutrients, and (4) tree roots, through mycorrhizal associations, are more efficient than agricultural plants at extracting nutrients. In spite of these problems, forest soils are routinely analyzed for their nutritional characteristics. Some of the more common analyses include cation exchange capacity, exchangeable cations, extractable P, total N, mineralizable N, pH, and organic matter. While the absolute values from such analyses are not always meaningful, the comparative values can be. Soil analysis may also show excessive concentrations of elements that can be detrimental to growth under some circumstances.

Nutrient Uptake Rates for Western Species

While foliage nutrient concentrations can serve to indicate nutrient sufficiency and deficiency levels, these values in themselves are poor indicators of nutrient uptake. The amount of nutrients contained within tree components, especially the foliage, depends on a number of factors, including stand age and foliage retention. The role these factors can play in impacting uptake is evident in Table 4.

These results show that maximum uptake coincides with canopy closure, which is at about age 20 for the site represented in Table 4. Douglas-fir also has the interesting characteristic of increasing the duration of needle retention as the tree matures. For the stands on the Cedar River Watershed, needle retention increased from 1-2 years at age 9 to approximately 6 years at age 95 (Table 4). With greater needle retention time, the tree needs less uptake to produce the same amount of biomass. From limited studies on silver fir (*Abies amabilis*), annual N uptake rates of 10 kg/ha at age 22 and 25 kg/ha at age 175 were reported by Meier (1981). Annual N uptake for 35-year-old red alder (*Alnus rubra*) is 115 kg/ha (Cole et al. 1978). From our research on the Cedar River Watershed (Thompson Research Center), it would

Table 3—Nutrient deficiency levels (% concentration) for western conifer seedlings grown in solution cultures. Adapted from Walker and Gessel (1991).

Element	Species				
	Douglas-fir	Hemlock	Western Redcedar	Sitka Spruce	True Fir
Nitrogen	1.25	1.8	1.5	1.8	1.15
Phosphorus	0.16	0.25	0.13	0.09	0.15
Potassium	0.6	1.1	0.6	0.4	0.50
Calcium	0.25	0.18	0.20	0.06	0.12
Magnesium	0.17		0.12	0.06	0.07
Sulfur	0.35		0.4	0.15	

Table 4—Annual nitrogen uptake and needle retention for Douglas-fir stands of various ages growing on a similar soil type on the Cedar River Watershed. Adapted from Turner (1975).

Stand Age (years)	Nitrogen Uptake (kg/ha)	Needle Retention (years)
9	3.7	1-2
22	33.7	2-3
30	32.1	3
42	32.8	3
73	37.3	5
95	23.7	6

Table 5—Annual uptake of nutrients (kg/ha) by temperate coniferous and deciduous forests. From Cole and Rapp (1981).

Forest	N	K	Ca	Mg	P
Deciduous	70	48	84	13	6
Coniferous	39	25	35	6	5

appear that most of this uptake is met through symbiotic N fixation.

In general, conifers take up less nutrients than deciduous species. In a comparison of mature stands of deciduous and coniferous forests in the temperate region, for nearly all nutrient elements Cole and Rapp (1981) found almost twice the uptake for deciduous species (Table 5). It was their conclusion that this higher uptake value for deciduous species was driven primarily by the annual replacement of the canopy foliage.

Sources of Nutrients in Forest Ecosystems

The forest ecosystem derives its nutritional supply from several potential sources, including weathering of minerals, nitrogen fixation, atmospheric deposition, and decomposition of organic matter. We will discuss each of these.

Weathering

Most cations (Ca, Mg, K) and some anions (PO_4 , SO_4) become available for plant uptake following a weathering process from primary and secondary minerals of the soil system. The rate of weathering varies widely between sites depending on many considerations, including the mineralogy and age of the parent material and the intensity of the weathering process. Zabowski (1990) summarized information on weathering rate as reported in the literature for 24 forest ecosystems worldwide. April and Newton (1992) studied the weathering rates for 17 of the Integrated Forest Study sites and found that the glaciated sites had a significantly higher weathering potential than the nonglaciated sites.

Mineral weathering does provide a significant supply of essential nutrients for plant uptake, typically at a rate faster than what is lost through leaching. While this is generally true of most soils, it might not be true for soils that are very young, heavily weathered, or derived from parent materials low in base elements (Zabowski 1990). In addition, soils that have high anion inputs from atmospheric deposition or nitrification could have high rates of leaching losses—rates potentially exceeding the resupply of these ions from the weathering process (Johnson and Lindberg 1992).

Although there are several ways to address rates of weathering, in many mineral cycling studies it is assumed that the soil available nutrient pool is in a steady state and the rate of nutrient addition by weathering is equal to the rate of removal by uptake and leaching. This assumption, at best, is a crude approximation of weathering. It is made primarily because of the difficulty of determining actual weathering values.

Nitrogen Fixation

An ecosystem can receive nitrogen through fixation of atmospheric nitrogen by either free-living or symbiotic organisms. Fixation by free-living organisms is a far less effective means of adding nitrogen to a site than through a symbiotic process. Free-living fixation seldom results in the annual accumulation of more than 1 to 2 kg/ha even under ideal conditions, and thus is not a significant process in increasing the nitrogen capital of an ecosystem.

However, fixation through symbiotic organisms can have an immediate effect on the nitrogen capital of an ecosystem. In the Pacific Northwest, annual symbiotic fixation rates ranging from 50 to 150 kg/ha are reported for red alder. This can result in doubling the nitrogen capital of the ecosystem well within the life cycle of a red alder forest. For example, Cole et al. (1978) reported that a 35-year-old alder stand of moderate productivity increased the soil nitrogen from 3,000 kg/ha to 5,600 kg/ha within this 35-year period (Figure 2). In a chronosequence study at Glacier Bay, Alaska, Crocker and Major (1955) clearly demonstrated the capacity of alder ecosystems to accumulate nitrogen. Similar rates of nitrogen accumulation have been reported by a num-

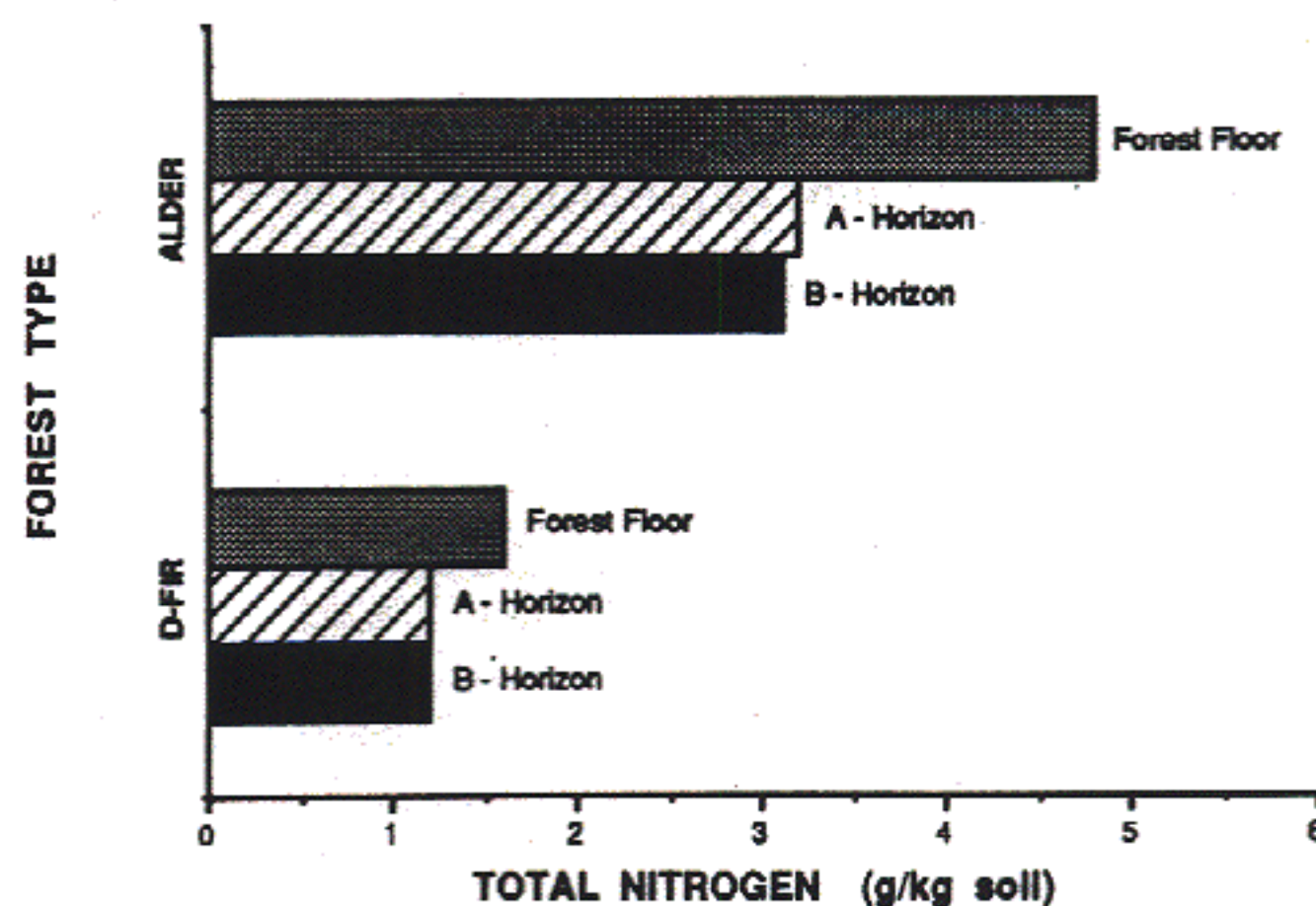


Figure 2. Comparison of total soil nitrogen and organic carbon under alder and Douglas-fir. The higher N values under alder are attributed to 55 years of N fixation. Adapted from Van Miegroet and Cole (1988).

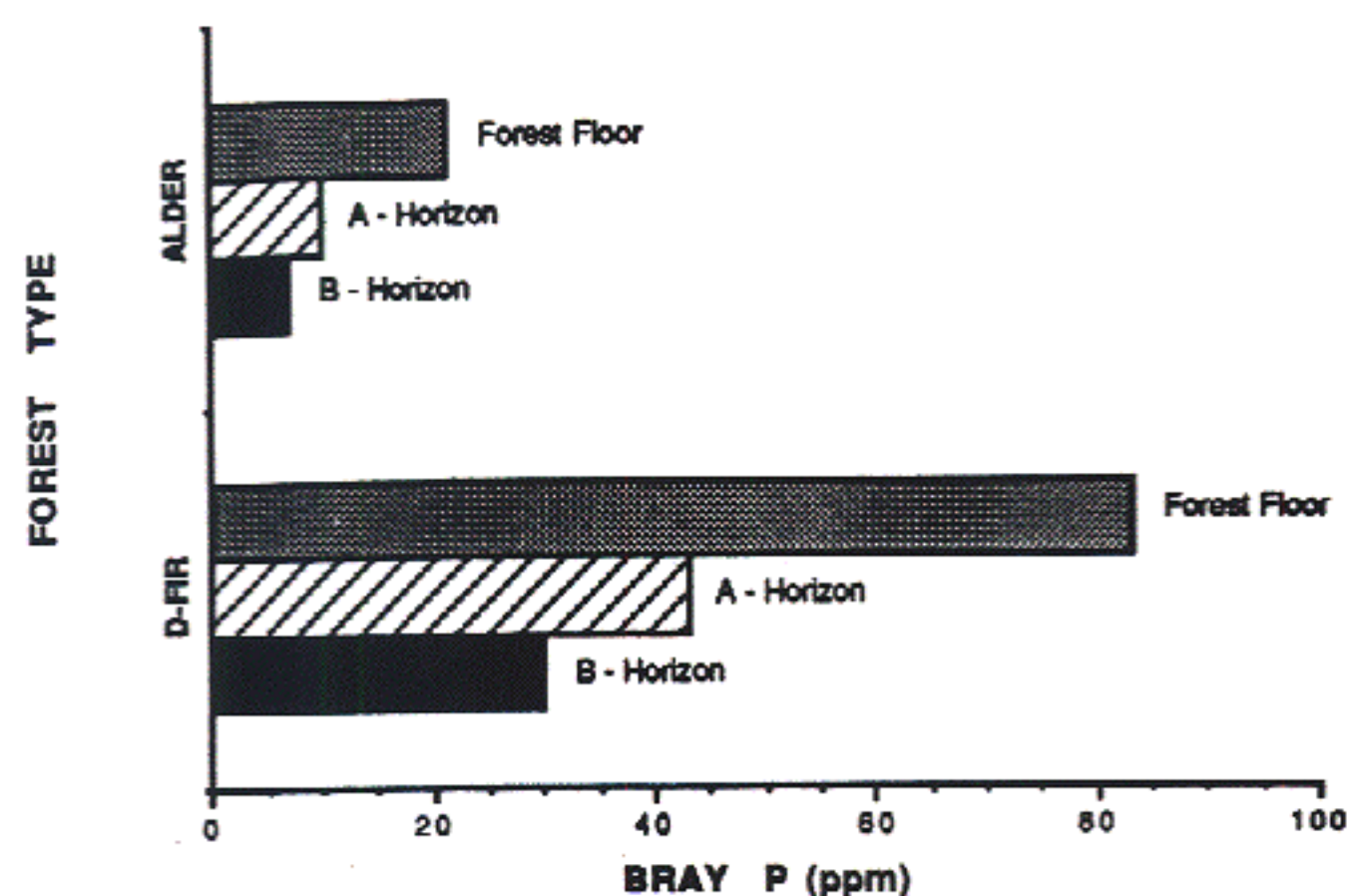


Figure 3. Comparison of Bray P under mature red alder and Douglas-fir at the Thompson Research Center. The decrease under red alder is attributed to organic incorporation and a decrease in soil pH. From Cole et al. (1990).

ber of other investigators, including Bormann and DeBell (1981) and Zavitkovski and Newton (1977). Douglas-fir will respond to the nitrogen accumulated in the soil through this mechanism (Tarrant and Miller 1963).

But excess nitrogen accumulation under red alder may lead to several problems. As reported by Van Miegroet et al. (1990), nitrification under red alder can result in high rates of nitrate leaching, exceeding at times EPA drinking water standards. This nitrate leaching process will also cause a downward displacement of cations in the soil profile, an acidification of the soil, and a decrease in the phosphorus availability (Figure 3). In a forest conversion study, Cole et al. (1990) found that these changes in the soil chemistry caused by the nitrification and nitrate leaching resulted in a striking decrease in the growth of second rotation alder (Figure 4). They attributed this reduction in alder productivity to a decrease in the phosphorus availability of the site. Apparently Douglas-fir can tolerate lower soil phosphorus levels than alder, perhaps because of the mycorrhizal association. Further supporting evidence for this hypothesis is the study by Radwan (1987) in which he demonstrated a growth response by alder to phosphorus addition. This is not to say that other environmental factors could not have been responsible for this decrease in productivity of second rotation alder stands. Potentially, the higher soil acidity under the original alder forest could cause aluminum toxicity to the fine roots or a decrease in the rate of nitrogen fixation.

Atmospheric Additions

Additions of essential elements through atmospheric deposition have historically been low compared to

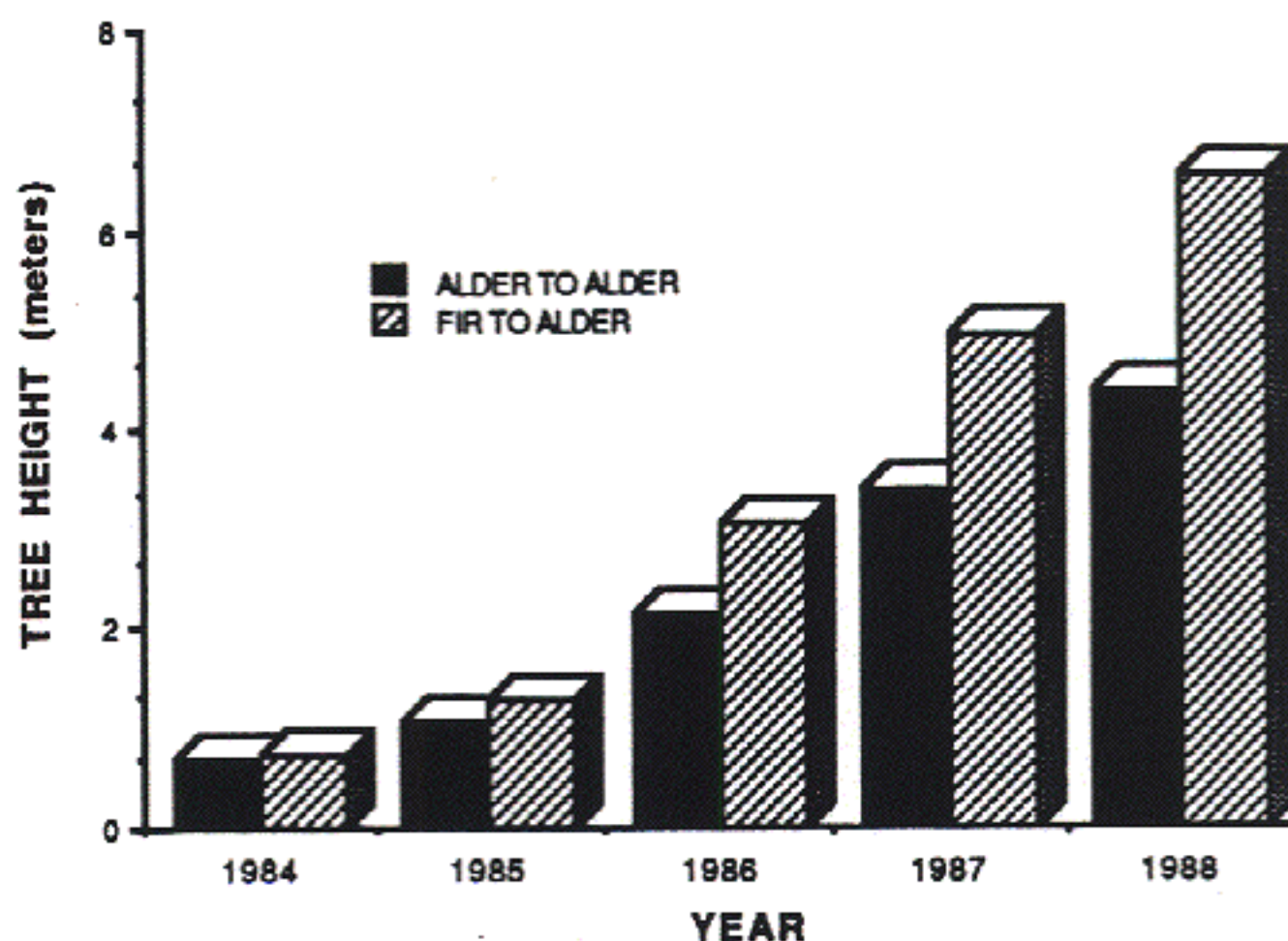


Figure 4. Initial growth of alder established on sites formerly occupied by Douglas-fir and alder. Differences in growth between these two plots are attributed to differences in soil properties caused by 50 years of nitrification and nitrate-N leaching under alder. From Cole et al. (1990).

nitrogen fixation or mineral weathering. However, higher deposition rates in recent years have made this source significant for some forest regions. For example, annual additions of nitrogen as high as 30 to 40 kg/ha are reported in Europe. Within the eastern United States and Canada there are many forest sites receiving a significant atmospheric input of nitrogen, as shown in Table 6. These inputs represent a major nitrogen addition to the ecosystem and potentially provide a significant part of the annual nitrogen requirements for many of our forest species. However, in the Pacific Northwest the annual input of nitrogen is less than 5 kg/ha. Considering that RFNRP (Regional Forest Nutrition Research Project) recommends a 224 kg/ha addition of nitrogen every five to eight years, equivalent to an annual input of 28 to 44 kg/ha, atmospheric additions in the North-

Table 6—Annual nitrogen input through atmospheric deposition as reported for the Integrated Forest Study (IFS) sites. From Johnson and Lindberg (1992).

Site (Location)	Nitrogen Input (kg/ha)
Lower Cedar River (Washington)	4.8
Upper Cedar River (Washington)	4.2
Coweeta (North Carolina)	7.2
Turkey Lake (Ontario, Canada)	11.4
Whiteface (New York)	15.9
Duke Forest (North Carolina)	15.0
Great Smoky Mountains (Tennessee)	26.8

west fall short of alleviating the chronic nitrogen deficiency problems that we encounter. At sites where high rates of nitrogen are added through atmospheric deposition, it is possible that nitrogen saturation and nitrate leaching will take place as discussed above for red alder.

Mineralization

In order for nitrogen to be available for plant uptake it has to be in an available form either as nitrate (NO_3) or ammonium (NH_4). Most of the soil nitrogen is stored in an organic form and is not available until the organic matter has been broken down and the nitrogen mineralized through biological processes. Typically this is a two-step process: an initial fauna-mediated chopping process followed by microbial mineralization. In the Pacific Northwest, the rate of mineralization ranges from 1 to 2% of the total per year. However, far different rates will be found in forest ecosystems of the northern and southern regions. For example, the mean residence time for organic matter in the forest floor ranges from less than a year in the tropics to 350 years in the boreal coniferous forest (Table 7).

Since many of the forest soils in the Pacific Northwest may have 2,000 to 4,000 kg/ha of total nitrogen, a 2% mineralization rate would result in 20 to 80 kg/ha of nitrogen available annually for uptake by the higher plants. While 80 kg/ha is probably an adequate amount of available nitrogen for excellent growth of our western conifers, 20 kg/ha would undoubtedly result in a nitrogen deficiency. In a parallel way, phosphorus and sulfur can also be supplied by mineralization.

Table 7—Mean residence time (years) of organic matter and nutrients in the forest floor for a wide range of forest ecosystem types.

Forest Type	OM	N	K	Ca	Mg	P
Boreal coniferous	350	230	94	150	455	324
Boreal deciduous	25	26	10	14	14	15
Subalpine coniferous	18	37	9	12	10	21
Temperate coniferous	17	18	2	6	13	1
Temperate deciduous	4	6	1	3	3	6
Mediterranean	3	4	1	4	2	1
Tropical	0.7	0.6	0.2	0.3		0.6

Mechanisms for Meeting Nutritional Needs

As discussed above, the nutrient needs of a tree are met in part through uptake and in part through internal translocation. The relative importance of these two processes in a given forest depends on several factors, including the nutrient element under consideration, the tree age and species, and the nutritional conditions of the site.

Uptake

Several conditions and processes involving the root system affect nutrient uptake by the tree. These include nutrient availability from the soil solution and the exchange sites, imbalances between nutrients, blockage of uptake by certain ions, and the special role mycorrhizae play in nutrient uptake.

The nutrients must be in an ionic form within the soil system. This can take the form of ions residing within the soil solution or on the cation exchange complex. Clearly there is an ionic equilibrium between the soil solution and the exchange complex. In order for nutrient elements to be a part of this ionic system, they have to be released from the solid phase of the soil through mineralization, as is the case with nitrogen, or through weathering of primary or secondary minerals, as discussed previously for the base elements. Some nutrient elements are released through both of these mechanisms. Phosphorus is an excellent example. In a very young soil, most of the phosphorus is associated with the mineralogy of the system. However, as the soil matures, a greater percentage of the phosphorus is associated with the organic component.

Internal Translocation of Nutrients (Mobility of Elements)

The ability of a tree to translocate nutrients prior to foliage senescence allows the tree to decrease the need for external nutrients and directly reuse the nutrient through its internal recycling mechanism. There are major differences between species and between nutrients in the amount of internal translocation that takes place. In part, the limiting factor regulating nutrient translocation is the role that the element plays within the plant. Nutrients that remain in an ionic form within the foliage, such as potassium, are very mobile and can be translocated easily. Elements such as calcium are tightly combined with other compounds such as oxalates and sulfates, and thus remain immobile within the foliage.

Nitrogen mobility is variable between species. For example, there is little to no translocation of nitrogen from alder foliage prior to senescence. However, larch

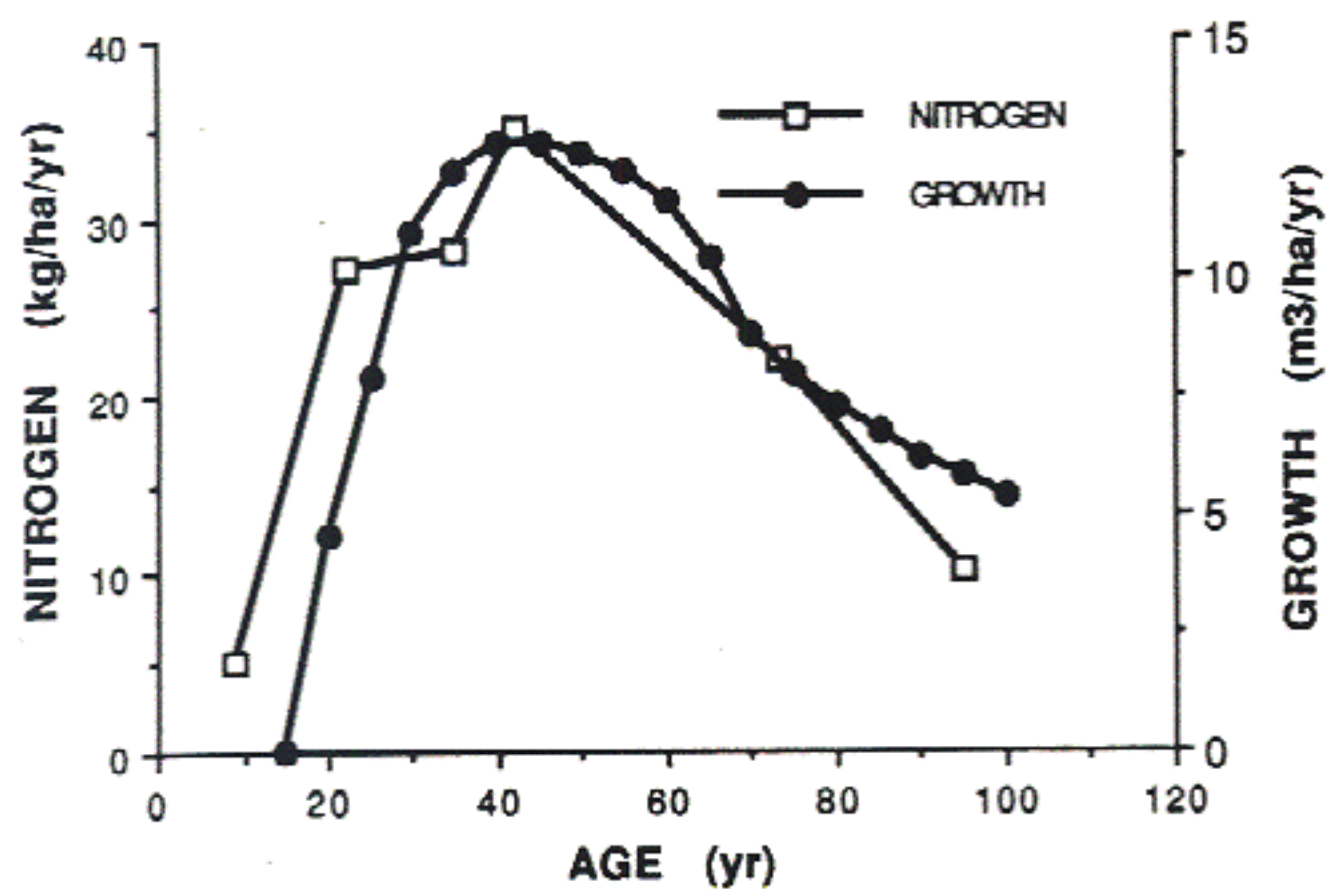


Figure 5. Relationship between growth as periodic annual increment (Curtis et al. 1982) and N uptake (Turner 1975) by site IV Douglas-fir during stand development.

will translocate 60 to 80% of foliage nitrogen prior to the abscission of its needles in the fall of the year (Gower 1987). These differences can perhaps be explained by the contrasting importance of nitrogen in these two species. Symbiotic nitrogen fixation associated with red alder appears to be sufficient to meet the annual nitrogen requirements of this species. In contrast, larch is a deciduous conifer which must replace all of its foliage each year. Since this species is typically found in a harsh environment where organic matter decomposition is very slow, nitrogen availability in the soil is minimal and the external cycling of most nutrients is slow. Apparently this species has evolved a very efficient means for the internal translocation of nitrogen, as well as other nutrients and carbohydrates, to provide the nutritional base for its growth and metabolism.

There is far more nutrient translocation from the foliage of deciduous species than of conifers (Cole and Rapp 1981). This translocation process in deciduous species is primarily driven by the annual turnover of the

canopy foliage. Where internal translocation is minimal and a single nutrient element is deficient, there should be a reasonable relationship between the uptake of this element and the productivity of the forest. As illustrated in Figure 5, such a relationship appears to exist between the productivity of Douglas-fir (as measured by the periodic annual increment) and nitrogen uptake.

Nutrient Conservation Retention Processes by Forest Ecosystems

In considering mechanism of retention, it must be recognized that nutrients typically do not behave independently of each other. While in soil solution they move as ions, thus there must always be a charge balance (cations must equal anions). In addition, there are selectivity relationships between ions in most adsorption, uptake, and leaching reactions. Consequently, it is somewhat meaningless to speak of the cycling of individual elements such as nitrogen or calcium if one is trying to understand how the system functions and why a given element is lost or retained by the system. It is with this concept in mind that one has to consider the processes associated with nutrient retention and loss.

Rates and Pathways of Loss

To maintain the long-term productivity of a forest ecosystem, the rate of nutrient input has to equal or exceed any losses that might occur by leaching, erosion, fire, or through harvest removal. Fortunately for most forest ecosystems, the rate of loss by leaching is very low. It is only when a system is overmature, harvested, burned, or there is an excessive rate of input from fixation or atmospheric deposition that high loss rates are experienced. For example, from the recent Integrated Forest Study (Johnson and Lindberg 1992), it is evident that nutrient leaching losses seldom occur from young, vigorous forests. It was found that only mature

Table 8—Annual nitrogen additions and loss (kg/ha) from a variety of forest sites as reported for the Integrated Forest Study (IFS) sites. From Johnson and Lindberg (1992).

Site Location	Atmospheric Input	Leaching Loss	Reason for Loss
Douglas-fir (Washington)	4.8	<1	
Red alder (Washington)	4.8	39	N fixation, 85 kg/ha/yr
Upper Cedar River (Washington)	4.2	<1	
Coweeta (North Carolina)	7.2	<1	
Turkey Lake (Ontario, Canada)	11.4	23	Mature; high deposition
Whiteface (New York)	15.9	3	
Duke Forest (North Carolina)	15.0	<1	
Great Smoky Mountains (Tennessee)	26.8	18	Overmature; high deposition

to overmature ecosystems that also had high rates of atmospheric input (The Smokies and Turkey Lake) or a high rate of N fixation (red alder site) experienced any significant leaching losses (Table 8). The sites with relatively young, rapidly growing forest did not experience leaching losses irrespective of the rate of deposition (Johnson and Lindberg 1992). Although examples were not included as part of the Integrated Forest Study program, sites with high calcareous soil or bedrock conditions could potentially experience high leaching losses due to the presence of the carbonate or bicarbonate anion.

Processes Associated with Nutrient Loss

The process of elemental loss through leaching is one that is limited by the production and mobility of anions within the soil solution (Johnson and Cole 1980). In order for a cation (i.e., Ca^{+2} , Mg^{+2} , K^{+}) to leach through the soil, it must be associated with an equivalent number of anions. The role that various anions play in this leaching process is indicated below:

Bicarbonate	Important in low elevation coniferous and deciduous forest stands. The pH must be above 5 for this to be significant in the leaching process.
Nitrate	Important where nitrification is taking place, primarily in sites with high rates of nitrogen fixation, overmature forest stands, or where high atmospheric depositional rates of nitrogen are taking place.
Organic acids	Important primarily at higher elevations and/or cold and wet environments. This anion is formed from the incomplete decomposition of organic matter.
Sulfate	Occurs primarily at sites experiencing high atmospheric depositional rates of sulfate.
Chloride	Found only at sites adjacent to the influence of ocean air.

Each of these anions plays a very different role in the leaching process. In soils associated with the forests of the Northwest, bicarbonate tends to be the dominant anion in our lower elevation coniferous forests. Since bicarbonate is the anion of a very weak acid, soil solutions dominated by the bicarbonate ion are also weakly acidic, seldom lower than pH 5. At a pH 4.5, the bicarbonate ion largely disappears from the soil solution, removing a H^{+} ion and forming carbonic acid.

At higher elevations or higher latitudes, where there is a significant organic accumulation, organic acids form the dominant anions. Because of their high dissociation

Table 9—Annual anion leaching processes and rates (keq/ha) at 10 cm depth under high elevation conifers, low elevation Douglas-fir, and red alder.

Forest Type	HCO_3	Organic Acids	NO_3	Total
Douglas-fir, low elevation	0.42	TR	TR	0.42
Red alder	0.28	TR	3.45	3.75
Conifers, high elevation	0.65	1.33	TR	1.89

constants, organic acids can remain deprotonated in soil solutions with pH values less than 4 and function as anions and produce very acid soils.

One of the most acidic soil environments in the Northwest and the one with the greatest leaching potential is associated with red alder. The symbiotic N-fixation process of this species results in an accumulation of available soil nitrogen initially in the ammonium form. Ammonium is readily transformed to nitrate through the nitrification process. This process releases two protons (H^{+}) for each nitrate ion formed. Consequently, this process not only produces a very acidic soil solution (pH as low as 3.5) but also results in the formation of a highly mobile anion, causing the downward displacement of cations in the soil profile (Van Miegroet and Cole 1984, 1985).

It follows from this discussion that only minimal leaching losses are found in the bicarbonate-dominated soils of the low elevation coniferous forests. This is consistent with studies where leaching losses have been directly measured for many years (Cole and Gessel 1968). A somewhat higher leaching potential exists in soils associated with organic acids at the higher elevations (Johnson et al. 1977). Clearly, the highest leaching rates in the Northwest are found under nitrate-dominated systems associated with red alder (Van Miegroet and Cole 1985). The contrast between these three systems in their leaching processes and the amount of leaching that takes place is shown in Table 9.

These results suggest that there is a far higher potential for cation leaching under red alder than for either Douglas-fir or high elevation forest sites. This leaching is driven in each case by a specific anion. Should the anion change through some management process, the leaching process and potential would also change (Cole et al. 1975).

Processes of Nutrient Retention

Processes which retain nutrients within the ecosystem vary widely depending on the nutrient involved. For example, the retention of nitrogen is heavily dependent on the biological processes associated with the

cycling of this nutrient. By retaining much of the nitrogen supply within the biomass and organic matter of the system, losses other than through fire are minimal. Nitrogen is readily removed from the soil solution when present in ionic form through immobilization by microorganisms or uptake by higher plants. This is especially true when the system is deficient in this nutrient. It is only when there is an overabundance of nitrogen, as in the case of red alder and with overmature forest ecosystems, that we find that nitrogen losses occur. With excess nitrogen in the soil, the ammonium ion is released through microbial decomposition from the organic matter. The ammonium ion is readily converted to the nitrate form through the nitrification process. Once it is in this form it can be lost from the soil through leaching. As discussed above, this is also an acidifying process that can affect the availability of other elements, such as phosphorus.

Some nutrients, such as calcium, magnesium, and potassium, are primarily retained through soil cation exchange processes. The cation exchange reaction of the soil is not only an effective process for the retention of these nutrients in an ionic form but also allows for the release of these ions for uptake through an ion exchange process with the tree roots. The storage of cations on exchange sites can be considerable. For the young glaciated soils of the Pacific Northwest, over 600 kg/ha of calcium, 200 kg/ha of magnesium, and 100 kg/ha of potassium can be stored in this way. However, in heavily weathered soils with very low base saturation or exchange capacities, the storage potential of cations through this mechanism is not nearly as great. For example, Johnson et al. (1988) found exchangeable calcium levels in some heavily weathered soils of Tennessee to be minimal, suggesting the strong possibility that these ecosystems could be calcium deficient.

Other nutrients, such as phosphorus, are readily retained in both the organic and inorganic forms. Inorganic phosphate retention is generally thought of as a surface adsorption-complexation phenomenon of orthophosphate retained on aluminum and iron hydroxide surface sites (Barrow 1983). The relative strength of adsorption of phosphate depends both on the extent of development of that surface complex and on other chemical soil factors that affect the surface, such as pH, organic matter content, presence of other adsorbed anions, and ionic strength (Larsen et al. 1959). The retention of phosphorus in soils generally increases with decreasing soil pH below 7. In some soils, phosphorus is primarily retained in an organic form. As such, the dynamics of the organic matter becomes an important

process in governing the release of phosphate into the soil solution for plant uptake. The conditions in the soil with regard to microbial activity can therefore directly affect the rate of phosphorus mineralization (e.g., lower pH, high C, high N).

Conclusions

Trees differ greatly from agronomic crops in their nutritional needs and in the way these needs are met. As a perennial system that typically lives for many decades, a tree has a number of mechanisms that minimize nutritional requirements for the production of structure and biomass. These mechanisms, which include cycling and internal translocation of nutrients, provide for a greater nutrient use efficiency than typically found in agronomic crops. Although trees are efficient in the use of nutrients, when they reach deficiency levels they respond by growing more slowly. In the Pacific Northwest most of our forests are deficient in nutrients, especially nitrogen. Management practices that aggravate this deficiency will probably result in the further erosion of site productivity. Likewise, management practices that increase the availability of the deficient nutrients will probably result in growth enhancement.

Tree species vary greatly in their relative dependence on internal processes to meet nutrient requirements. Because trees are part of an ecosystem, we must understand how the total ecosystem functions in order to understand how these nutritional needs are met. In part they are met through an internal process of storage and translocation and in part through external processes of atmospheric additions, organic decomposition, mineral weathering, and the cycling of nutrients between the tree and the rest of the ecosystem.

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