7

Nutrient Cycling in Forests of the Pacific Northwest

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INTRODUCTION

Ecosystem analysis has established nutrient cycling as an important area of ecology involving biological, chemical, and geological interactions. Studying the flow of elements through ecosystems provides us with a tool for understanding the functioning of ecosystems. For example, if an ecosystem component has a rapid flux of elements through it, or if it stores large amounts of an element, that component is clearly important in ecosystem function. Nutrient cycling strongly influences ecosystem productivity since nutrient flows are closely linked with transfers of carbon and water. In addition nutrient cycling may also affect succession and evolution in forest ecosystems.

Various distinct processes are involved in nutrient cycling, such as decomposition, weathering, uptake, leaching, and so on. Each is a precursor to another and the flow of nutrients follows a set of interconnected steps. Although the basic nutrient cycling processes are common to all ecosystems, the rates of the processes vary from one forest ecosystem to another. This variation plays an important role in forest succession and evolution. For example, long-term foliage retention by conifers may allow a species to exist where only a marginal nutrient supply is available from the soil. Nitrogen-fixing species, on the other hand, can occupy sites where nitrogen availability is low because they can provide their own nitrogen. An understanding of nutrient cycling is thus essential for the rational management of forest ecosystems.

Nitrogen is recognized as the most limiting element for forest growth in the Pacific Northwest, particularly in Douglas-fir *(Pseudotsuga menziesii)* ecosystems (Gessel and Walker 1956; Gessel et al. 1969). For this reason this chapter focuses largely on nitrogen cycling. Cycling of other elements such as potassium and calcium are compared with that of nitrogen, where contrasting behavior may provide insight into nutrient-cycling processes.

The objectives of this chapter are to (1) briefly describe the important nutrient cycling processes; (2) contrast nutrient cycles in different forest eco-

systems; (3) contrast nutrient cycles in relation to stand development; and (4) assess the impact of forest-management practices on nutrient cycling.

KEY PROCESSES IN FOREST NUTRIENT CYCLES

Study of nutrient cycles in forest ecosystems requires a basic conceptual framework to organize the nutrient capitals and transfer processes. Diagrams of nutrient cycles in forests have been presented before, for example, by Duvigneaud and Denaeyer-DeSmet (1970). The scheme followed by coniferous forest biome researchers is similar (Figure 7.1). As Figure 7.1 shows, there are many important biological and physical processes involved. In particular the importance of belowground processes is recognized. In this section nutrient inputs, nutrient transfers within ecosystems, and nutrient outputs are briefly discussed. More detailed discussions of the processes controlling nutrient availability and conservation follow.

Inputs

Input of mineral nutrients by dry particulate deposition, precipitation, and gaseous fixation can be an important source of new nutrient elements for ecosystems. This and release of nutrients by weathering of soil parent material constitute the only two sources of new nutrients for forest ecosystems. These sources must replace any losses that occur as well as provide for nutrient accumulation.

Atmospheric Inputs

Inputs by dust, dry aerosol impaction, and precipitation are generally low in the coniferous biome compared with those in the eastern United States. For example, inputs of nitrogen are generally less than $3 \text{ kg} \cdot \text{ha}^{-1}\text{yr}^{-1}$ throughout much of western Oregon and Washington. In contrast nitrogen inputs in excess of $6 \text{ kg} \cdot \text{ha}^{-1}\text{yr}^{-1}$ are routinely reported for northeastern hardwood forests (Likens et al. 1977). One exception to the low atmospheric nutrient inputs for northwestern forests is coastal ecosystems. In these, nutrient input originating as sea spray contributes up to $10 \text{ kg} \cdot \text{ha}^{-1}\text{yr}^{-1}$ of nitrogen and large amounts of other nutrients (Grier 1978a).

Nitrogen Fixation

Nitrogen fixation occurs throughout the coniferous biome by free-living algae and bacteria, by canopy epiphytes, and by symbiotic associations with
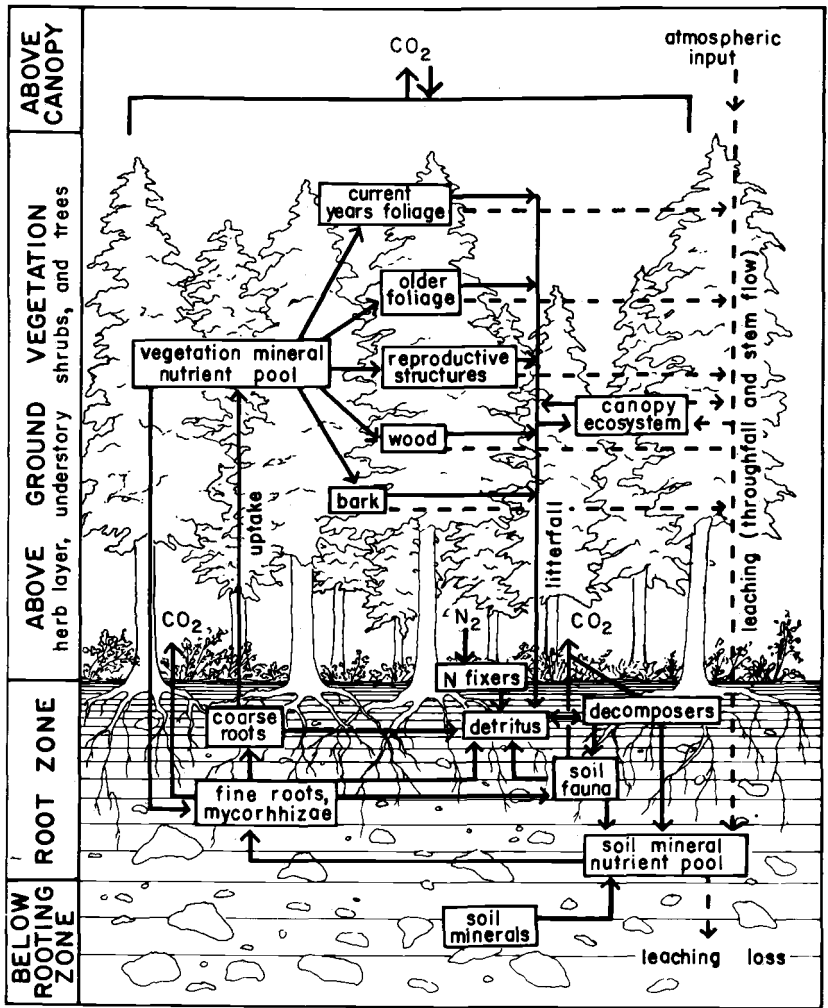
FIGURE 7.1 *Conceptual model of nutrient transfers in coniferous forests.*

roots of plants such as red alder *(Alnus rubra)*. Red alder is a widespread deciduous tree species in the Pacific Northwest. It has been known for many years that symbionts associated with red alder roots fix nitrogen (Bond 1954) and that an alder sere can improve site fertility for succeeding nonnitrogen-fixing species (Tarrant and Miller 1963; Newton et al. 1968).

Organic matter production and nitrogen fixation by red alder appear to be correlated. Maximums in both occur at a stand age of about twenty years. Estimates of the amounts of nitrogen fixed by alder stands vary considerably. Tarrant and Miller (1963) calculated an average nitrogen accretion of $41 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ during thirty years of site occupancy by red alder, while New-

ton et al. (1968) reported an extremely high accumulation of up to 321 kg·ha^{-1}·yr^{-1} over fifteen years of alder occupancy on sites near the Oregon coast.

In a study conducted by the coniferous forest biome researchers, Cole et al. (1978) estimated an average annual fixation rate of 85 kg·ha^{-1}yr^{-1} over thirty-five years. These values were obtained by comparing nitrogen capitals of thirty-five-year-old red alder and Douglas-fir stands on the same soil series at the Thompson site in Washington.

Another northwestern species known to host nitrogen-fixing symbionts is snowbush *(Ceanothus velutinus)*. This species occupies drier sites than alder and typically grows from buried seed activated by fire. Youngberg and Wollum (1976) found nitrogen accretion of about 1080 kg/ha over ten years of snow-bush occupation of a burned clearcut in Douglas-fir and 715 kg/ha for ten years in a burned ponderosa pine clearcut in the Oregon Cascades. At these rates of fixation, they calculate that the nitrogen lost during burning is replaced in about seven years. Other *Ceanothus* species may also host nitrogen-fixing symbionts.

Contributions to ecosystem nitrogen capital by free-living microbes in the soil were not examined by coniferous forest biome researchers. However, microbe contribution is thought to be less than that of nitrogen-fixing organisms hosted by green plants.

In-depth studies on nitrogen fixation in forest canopies as well as other nutrient-cycling aspects of canopy-dwelling organisms were conducted in old-growth Douglas-fir forests in Oregon (Denison 1973). Significant fixation was found to occur in at least one species of epiphytic lichen, *Lobaria oregana*. A conservative nitrogen fixation rate of 3.8 kg·ha^{-1}·yr^{-1} was estimated using acetylene reduction methods. Fixation rates were positively correlated with moisture content of the lichen thallus. This was in turn related to precipitation and atmospheric vapor pressure deficit.

Another possible site for nitrogen fixation in the coniferous biome is in decaying logs. Several studies (Grier 1978b; Cromack, pers. comm.) showed nitrogen accumulation occurring in fallen trees both in coastal and Douglas-fir forests. Some evidence suggests this may result, in part, from nitrogen fixation. Specific nitrogen-fixing organisms residing in fallen logs are unknown. But, Aho et al. (1974) have shown that nitrogen-fixing bacteria do inhabit decaying heartwood of white fir *(Abies concolor)* in southwestern Oregon. The same or similar organisms may account for nitrogen accumulation in fallen logs.

Soil Weathering

Weathering of soil parent material is a major source of new cation nutrients and can often be the major source of new phosphorus and sulphur in an ecosystem. Weathering of soil primary minerals and other soil-forming processes were studied within the biome program; a large part of the effort going into a

study of podzolization processes in a mature *Abies amabilis* stand at Findley Lake (Singer and Ugolini 1974; Ugolini et al. 1977a, b; Singer et al. 1978).

The term "weathering" is used here to describe nutrient release from primary soil minerals. This release constitutes a functional nutrient input to the ecosystem, since it adds previously unavailable nutrients to the available nutrient pool. Rates of nutrient release are difficult to measure *in situ* because of the masking effects of nutrient uptake by vegetation and microorganisms. Release rates can be calculated as the normally small difference between other major nutrient transfers, but the accuracy of such measurements is questionable in view of the errors associated with the other measurements.

Rough estimates of mineral weathering in one soil were obtained as a result of long-term plot studies conducted in young Douglas-fir stands at the Thompson site. Measurements of nutrient-cycling processes in a second growth Douglas-fir stand at the Thompson research site were initiated in 1962. Remeasurements of exchangeable cations in 1976 indicated that soil weathering input to exchangeable nutrient pools was not keeping pace with immobilization of cations in living biomass or their loss by leaching (Table 7.1). In the surface horizons there was a general decrease in amounts of exchangeable calcium, potassium and magnesium over the fourteen-year span of this study. But, in this interval, cation-exchange capacity remained the same. These data indicate that an assumption of steady state in soil exchangeable cations may not be justifiable. Thus weathering rate calculations based on this assumption (Duvigneaud and Denaeyer-DeSmet 1970, Likens et al. 1977) may be in error.

Nutrient Transfers Within Coniferous Ecosystems

Once nutrients have entered an ecosystem they are subject to transfer by a large number of processes. Clearly, all the steps involved, that is, litterfall, decomposition, uptake, and internal translocation, are highly interdependent. In the following sections we consider these processes individually and discuss how they interact to regulate nutrient cycling in stands subjected to very different climatic conditions.

Litterfall and Crownwash

Litterfall and its components are part of a spectrum of organic matter and nutrient return to the forest floor ranging from nutrients in small particles returned in canopy wash to those returned in logs and other large woody material. The different components of this spectrum vary widely in nutrient concentration and, when they reach the forest floor, also vary in the amount of time required for decomposition and nutrient mineralization to occur. Nutrients dissolved in canopy wash may be in immediately available ionic form whereas

TABLE 7.1 *Cation exchange capacity and exchangeable cations in the Everett soil at the Thompson Research Center, Washington, in 1962 and 1976. Standard deviations are in parentheses.[a]*

Horizon and depth (cm)	Cation exchange capacity			CA^{2+}			Mg^{2+}			K^+		
	1962a[b]	1962b[c]	1976[d]	1962a	1962b	1976	1962a	1962b	1976	1962a	1962b	1976
						meq/100 g soil						
A	9.78	—	9.50	1.33	—	0.90	0.26	—	0.12	0.17	—	0.11
(0 to 15)	(0.556)	—	(0.995)	(0.192)	—	(0.20)	(0.48)	—	(0.022)	(0.011)	—	(0.016)
B21	6.99	6.23	6.21	0.44	0.43	0.30	0.13	0.10	0.06	0.08	0.08	0.05
(15 to 30)	(2.912)	—	(0.613)	(0.213)	—	(0.042)	(0.052)	—	(0.005)	(0.018)	—	(0.002)
B21	6.52	5.01	4.43	0.32	0.22	0.18	0.09	0.05	0.04	0.06	0.05	0.03
(30 to 45)	(0.979)	(0.662)	(0.578)	(0.114)	(0.100)	(0.081)	(0.025)	(0.010)	(0.015)	(0.006)	(0.005)	(0.008)
B22	3.15	2.56	3.64	0.15	0.90	0.17	0.04	0.03	0.04	0.04	0.03	0.03
(45 to 60)	(1.223)	(0.769)	(0.591)	(0.033)	(0.015)	(0.044)	(0.019)	(0.010)	(0.003)	(0.026)	(0.016)	(0.005)

[a] D. W. Cole and R. L. Lamon, unpublished data.
[b] 1962a: sampled and measured in 1962.
[c] 1962b: sampled in 1962, measured in 1976.
[d] 1976: sampled and measured in 1976.

nutrients incorporated in woody material may require prolonged decomposition before they are available for uptake.

The proportion of a given nutrient returned along various pathways is different for different elements (Will 1959; Cole et al. 1968). For example, Cole et al. found that after canopy closure, 8 to 12 percent of the nitrogen, 65 to 85 percent of the potassium, and 15 to 20 percent of the calcium moved to the forest floor from the canopy by way of crown leaching and stemflow. The remainder was returned in litterfall.

Detailed studies were conducted on nutrient dynamics within the canopy of old-growth Douglas-fir forests (Denison 1973). Entire ecosystems occupy niches within old-growth canopies. These ecosystems contain all the major elements of the larger ecosystem including primary producers, such as lichens, mosses, and occasional ferns, decomposers, and consumers, mainly microarthropods. These microecosystems also have many of the same properties as larger ecosystems; they cycle and conserve nutrients and thus exert a strong influence on nutrient return via crownwash and, to a lesser extent, litterfall. A full discussion of this intricate system is well beyond the scope of this chapter, but a summary diagram of the canopy ecosystem is presented in Figure 7.2. The diagram is largely self-explanatory, but the point to be stressed is that neither crownwash nor litterfall can be considered as a process solely regulated by the trees. What the researcher observes in ground-level collectors is the output of complex microecosystems that thrive within many forest canopies. Unfortunately, it is difficult to measure these intricate fluxes and few of them have been directly quantified as yet.

Decomposition Processes

Organic-matter decomposition and subsequent nutrient release are key processes in forest ecosystems, and the rate at which carbon and nutrients flow through the forest floor can play a large role in regulating ecosystem productivity. This regulatory role is particularly important in systems that operate on a very low nutrient capital and in those where decomposition processes are limited by environmental extremes.

Factors known to influence decomposition and mineralization rates of litter components are: (1) environmental factors (temperature, moisture); (2) litter nutrient content, particularly N; (3) C/N ratio; and (4) lignin content. These factors and nutrient release from decomposing litter are discussed in more detail in later sections along with the role of mycorrhizae.

Uptake and Internal Translocation

Uptake processes were studied in the biome program from both short- and long-term perspectives. Long-term information can be gleaned from nutrient
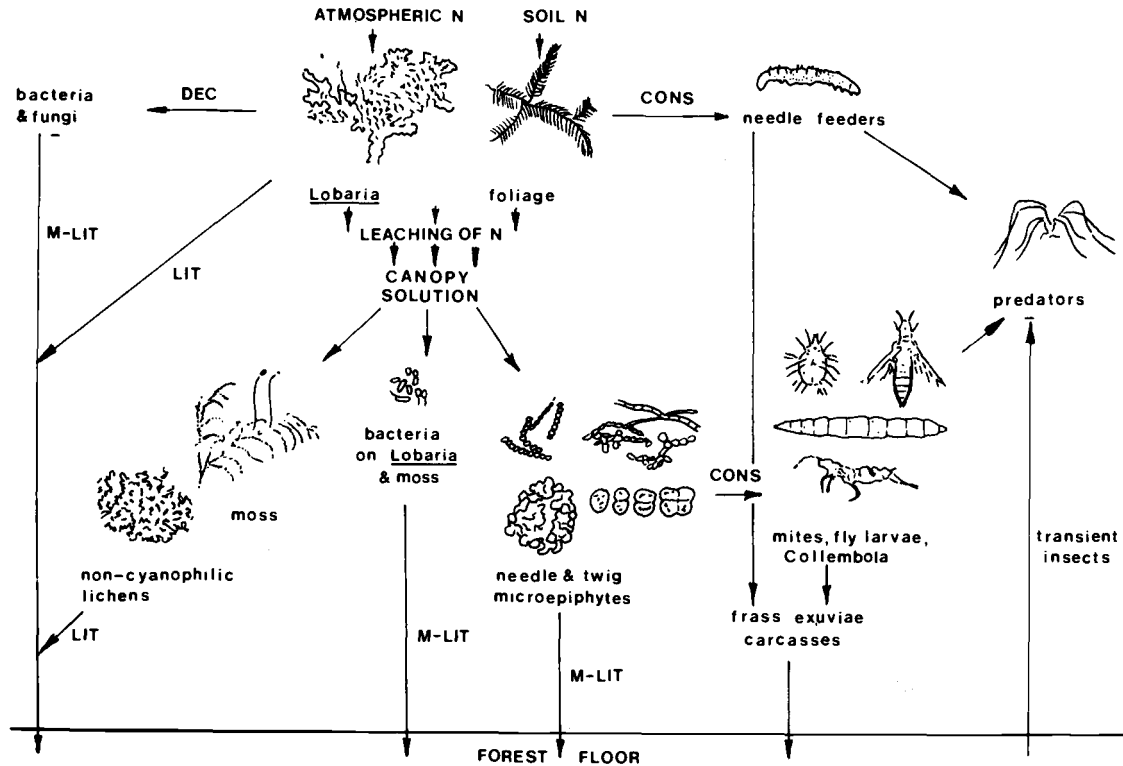
FIGURE 7.2 *Scheme of canopy N flow.* Key: *DEC = decomposition, CON = consumption, LIT = macrolitterfall, M-LIT = microlitterfall (after G. C. Carroll, pers. comm.).*

budgets in stands of various ages and this approach is pursued later in this chapter. Highlights of the short-term studies are reported here.

Most attention was paid to the uptake of nitrogen since it plays such an important role in the functioning of ecosystems in the biome. Nitrogen-uptake processes, however, are not well understood. Trees can utilize either ammonium or nitrate, but there is still some controversy over which is the preferred form. In the biome program nutrient uptake was studied using nonmycorrhizal Douglas-fir seedlings in solution culture.

These solution-culture studies revealed that nutrient-uptake rates increased with increasing ion concentrations until a plateau was reached (Cole and Bledsoe 1976). Nitrogen, either in NH_4^+ or NO_3^- form, was taken up more rapidly than other nutrients. Ammonium was taken up more rapidly than NO_3^-. Uptake of NH_4^+ temporarily depressed or precluded the uptake of other cation nutrients (presumably by ion competition), whereas NO_3^- uptake occurred simultaneously with cation uptake. In addition, it was shown that the seedlings were efficient at removing nitrogen at low levels, since nitrogen uptake rates decreased little even as concentration decreased.

Preferences for NH_4^+ or NO_3^-, however, may be different in soils than in solution culture. Van den Driessche and Dangerfield (1975) reported that Douglas-fir seedlings grew well in sand culture in both NH_4^+ and NO_3^-. However, well-irrigated seedlings favored NH_4^+ as the nitrogen source, while less irrigated seedlings favored NO_3^-, apparently because NH_4^+ is less mobile than NO_3^- in soils. In addition mycorrhizae in soils may influence nitrogen preference because of their ability to produce extensive hyphal networks in the soil. Uptake of organic nitrogen by forest trees is also possible but we know very little about this process.

In the solution-culture studies, the form of nitrogen supplied to Douglas-fir seedlings had a significant effect on final distribution of mineral nutrients. Figure 7.3 illustrates the concentrations of N, P, Ca, K, and Mg in parts of harvested seedlings. Although seedlings grown in NH_4^+–N accumulate considerably more nitrogen than do those grown in NO_3^--N, the accumulation of cations in the former is usually lower. This may be because of the charge-balance problem presented to seedlings that are taking up nitrogen as a cation (NH_4^+) and therefore have to limit their uptake of K^+, Ca^{2+}, and Mg^{2+}.

Analyses of xylem sap from roots of decapitated seedlings suggested that nitrate reduction occurred in the root tissues (Riekerk 1977). When nitrate was supplied in solution culture to seedling roots, ammonium predominated in the sap. Concentrations of potassium in xylem sap were also high, presumably because of the use of K^+ for carbohydrate and anion transfer through the xylem.

In addition to nutrient uptake by roots, internal translocation, or the withdrawal of nutrients from older tissues for use in production of new tissues, also constitutes a mechanism by which trees obtain nutrients for growth. It is also an important mechanism for nutrient conservation by trees. Nutrient requirements thus can be met in part by internal translocation. This partially short-circuits the more tortuous and less certain route of litterfall return, decomposition, and
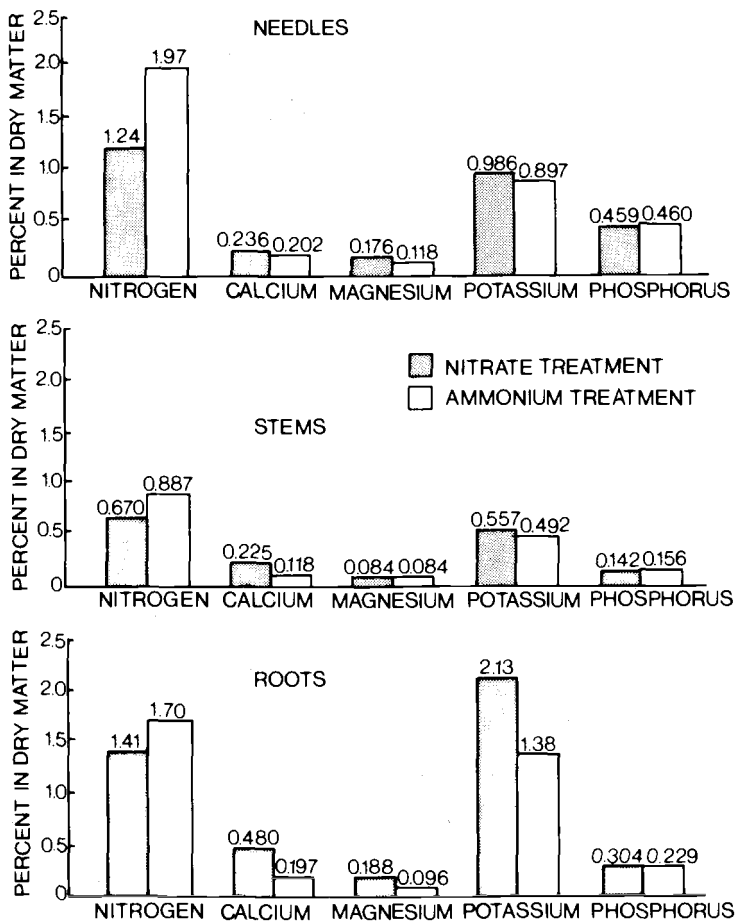
FIGURE 7.3 *Nutrient distribution in Douglas-fir seedlings given NH_4^+ and NO_3^- sources of N from solution culture (after C. S. Bledsoe, pers. comm.). Values are significantly different at the 99 percent level.*

uptake. Internal translocation is discussed in more detail later in the section on nutrient conservation mechanisms.

Outputs

Soil Leaching Processes

Soil-leaching processes were studied in some detail during the biome program. These processes are important for a number of reasons: (1) leaching

is important in regulating nutrient losses from the rooting zone; (2) leaching and exchange reactions make nutrients available for plant uptake by bringing them into solution; (3) soil leaching processes play a large role in regulating the chemistry of water entering aquatic ecosystems.

Conceptually, the rate of soil leaching can be viewed as a function of the level of mobile anions in soil solution (Shilova 1959; McColl and Cole 1968). The cation-exchange capacity of most soils is greater than their anion exchange capacity. Because of this, cation leaching is restricted by exchange reactions and since total cations must equal total anions in solution, it is usually more convenient to consider factors affecting the level of anions in the soil. Shilova (1959) and McColl and Cole (1968) showed that bicarbonate was the major anion involved in soil leaching at their temperate forest sites and deduced that carbonic acid was the major leaching agent.

Carbonic-acid leaching operates as shown in Figure 7.4. Because of respiration and reduced CO_2 diffusivity in the soil, CO_2 pressure builds up relative to the ambient atmosphere. An incoming wetting front encounters this higher CO_2 pressure and may increase it by further reducing CO_2 diffusivity. Carbonic acid forms as CO_2 dissolves. Carbonic acid in turn dissociates into hydrogen (H^+) and bicarbonate ions (HCO_3^-), H^+ displaces cations from exchange sites, and a bicarbonate-cation solution leaves the system.

Soil-leaching processes were investigated at three sites within the coniferous biome and at a tropical site near La Selva, Costa Rica (Johnson et al. 1977). The temperate forest site, the A. E. Thompson site where McColl and Cole (1968) worked, was used as a basis of comparison with a subalpine site at Findley Lake, a high latitude, low-elevation site near Petersburg, Alaska, and the tropical site. At each site, all major anions in solution were balanced against major cations so that the relative roles of various leaching agents could be deduced (Figure 7.5).

Bicarbonate dominated soil solutions at the tropical (La Selva) and temperate (Thompson) sites (Figure 7.5). Because of high soil respiration and CO_2 pressure, soil solution bicarbonate concentrations were greatest at the tropical site (Johnson et al. 1975, 1977). Precipitation was acid (pH 4.5 to 4.8) at the La Selva and Thompson sites, presumably because of inputs of sulfuric acid from nearby SO_2 sources (volcanic at the La Selva site and industrial at the Thompson site).

The pH of solutions rose as they passed through the forest canopy and soil (pH 5.5 to 6.0) presumably by H^+ exchange processes. Increased pH allowed bicarbonate to dominate soil solutions at both sites (Figure 7.5).

Precipitation pH was near normal (5.7) for atmospheric CO_2 levels at the subalpine (Findley Lake) and northern (Alaska) sites, but was reduced to 4.1 to 4.8 in passing through the canopy and forest floor. Coincident with pH lowering, solution color increased and an anion deficit (total cations minus total anions) developed (Figure 7.5). These observations imply that organic acids leaching from the forest canopy and forest floor lower pH and bicarbonate
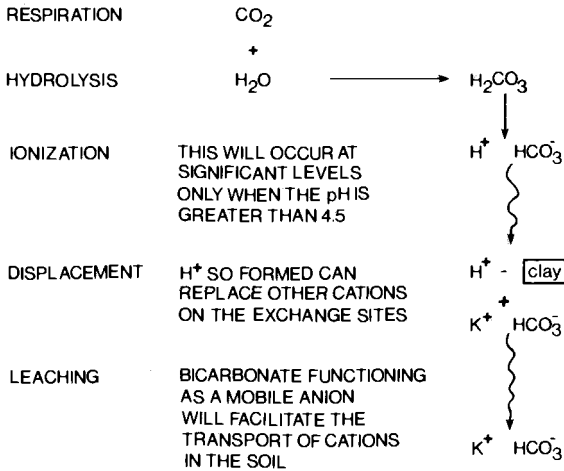
RESPIRATION CO_2

                         +

HYDROLYSIS H_2O $\longrightarrow$ H_2CO_3

IONIZATION   THIS WILL OCCUR AT H^+ HCO_3^-
                       SIGNIFICANT LEVELS
                       ONLY WHEN THE pH IS
                       GREATER THAN 4.5

DISPLACEMENT H^+ SO FORMED CAN H^+ - ⬛ clay
                       REPLACE OTHER CATIONS   +
                       ON THE EXCHANGE SITES K^+ HCO_3^-

LEACHING   BICARBONATE FUNCTIONING
                       AS A MOBILE ANION
                       WILL FACILITATE THE
                       TRANSPORT OF CATIONS K^+ HCO_3^-
                       IN THE SOIL

FIGURE 7.4   *Schematic representation of soil carbonic acid leaching (after Cole et al. 1975).*
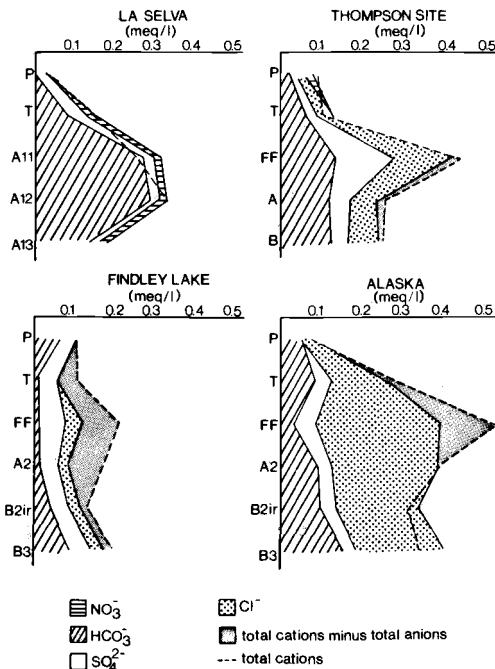

FIGURE 7.5   *Anion and total cation concentrations of solutions from four forest ecosystems (from Johnson et al. 1977).* Key: *P = precipitation, T = throughfall, FF = forest floor; soil horizons are indicated.*

levels and thus account for the anion deficit (Shilova 1959, Johnson et al. 1977). In and below the B2ir soil horizon, where organic acids and their chelated cation associates precipitate (Kononova 1966), pH and bicarbonate concentrations rise. Thus organic acids appear to play a significant role in throughfall and upper soil horizons at these cold sites, both in cation transport and in reducing pH and the role of bicarbonate. In fact, it appears that organic anions dominated upper horizon soil solutions at the subalpine site. Ugolini et al. (1977b) verified the presence of fulvic acids in soil solutions from upper horizons at Findley Lake. Moreover, fulvic-acid concentrations were reduced 60 to 70 percent as soil solutions passed through the B2 soil horizon. The chloride ion dominated solutions at the Alaskan site, presumably because of its proximity to salt water (4 km).

In total, the intensity of carbonic-acid leaching corresponded with the intensity of biological activity at the various sites. In cold forest ecosystems, the production of organic acids served to conserve nutrients by suppressing carbonic-acid leaching within the rooting zone. This is particularly important in cold forest soils since CO_2 pressures can build to very high levels beneath melting snowpacks, creating a great potential for carbonic-acid leaching if pH conditions were to allow it (Marakov 1966, Johnson et al. 1977).

Other Nutrient Outputs

Gaseous inputs and outputs can be very important to the cycling of nitrogen and sulfur in forest ecosystems (Likens et al. 1977; Shriner and Henderson 1978). Unfortunately, these outputs are extremely difficult to measure and quantify, and little is known about their importance in forests of the Pacific Northwest. This is an area that clearly deserves further research.

Another area worthy of more research is migration of particulate matter through soils. A major finding of Ugolini et al. (1977a), working at Findley Lake, was that suspended material in soil solutions reflected the same trends as the dissolved material. They demonstrated that soil leachates in upper horizons contained organic particles associated with aluminum, iron, silicon, and sulfur. The downward transport of these particles was arrested in the B2hir horizon, below which phyllosilicates, quartz, and silicate minerals dominated suspended materials. Their results provided direct evidence for the mechanism of podzolization. They demonstrated the crucial importance of the B2hir horizon as an illuvial horizon for suspended organics and their complexed metals, and as an eluvial horizon for silicates.

Erosion is also an important process in terms of nutrient output from terrestrial systems and input to aquatic ecosystems. Unlike the other processes discussed in this section, erosion is primarily episodic in nature in forest ecosystems and its study must be approached in unique ways. Because of its episodic nature, erosional nutrient losses are difficult to quantify and express on

a yearly basis as other nutrient transfers traditionally are. Researchers at Oregon State University spent a great deal of effort studying erosional processes and their impacts on aquatic ecosystems. This subject is discussed in Chapter 9, which deals with terrestrial/aquatic interface studies.

NUTRIENT CYCLES IN DIFFERENT FOREST ECOSYSTEMS IN THE BIOME IN CONTRASTING ENVIRONMENTS

General Nutrient Cycles in Various Ecosystems in the Biome

Coniferous forests tend to dominate in the biome. These forests occupy a wide range of habitats including wet warm coastal, wet cold subalpine, boreal, and dry hot interior. Moreover, there are also significant areas supporting deciduous forest species such as red alder in the biome, and the nutrient cycles in these ecosystems provide an interesting contrast with those of coniferous ecosystems.

As previously indicated, nutrient-cycling processes are broadly similar in most northwestern ecosystems, but the rates of these processes vary considerably from one ecosystem to another. These variations produce different nutrient distributions among the compartments indicated in Figure 7.1. Also, because nutrient and carbon pools are closely linked, organic matter pools tend to vary from one ecosystem to another.

The abiotic environment an ecosystem occupies has a great influence on the processes controlling nutrient availability to trees and thus will also have a great influence on tree growth. Belowground processes, including decomposition, mineralization and the presence of mycorrhizae, are particularly important in controlling nutrient availability. These are relatively sensitive to differences in abiotic environments. Many ecosystems have developed nutrient-conservation mechanisms, particularly fungal nutrient immobilization and nutrient redistribution inside trees.

We will first examine some contrasting ecosystems. Table 7.2 shows organic-matter and nitrogen distributions for two Douglas-fir ecosystems, a coastal western hemlock/Sitka spruce ecosystem and a subalpine Pacific silver fir ecosystem. Additional data from other ecosystems in the biome are presented in Cole and Rapp (1980). It is immediately apparent that the distribution of organic matter and nitrogen in these ecosystems differs considerably. Although the old- and young-growth Douglas-fir ecosystems have similar foliar biomasses the old-growth ecosystem has considerably more organic matter and nitrogen, particularly in the forest floor and soil. This is largely due to age differences. The other two ecosystems have even greater accumulations of organic matter and nitrogen than the Douglas-fir ecosystems, again with large

TABLE 7.2 *Organic matter and N (in parentheses) distribution (kg/ha) for young- and old-growth Douglas-fir, western hemlock/Sitka spruce, and Pacific silver fir ecosystems.*

	Ecosystem			
Component	36-year-old Douglas-fir (Thompson site)[a]	450-year-old Douglas-fir (H. J. Andrews)[a]	121-year-old western hemlock/Sitka spruce (Cascade Head)[b]	170-year-old Pacific silver fir (Findley Lake)[c]
OVERSTORY				
Foliage	9,097	8,906	8,100	15,700
	(102)	(75)	(85)	(173)
Branches	22,031	48,543	50,600	17,710
	(61)	(49)	(91)	(18)
Stemwood	121,687	472,593	856,900	265,010
	(77)	(189)	(589)	(116)
Bark	18,728	472,593	856,900	38,710
	(48)	(189)	(589)	(13)
Roots	32,986	74,328	186,700	—
	(32)	(162)	(157)	
Total Overstory	204,529	604,370	1,102,300	337,130
	(320)	(375)	(922)	(320)

SUBORDINATE VEGETATION (including lichens)	1,010 (6)	9,864 (58)	4,300 (15)	3,670 (28)
FOREST FLOOR				
Wood	6,345 (14)	55,200 (132)	24,700 (180)	137,710 (104)
Litter and humus	16,427 (161)	43,350 (434)	34,000 (265)	43,520 (571)
SOIL	111,552 (2,809)	79,250 (4,300)	776,000 (34,900)	243,960 (15,855)
TOTAL ECOSYSTEM	339,863 (3,310)	792,034 (5,300)	2,128,300 (36,282)	765,990 (16,878)

[a]Grier et al., 1974.
[b]Grier, 1976.
[c]Turner and Singer, 1976.

accumulations in the soil. The reasons for these similar accumulations, however, are different in the coastal hemlock/spruce ecosystem than in the subalpine ecosystem. The coastal forest is considerably more productive than the subalpine forest and as a result the overstory biomass accumulation is greater. This, of course, results in a greater litterfall (Table 7.3) and significant litter accumulation in spite of higher decomposition rates. Dead roots also contribute a considerable amount of organic matter, especially to the soil. Once on the forest floor, the litter is subject to decomposition and mineralization and this critical process determines the rate of accumulation of organic matter and nitrogen in the soil. Although decomposition rates are faster in the western hemlock ecosystem than the Pacific silver fir ecosystem the greater productivity in the hemlock system offsets this, resulting in large soil accumulations. Nitrogen accumulations in the hemlock soil are about an order of magnitude higher than those in the Douglas-fir soils.

Contrasts between the red alder and Douglas-fir ecosystems are interesting because these species occupy similar habitats and soils. Table 7.2 and 7.4 compare nutrient distributions in adjacent alder and Douglas-fir stands. While the Douglas-fir ecosystem is of similar age to the red alder ecosystem, it has accumulated only half the nitrogen and slightly less organic matter than the red alder ecosystem. The additional nitrogen in the red alder stand appears to result from nitrogen fixation by symbionts associated with alder roots. Nitrogen returned to the forest floor via litterfall is considerably greater in the red alder ecosystem, as are losses from the forest floor (Tables 7.3 and 7.4).

Nitrogen cycling strategies are thus different in the red alder and Douglas-fir ecosystems and also among coniferous ecosystems. This implies that the critical belowground processes influencing nutrient availability, including N inputs, decomposition, mineralization, nutrient immobilization, mycorrhizal uptake, and redistribution within trees also vary from ecosystem to ecosystem.

Critical Processes Influencing Nutrient Availability

Nitrogen fixation was discussed previously and will not be elaborated upon. Rates of litter decomposition and nitrogen mineralization in coniferous biome ecosystems, however, do need further discussion. Decomposition rates of various litter components including needles, leaves, twigs, cones, roots, and wood, and the factors controlling them, were assessed in various ecosystems.

After two years of decomposition, k values (decomposition constants based on the equation $x = x_o e^{-kt}$; Olson 1963) were 0.44 for red alder leaves and 0.42 and 0.38 for Douglas-fir and western hemlock needles, respectively, at the Thompson research site (Edmonds 1980). In a variety of Douglas-fir ecosystems in Oregon and Washington, k values for needles ranged from 0.22 to 0.56 (Fogel and Cromack 1977; Edmonds 1979) with highest values on

TABLE 7.3 *Nitrogen transfers (kg·ha⁻¹·yr⁻¹ in young- and old-growth Douglas-fir, mature western hemlock/Sitka spruce and mature Pacific silver fir ecosystems.*

	Ecosystem			
Component	42-year-old Douglas-fir (Thompson site)[a]	450-year-old Douglas-fir (H. J. Andrews)[b]	121-year-old western hemlock/Sitka spruce (Cascade Head)[c]	170-year-old Pacific silver fir (Findley Lake)[d]
INPUT (precipitation and dry fall)	1.67	2.0	5.5	1.3
RETURN TO FOREST FLOOR				
Throughfall plus stemflow	0.53	3.4	—	1.3
Litterfall	25.4	25.6	—	16.3
Total	25.93	29.0	35.8	17.6
WITHIN VEGETATION				
Requirement	45.8	33.3	39.9	23.1
Redistribution	20.7	18.5	0.0	12.4
Uptake	25.1	14.8	39.9	11.9
SOIL TRANSFERS				
Loss from forest floor	7.3	4.7	—	10.3
Loss from rooting zone	3.4	1.5	1.5–2.5	2.7

[a] Turner 1975.
[b] Sollins et al. 1980.
[c] Grier 1976.
[d] Turner and Singer 1976.

TABLE 7.4 *Organic matter and N budgets and N transfers in a 34-year-old red alder ecosystem at the Thompson site.*

Component	Budgets (kg/ha)	
	Dry Weight	N
OVERSTORY		
Foliage	4,060	100
Branches	20,530	23
Stemwood	135,150	144
Bark	23,550	165
Roots	35,230	176
Total Overstory	209,800	589
SUBORDINATE VEGETATION	9,530	103
FOREST FLOOR		
Wood	27,740	264
Leaves	13,040	195
Humus	21,220	361
Fern Branch	4,350	57
Total Forest Floor	66,350	877
SOIL	158,520	5,450
TOTAL ECOSYSTEM	444,200	7,019

	N Transfers $(kg \cdot ha^{-1} \cdot yr^{-1})$
LITTERFALL	
Tree: Foliage	61
Wood	18
Stem	8
Understory	24
Total Litterfall	111
LEACHING	
Precipitation	1.7
Stemflow	0.1
Throughfall	8.8
Total Return to Forest Floor	122.0

moister sites. Decomposition of Douglas-fir needles was also studied in differing habitats in four communities dominated by an overstory of old-growth Douglas-fir at the Andrews site (Fogel and Cromack 1977). Rates of needle decomposition shown in Table 7.5 were greatest in the cool moist habitat ($k = 0.28$) and least in the warm-dry habitat ($k = 0.22$). Slow decomposition rates were also observed for Pacific silver fir needles at the cold Findley Lake site ($k = 0.31$), but decomposition did occur under snow (Vogt et al. 1980; Edmonds 1980).

TABLE 7.4 *Continued.*

	N Transfers $(kg \cdot ha^{-1} \cdot yr^{-1})$
LEACHED FROM FOREST FLOOR	15.0
REQUIREMENT	
Uptake: Foliage	78.8
Branches	0.8
Wood	5.3
Bark	7.1
Understory	21.8
Total Uptake	113.8
REDISTRIBUTION	
Tree: Foliage	29.9
Branches	1.7
Wood	10.7
Bark	13.5
Understory	12.2
Total Redistribution	68.0
TOTAL REQUIREMENT	
Foliage	99.9
Branches	2.5
Wood	16.0
Bark	20.6
Understory	34.0
Total Stand Requirement	173.0

TABLE 7.5 *Decomposition constants (k, yr^{-1}) for Douglas-fir litter components in different environments in the H. J. Andrews Forest, Oregon, 1973–1975.[a]*

	Site and community[b]			
	——————Increasingly warmer and drier——————▶			
	Tshe/[c] Pomu– Oxor	Tshe/ Rhma– Bene	Tshe/ Cach	Psme/ Hodi
Needles	0.28	0.28	0.24	0.22
Branches	0.07	0.09	0.06	0.08
Cones	0.06	0.07	0.06	0.08
Bark	0.03	0.04	0.03	0.01

[a]After Fogel and Cromack 1977; based on 2 years' cumulative weight loss.
[b]Means of two sites per community except for Psme/Hodi.
[c]Tshe = *Tsuga heterophylla;* Pomu = *Polystichum munitum;* Oxor = *Oxalis oregena;* Rhma = *Rhododendron macrophyllum;* Cach = *Castanopsis chrysophylla;* Psme = *Pseudotsuga menziesii;* Hodi = *Holodisus discolor.*

Both temperature and moisture were found to regulate litter decomposition rates. Moisture was particularly limiting in Douglas-fir ecosystems, with the effect being more pronounced in Oregon than Washington. Temperature plays a more important role in cold high-altitude ecosystems. Little decomposition occurred in the summer in many ecosystems in the biome due to dry conditions.

The chemical constituents of litter also influence decomposition rates, particularly lignin content. As lignin values increase, k values decrease. This is illustrated in Table 7.5 for Douglas-fir branches, cones, and bark. Initial lignin content appeared to be better related to woody litter decomposition rates than C/N ratios (Fogel and Cromack 1977). Edmonds (1980), however, found that needle and leaf decomposition rates were better related to initial C/N ratios than lignin content.

Data on the decomposition rates of fine roots and logs in the biome were also obtained. The decomposition rate for Douglas-fir fine roots was similar to that for needles ($k = 0.24$). For Douglas-fir logs at the Andrews site, decomposition rates were very slow, with k values ranging from 0.008 to 0.043 depending on the state of log decay. These values are similar to those found by Grier (1978b), who found an average k value of 0.012 for western hemlock logs in a coastal site at Cascade Head in Oregon. Logs, of course, have a high lignin content.

Since litter-decomposition rates varied from one ecosystem to another it is not surprising that nitrogen mineralization rates also varied (Table 7.6). Nitrogen was most rapidly released from red alder leaves, with next most rapid release occurring from Douglas-fir needles. On the other hand, nitrogen accumulated in western hemlock and Pacific silver fir needles during two years of decomposition. Nitrogen mineralization rates were related to C/N ratios, with mineralization occurring when ratios fell below about 25.0 to 30.1 (Edmonds 1979; 1980). Above this ratio microbial immobilization occurred. The nitrogen content of decaying western hemlock logs also increased with time (Grier 1978b). Even after forty years, log nitrogen contents were higher than those of freshly fallen logs. This increase may result from nitrogen fixation (Cornaby and Waide 1973; Aho et al. 1974); from translocation of nitrogen from adjacent litter by fungi inhabiting the fallen logs; or from inputs to log surfaces through litterfall and throughfall.

Fungal immobilization by decomposer and mycorrhizal fungi and nutrient redistribution within the tree are important processes in retaining nutrients within ecosystems as discussed below.

Critical Processes Influencing Nutrient Retention in Ecosystems

Fungi dominate the microflora in coniferous forests and they play important roles in cycling and conserving nutrients. Fungal immobilization of nutri-

TABLE 7.6 *Carbon-to-nitrogen ratios and percentage of initial N remaining in red alder leaves and Douglas-fir and western hemlock needles at the Thompson Research Center, in Pacific silver fir needles at Findley Lake, and in Douglas-fir needles at the H. J. Andrews Forest after 1 and 2 years in litterbags.*

Site	Community[a]	Litter species	C/N ratio after 1 yr	C/N ratio after 2 yr	Percent of initial N remaining after 1 yr	Percent of initial N remaining after 2 yr
A. E. Thompson, Wash.[b]	Alru/Pomu	Red alder	19	20	74	67
	Psme/Gash	Douglas-fir	25	24	108	83
	Tshe/Pomu	Western hemlock	51	37	103	103
Findley Lake, Wash.[b]	Abam-Tsme/ Vade	Pacific silver fir	34	28	106	126
H. J. Andrews, Oreg.[c]	Tshe/Rhma-Bene	Douglas-fir	42	37	110	100

[a] Alru = *Alnus rubra;* Gash = *Gaultheria shallon;* Abam = *Abies amabilis;* Tsme = *Tsuga mertensiana;* Vade = *Vaccinum deliciosum;* Bene = *Berberis nervosa;* for other abbreviations see Table 7.5.
[b] Edmonds, 1980.
[c] K. Cromack, unpublished data.

ents varies from ecosystem to ecosystem in the biome. Immobilization occurs when nutrients are incorporated into fungal biomass, as during periods of active growth. Vogt and Edmonds (1980) found greater fungal immobilization of nitrogen, phosphorus, calcium, and potassium occurring in lowland western hemlock and subalpine Pacific silver fir ecosystems than in lowland Douglas-fir and red alder ecosystems. Maximum immobilization occurred in winter and spring and appeared to correlate with active fungal growth. Immobilization in these seasons may serve to prevent leaching losses during the wet period of the year, particularly during snowmelt. Phosphorus may also be conserved in terrestrial ecosystems as a result of calcium oxalate production by fungi (Graustein et al. 1977).

Although mycorrhizae received only limited attention from biome researchers, their importance and the importance of the belowground ecosystem should not be underestimated. Mycorrhizae are important in nutrient immobilization and tree uptake. Fogel and Hunt (1979) recently pointed out their importance in Douglas-fir ecosystems.

Another method that trees use to conserve nutrients is internal translocation. This was amply demonstrated by Turner (1977), who observed the effects of soil nitrogen availability on nitrogen transfers in a low-site-quality, forty-

two-year-old Douglas-fir stand. He used a number of treatments to vary nitrogen availability. The five treatments consisted of 0 (control), 220, and 880 kg/ha of urea-N; a sugar and sawdust application; and a sugar, sawdust, phosphorus, potassium, sulfur, and calcium treatment. The last two treatments were intended to stress the nitrogen supply by stimulating microorganism activity and possibly inducing growth responses to other nutrients.

In the 880 kg/ha nitrogen treatment, growth requirements were entirely met by uptake and internal translocation became negative. Nitrogen uptake exceeded growth requirement thus nitrogen accumulated in older tissue. In the 220 kg/ha nitrogen treatment, growth nutrient requirement was greater than uptake and the difference was provided by translocation. The difference between requirement and uptake increased in the control and carbohydrate treatments. This study indicates that internal translocation provides a mechanism by which trees can maximize growth under nutrient-poor conditions.

On a broader, long-term scale, one might expect that forests in habitats where nitrogen mineralization is slow might slowly accumulate large foliar nitrogen reserves. These reserves would provide for within-tree translocation during periods of low nitrogen availability, for example, during unusually dry or cold growing seasons, when decomposition and nitrogen mineralization rates are very slow. The absolute values of foliar nitrogen pools, however, may not be controlled by forest floor nitrogen availability. Grier and Running (1977) showed that leaf-area index is strongly related to site water balance for a variety of ecosystems in Oregon. Since foliar biomass is closely related to leaf-area index, and since foliar nitrogen concentration varies much less than biomass, it would seem that foliage nitrogen content is dictated by site water balance.

Some of Grier and Running's data are shown in Figure 7.6 in the form of a transect from the wet Oregon coast to the very dry eastern slope of the Cascade Mountains. Foliar biomass and nitrogen content are quite high on the coast, but they drop off in the drier Willamette Valley, which lies in the rain shadow of the Coast Range. In the wetter, west slopes of the Cascades, foliar biomass and nitrogen content increase again and then rapidly drop on the dry, east slopes of the Cascades.

To properly assess foliar nitrogen reserves, however, total foliage nitrogen content must be viewed in terms of the flux into and out of that pool. One way to approach this is to calculate mean residence times (MRT) in years as indexes of relative foliar reserves. This is done by dividing total foliage content by litter plus throughfall transfer. Similarly, forest floor MRT values (calculated in a similar way) can serve as indexes of decomposition and nitrogen mineralization.

Forest floor MRT is not exclusively regulated by climatic conditions. Lignin content and nitrogen status have a strong effect on decomposition rate, as shown earlier. For instance nitrogen MRT values are different in the Douglas-fir and red alder stands at the Thompson site (6.5 and 1.5 years, respectively) even though the stands are adjacent to each other and are subject to the same climatic conditions. While it is obvious that climatic conditions
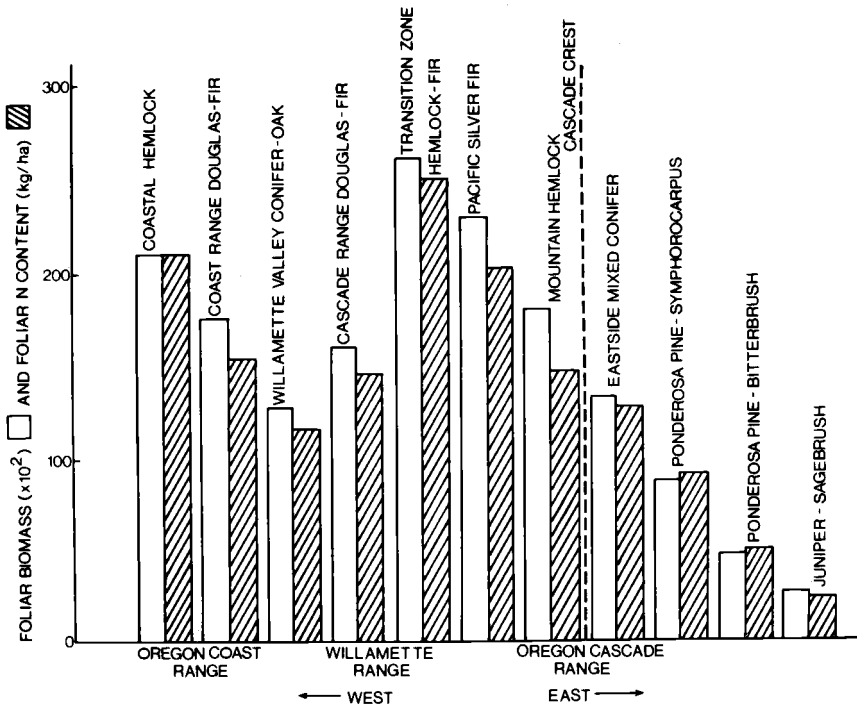
FIGURE 7.6   *Foliage biomass and N content along a transect from eastern Oregon to the Oregon coast (after Grier and Running 1977).*

affect decomposition and N mineralization rates, neither forest floor nor foliar MRT was well correlated with mean annual temperature or precipitation ($r^2 < 0.5$ in both cases). Thus, in this exercise, we view forest floor MRT as an independent variable (influenced by climatic conditions and species differences) and hypothesize that foliar MRT is correlated with it. Both nitrogen and forest floor MRT values for all the forest ecosystems studied in the coniferous forest biome are plotted in Figure 7.7. Although these ecosystems encompass a wide range of species and climatic conditions (deciduous and coniferous, subalpine to coastal), it is clear that good correlations exist. This does not prove cause and effect, but it supports the hypothesis that forest floor nitrogen availability affects the way trees handle foliar nitrogen reserves.

NUTRIENT ACCUMULATION AND CYCLING DURING STAND DEVELOPMENT

Douglas-Fir Ecosystems

It is clearly not feasible to measure productivity and nutrient cycling during the development of a single stand without the devotion of many generations of
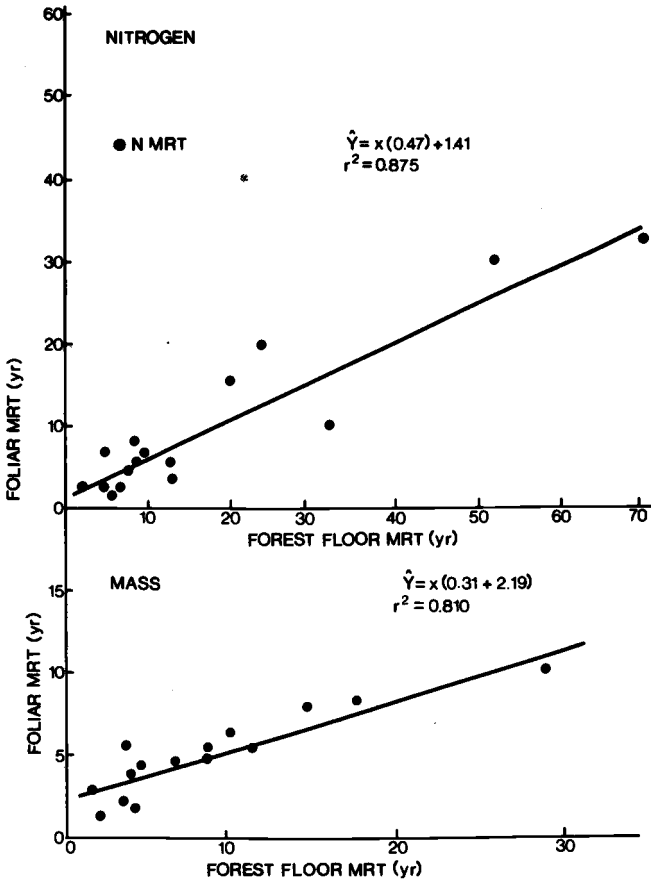
FIGURE 7.7 *Relation between foliar and forest floor mean residence time (MRT) among various deciduous and coniferous stands in a climatic-geographic gradient in the coniferous forest biome.*

researchers. Alternatively, stand development patterns can be inferred by studying stands of different ages within the same geographic, edaphic, and physiographic setting. Such an analysis was conducted in a series of low-site-quality Douglas-fir stands at the Thompson site (Long and Turner 1975, Turner and Long 1975, Cole and Rapp 1980). This analysis revealed many parallels between organic matter and nutrient accumulation patterns during Douglas-fir stand development.

A full discussion of organic matter production and accumulation during stand development is given in Chapter 5. Here accumulation of nutrients during stand development is compared with that of organic matter. Emphasis is on nitrogen, potassium, and calcium. Also considered are changes in key processes during this development sequence.

The accumulation of nitrogen and potassium within the foliage (Figure 7.8a) closely follows biomass accumulation described in Chapter 5, indicating that for more mobile elements (in this case nitrogen and potassium) a steady-state condition parallel to that found for biomass is achieved. Mobility of these two elements originates from two quite separate processes. Nitrogen is extensively translocated within the tree from older to current foliage while potassium is leached from foliage by throughfall. In the case of the immobile nutrient calcium, accumulation continues for at least the first seventy-five years of development.
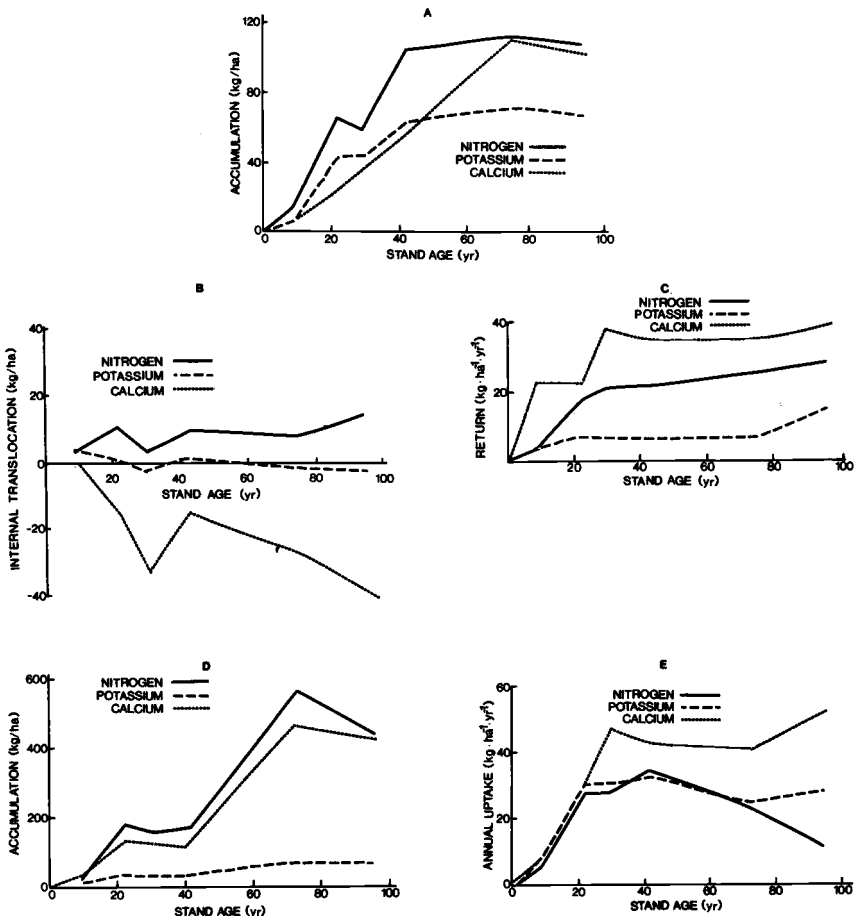

FIGURE 7.8   (A) Accumulation in foliage; (B) internal translocation; (C) return to the forest floor by both litterfall and crown leaching; (D) accumulation in the forest floor; and (E) annual uptake of N, K and Ca during Douglas-fir stand development (from Cole et al. 1968). Internal translocation was calculated using current tissue N concentrations minus N concentration in older tissue. Corrections were made for leaching losses.

There appears to be an increase in translocation of nitrogen with age, at least in low productivity, nitrogen-poor Douglas-fir ecosystems (Figure 7.8b). From these data it can be hypothesized that the Douglas-fir forest becomes significantly more efficient in nitrogen utilization as it matures. In that nitrogen is systematically being withdrawn from the cycling process and stored in such tissue as the bole and the bark, this increased efficiency could be of real nutritional importance to the trees in nitrogen-limited ecosystems.

Internal translocation of potassium and calcium is less than that for nitrogen. Large quantities of potassium are leached from the foliage by precipitation before translocation from the older to current tissue has occurred. Thus potassium requirements appear to be met mainly by uptake. Calcium, on the other hand, is largely incorporated in cell wall material. Thus there is no calcium transfer from older to younger foliage.

The increased amount of calcium in foliage of older stands appears to be related to an increase in needle retention time as stands age, thus allowing more time for calcium accumulation to occur in older foliage. Evidence for this increase in needle retention shows up in the leaf litter/standing foliar biomass ratio, which is low for younger stands and high for older ones. The twenty-two-year-old stand appears to retain needles for only two to three years while the ninety-five-year-old stand's retention time is nearer to six years.

The rate of litterfall and crownwash return in a Douglas-fir age sequence follows canopy development, reaching a maximum with crown closure, then remaining at nearly this level (Figure 7.8c).

There is a general pattern of high nutrient return by understory vegetation during the initial twenty to twenty-five years of the stand, which corresponds to the period when this part of the vegetation plays its most dominant role in the structure of the ecosystem (Chapter 5). With the closure of the forest canopy and corresponding decrease in the biomass of the understory species, there is a corresponding decrease in return from the understory species.

As the stand matures, the amount of woody litterfall increases even though leaf litter may remain relatively constant. Up to 90 percent of annual litterfall in a 450-year-old stand in Oregon consisted of wood, including tree stems (Grier and Logan 1977) while about 50 and 25 percent of total litterfall was woody in the 95- and 22-year-old stands at the Thompson site. Since wood has a low nutrient content, total nutrient return should not increase as rapidly as total organic matter return to the forest floor. This widens the C:N ratio and slows nutrient mineralization.

Needle decomposition rates increase until canopy closure and then slowly decrease (Table 7.7; Edmonds 1979). The k values determined after one year were statistically different at the 95 percent level among stands, but there were no differences in decomposition rates based on two years' data. This trend for decomposition rates is closely related to the annual ecosystem productivity in these stands as determined by Turner and Long (1975). The stands with the highest annual productivity also had the largest k values.

As shown in Chapter 5, biomass of woody tissue increases with time and

TABLE 7.7 *Decomposition rates of Douglas-fir needles in relation to stand age at the A. E. Thompson Research Center, Washington.*

Stand Age (yr)	Decomposition constant, k^a (yr^{-1})	
	1 year	2 year
11	0.48	0.41
22	0.69	0.56
44	0.57	0.49
75	0.53	0.53
97	0.56	0.40

[a]Based on the exponential model $x = x_0 e^{-kt}$ (Olson 1963)

will presumably continue to do so for at least several hundred years (Grier et al. 1974). Nutrient accumulation in the forest also increases as the total forest floor biomass increases (Figure 7.8d). One would expect this since the release of nitrogen and calcium is dependent on the decomposition of the forest floor. The accumulation rate for potassium is markedly lower, primarily because potassium is present in ionic form, not as part of organic structures. Thus its retention is dependent on ion exchange, not decomposition. These data suggest that a nitrogen deficiency could be progressively induced with time due to accumulation in the forest floor.

Since forest floor biomass and nutrient content increase during Douglas-fir stand development, it is interesting to speculate as to whether the forest floor is a source or sink of nutrients. Gessel and Balci (1965) speculated that the forest floor is a significant source of nitrogen for tree uptake in this region.

Calculations were made to estimate the proportion of nitrogen uptake derived from forest floor. This was done by assembling nutrient budgets from measured fluxes and changes in nutrient content in the age-sequence of Douglas-fir stands studied at the Thompson site. The results of this calculation suggest that an increasing proportion of uptake is being derived from the forest floor as stand age increases. Up to age 20, 55 percent of the nitrogen taken up is derived from the forest floor, but at age 70 almost 100 percent is taken up from the forest floor. Douglas-fir seems to become less and less dependent on the mineral soil for nutrient requirements as the stand matures and relies more on internal cycling processes and uptake from the forest floor.

The maximum annual uptakes of nitrogen, calcium, and potassium correspond closely to maximum development of the crown (Figure 7.8e). The annual uptake of nitrogen begins to decrease, however, at approximately forty years. By the time the stand is ninety-five years old, annual nitrogen uptake has decreased from a maximum of 40 kg/ha (at forty years) to 17 kg/ha. It is not known whether this reduced uptake pattern is due to decreased nutrient demands or decreased soil supply. In either case, the stand must continue to meet

its requirements. This is accomplished in two ways: by an increase in needle retention time and by a significant increase in internal translocation.

The accumulation patterns for the three nutrient elements within the understory closely follow that of understory biomass. Maximum nutrient accumulation is reached between ten and twenty-two years in age and then rapidly decreases as the tree canopy closes (Figure 7.9). A second period of biomass and nutrient accumulation occurs in the understory vegetation when the canopy begins to open in later years. Understory biomass in the 450-year-old Douglas-fir forests of watershed 10 was actually greater in some habitats than that found in young stands (Grier and Logan 1977).

Extrapolation to Other Forest Types

The patterns observed in the Douglas-fir age sequence analysis can be used as a model for other ecosystems as well. It is obvious, however, that two stands of the same age can be at very different stages of stand development. For example, Turner et al. (1976) compared nutrient distribution and transfers in a thirty-four-year-old red alder stand with those in a nearby thirty-six-year-old Douglas-fir stand. They found that tree biomass was comparable in the two stands at this age, but the nitrogen content of the alder was higher, presumably because of its nitrogen-fixing capabilities. The understory component was greater in the thirty-four-year-old alder stand than in the thirty-six-year-old Douglas-fir stand because the two stands appear to be in different stages of development. A thirty-four-year-old alder stand in this region is fully mature and possibly overmature. In contrast, Douglas-fir stands of this age are in their period of most rapid growth. The fact that alder is deciduous whereas Douglas-fir is evergreen may account for some understory differences, but comparisons with understory measurements made in 1963 (at age twenty-four) on the same stand (Balci 1964) indicate that the understory biomass at that time was smaller, more nearly comparable with that of the then twenty-six-year-old Douglas-fir stand. The authors postulate that the thirty-four-year-old red alder stand is at a stage of development somewhat analogous to that of the 450-year-old Douglas-fir stand. Since the life span of alder is about one-tenth that of Douglas-fir, a thirty-four-year-old alder stand might be compared to a 340-year-old Douglas-fir stand. Viewed this way, the development of these two stand types would proceed as shown in Figure 7.10.

EFFECTS OF SITE DISTURBANCE ON NUTRIENT CYCLING AND ITS MANAGEMENT IMPLICATIONS

To evaluate and attempt to predict the effects of various site manipulations on nutrient cycling, we must consider the processes involved in nutrient trans-
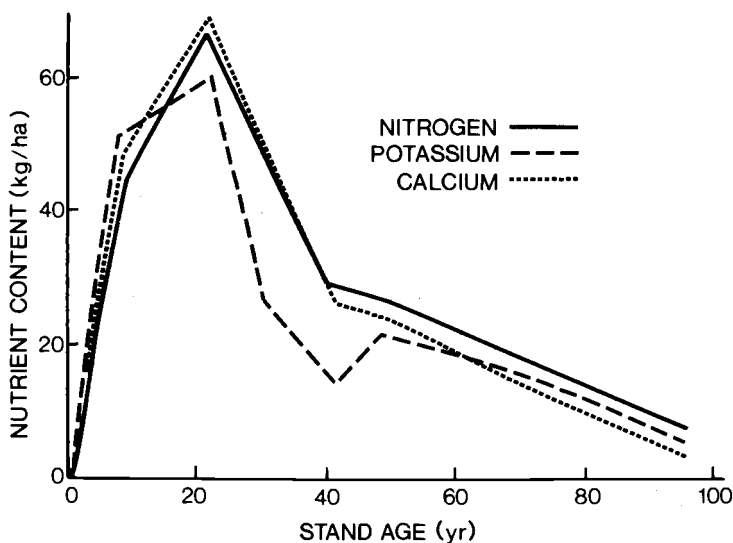
FIGURE 7.9 *Accumulation of N, K, and Ca in the understory vegetation of various aged stands of Douglas-fir (after Cole and Rapp 1980).*
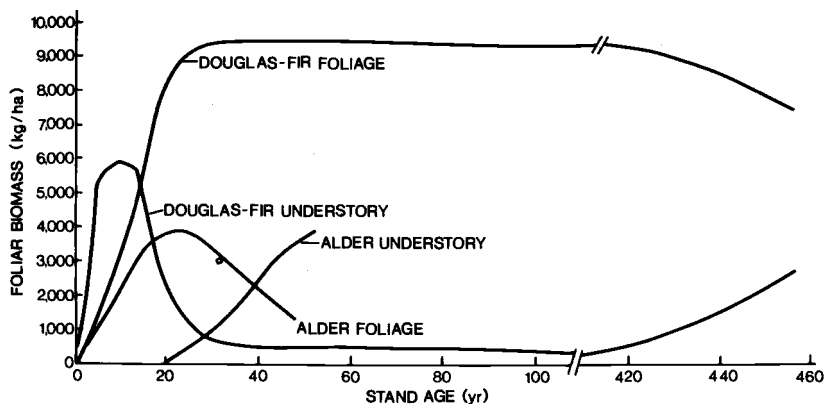

FIGURE 7.10 *Changes in overstory and understory foliar biomass for Douglas-fir and red alder during stand development (after Turner et al. 1976).*

fer. Very seldom are considerations of pool sizes and nutrient budgets useful in themselves in predicting or evaluating the effects of manipulations. An exception to this generality is clearcutting, where a nutrient pool, the tree bole, is removed from the site directly. Thus the following discussion focuses on the processes described previously and the way they are affected by manipulations.

Effect of Harvesting on the Nutrient Capital
of an Ecosystem

The most obvious immediate effect of clearcutting on nutrient distribution is the removal of part of one of the nutrient pools, that is, the trees. Assuming that all of the foliage is left on a site, clearcutting results in the removal of only a small percentage of the nutrient capital of a site, provided the site isn't burned. This is clearly illustrated in Table 7.8 for nitrogen for seventeen ecosystems in Washington and Oregon.

There is a further increase in net losses of nitrogen when the entire above-ground portion of the tree is removed, such as is done in some logging opera-

TABLE 7.8 *Ecosystem nitrogen capital remaining after bole only, whole tree and total vegetation removal in forest ecosystems in Washington and Oregon.*

				% Remaining		
Age (yr)	Ecosystem Species	State	Ecosystem Total (kg/ha)	Bole only removal[a]	Whole tree removal[b]	Vegetation removal[c]
9	Douglas-fir	WA	3017	99.6	98.9	97.4
22	Douglas-fir	WA	3281	95.6	93.1	91.0
30	Douglas-fir	WA	3232	95.6	93.2	91.7
30	Douglas-fir	WA	3477	95.1	90.9	90.1
42	Douglas-fir	WA	3366	93.3	89.4	88.3
49	Douglas-fir	WA	3538	95.3	90.6	89.9
73	Douglas-fir	WA	3751	95.4	90.7	90.2
95	Douglas-fir	WA	3686	92.5	87.9	87.7
95	Douglas-fir	OR	10805	97.5	95.2	95.1
130	Douglas-fir	OR	8775	97.9	95.6	95.5
450	Douglas-fir	OR	5725	93.9	90.1	89.9
30	Western hemlock/ Sitka spruce	OR	33781	99.5	98.6	98.6
121	Western hemlock/ Sitka spruce	OR	36315	98.4	98.0	97.9
130	Noble fir	OR	15500	97.5	96.0	96.0
130	Mountain hemlock/ silver fir	OR	6529	97.2	94.0	93.7
23	Pacific silver fir	WA	2868	99.0	94.1	93.1
170	Pacific silver fir/ Mountain and western hemlock	WA	4895	96.9	93.1	92.8

[a] Tree stems removed to a minimum top diameter inside bark of 10 cm.

[b] Tree stems, branches, foliage and reproductive structures removed from site for all trees greater than 5-cm-diameter breast height (1.4 m above soil surface).

[c] All living vegetation removed to surface of litter layer.

tions in the Pacific Northwest where "whole-tree yarding" is conducted so that tops and limbs may be more efficiently removed at a central landing. Almost 10 percent of the ecosystem nitrogen capital may be removed in some cases (Table 7.8). Only a small further increase is incurred if all living vegetation is removed to the surface of the litter layer.

The concept of whole-tree logging and almost total utilization of logging residues will, if adopted, have some impact on future forest growth, especially on those forest soils with a relatively low supply of essential elements. The reduced site fertility resulting from removal of forest litter for farm-use purposes is still observable in European forests.

In some soil systems this loss can be replaced by weathering or atmospheric input but in others alternative additions may need to be considered. Total loss from the system is determined not only by removal in a given harvest but also by frequency of harvest. Therefore areas managed under a so-called energy plantation concept may have more serious problems than those under less intensive management schemes.

It can be concluded that net loss from the system due to harvesting is nearly independent of the rotation period but highly dependent on degree of utilization of the trees. In general, extending the rotation period does not proportionally increase total elemental loss; however, increasing harvest removal from bole only to whole tree typically increases removals to the point where they become a significant portion of the total nitrogen capital of the ecosystem.

Calculations can be made for any stand where nutrient distribution data are available. These data are available for most major timber species in the biome. For example, in the subalpine area of the state of Washington, harvesting of the 170-year-old Pacific silver fir *(Abies amabilis)* studied at Findley Lake would result in a nitrogen loss of 130 kg/ha if only the boles were removed (Turner and Singer 1976). This is similar to removals estimated for Douglas-fir. With a rotation of one hundred years for these sites and a net annual addition from precipitation of 1 kg/ha, nitrogen loss from harvesting would nearly balance annual additions.

Total tree removal from these higher elevation sites would result in greater loss. These losses would also be greater than estimated for lower elevation Douglas-fir stands since nutrient-rich foliage biomass is appreciably greater. Total tree removal in Pacific silver fir stands would cause a total nitrogen loss of 330 kg/ha (Turner and Singer 1976), an annual net loss from the ecosystem over a 100-year rotation of 2.3 kg/ha. Thus total tree harvesting at these sites should result in a significant increase in nitrogen loss.

Similar calculations can be made for other nutrient elements. For Douglas-fir stands the losses of calcium, magnesium, and potassium are greater than those for nitrogen. Whether or not these ecosystems actually lose these quantities of nutrients from the available pool is largely dependent on the rate of soil mineral weathering. While the stands do not currently display any deficiency symptoms, losses of these nutrients, resulting from harvesting, could result in

deficiencies in future rotations. This is especially true in the case of potassium, where exchangeable potassium appears to be at a minimal level to meet uptake requirements and in view of the fact that weathering is apparently not keeping pace with uptake and leaching (see Table 7.1).

Effect of Harvesting on Soil Leaching

The input of foliage and branches to the forest floor compartment dramatically increases the carbon and nutrient content of that compartment. Coupled with an increase in surface temperature, this usually leads to accelerated decomposition (Gessel and Cole 1965). This, in turn, should lead to increased CO_2 evolution and carbonic acid production in soil solution. Experience showed, however, that increased ion leaching occurred only in the upper few centimeters of the soil (Gessel and Cole 1965). This was due to the more acid lower soil horizons donating hydrogen ions to solution, reducing bicarbonate concentration, and causing associated cations to occupy exchange sites (Cole et al. 1975).

Results to date from an experimental clearcut in the H. J. Andrews Forest indicate that immediately following cutting the total loss of nitrogen from the terrestrial system increased by a factor of 4.5. Particulate nitrogen, however, accounted for 72 percent of the loss, dissolved organic nitrogen accounted for 26 percent, and nitrate accounted for only 2 percent. Researchers in Oregon postulate that particulate nitrogen loss will rapidly diminish as the site stabilizes, but that dissolved organic nitrogen loss may remain high for longer periods (up to five years, according to studies by R. L. Fredriksen).

The patterns of dissolved nitrogen loss are interesting in themselves. It was found that losses varied considerably from site to site within the watershed (Figure 7.11). The greatest loss occurred from a toe slope with relatively sparse postlogging vegetative cover, but in the riparian zone between this site and the seep waters entering the stream a great deal of the nitrogen was reabsorbed. As a result, the riparian zone at the Andrews site has received intensive study. Results are presented in Chapter 9.

In a study on the effects of clearcutting, Likens et al. (1969) found large cation fluxes associated with nitrification and nitrate leaching in the Hubbard Brook watershed in New Hampshire. Leaching losses in both the Washington and Oregon studies reported here were much less dramatic. Factors affecting nitrification clearly deserve further study, however, especially in regard to clearcutting.

Effects of Fire

Fire, whether it be a wildfire or a slash burn used in forest management, has a strong influence on nutrient losses from an ecosystem. These losses are
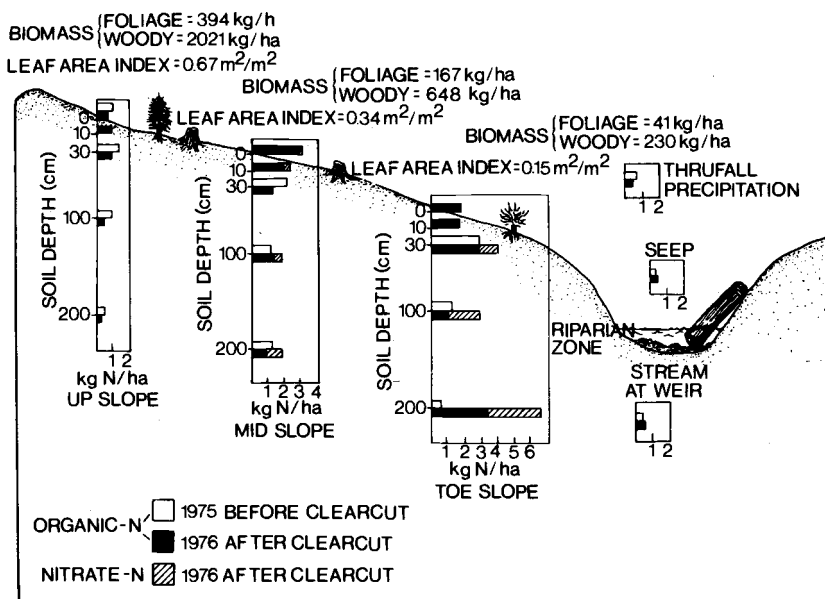
BIOMASS {FOLIAGE = 394 kg/h
{WOODY = 2021 kg/ha
LEAF AREA INDEX = 0.67 m²/m²

BIOMASS {FOLIAGE = 167 kg/ha
{WOODY = 648 kg/ha
LEAF AREA INDEX = 0.34 m²/m²

BIOMASS {FOLIAGE = 41 kg/ha
{WOODY = 230 kg/ha
LEAF AREA INDEX = 0.15 m²/m²

SOIL DEPTH (cm)
UP SLOPE   kg N/ha   1 2

SOIL DEPTH (cm)
MID SLOPE   kg N/ha   1 2 3 4

SOIL DEPTH (cm)
TOE SLOPE   kg N/ha   1 2 3 4 5 6

THRUFALL PRECIPITATION   1 2
SEEP   1 2
RIPARIAN ZONE
STREAM AT WEIR   1 2

ORGANIC-N ☐ 1975 BEFORE CLEARCUT
           ■ 1976 AFTER CLEARCUT
NITRATE-N ▨ 1976 AFTER CLEARCUT

FIGURE 7.11 *Profile of N content in a hillslope transect in watershed 10 and in throughfall precipitation, seep water, and stream water at the weir. Biomass and leaf area index data pertain to postlogging residual vegetation (F. M. McCorison pers. comm.).*

largely due to volatilization, particularly in the case of nitrogen, and increased leaching losses.

Table 7.9 shows nitrogen losses from Douglas-fir ecosystems due to slash burning and wildfire. Also included for comparison are nitrogen losses in undisturbed and clearcut-only ecosystems. There is no nitrogen loss from the undisturbed old-growth ecosystem; in fact nitrogen is accumulating. There is an increasing loss of nitrogen in the progression from a clearcut-only ecosystem (3.8 percent of the ecosystem total nitrogen) to a clearcut and slash-burned ecosystem (9.5 percent loss) to an ecosystem that has experienced an intense wildfire (27 percent loss).

Fire is an important decomposition agent in natural ecosystems and it results in considerably more nitrogen loss from an ecosystem than clearcutting alone. The practice of using fire as a management tool for slash burning needs to be closely examined in relation to its impact on nitrogen losses and tree productivity.

Urea-N Fertilization

The effects of urea fertilization have been studied in some detail prior to and during the IBP. Douglas-fir growth responses to nitrogen have been docu-

TABLE 7.9   *Total annual N losses from undisturbed, clearcut only, and clearcut and slash-burned Douglas-fir ecosystems, and a ponderosa pine/Douglas-fir ecosystem subjected to intense wildfire.*

Treatment and forest type	Age (yr)	Total N loss (kg· ha^{-1}·yr^{-1})	N loss (% of ecosystem total)	Mechanism of loss (in descending order of importance)
Undisturbed[a] Douglas-fir	450	–0.5	—	Accumulation; no loss
Clearcut only [b] Douglas-fir	42	123	3.8	Tree stem removal
Clearcut and slash-burned[c] Douglas-fir	42	299	9.5	Volatilization, tree stem removal, leaching
Intense wildfire[d] ponderosa pine/ Douglas-fir	>150	736	27	Volatilization, leaching

[a]Fredriksen 1975.
[b]Cole and Gessel 1965; Cole et al. 1968.
[c]Cole et al. 1968.
[d]Grier 1976.

mented for much of the region (Gessel and Walker 1956) and forest fertilization is rapidly becoming an accepted management practice (Gessel et al. 1969, 1973). In an initial effort to evaluate the effects of fertilization on nitrogen cycling in the region, Heilman and Gessel (1963) found that they could account for nearly all of the applied nitrogen in the vegetation and forest floor after two to ten years. They further concluded that the effect of fertilization on Douglas-fir growth response was long-lasting because of increased nitrogen cycling. Following this work, emphasis began to shift toward process-level research in an effort to characterize the mechanisms of nitrogen retention in these ecosystems.

Crane (1972) and Cole et al. (1975) examined the immediate effects of urea fertilization on soil leaching and nitrogen volatilization processes. Volatilization losses were small, but urea fertilization had profound effects on cation transfer in upper soil horizons. Urea is a highly soluble, nonionic, polar organic compound, and it is therefore readily leached if applied during rainy periods. Urea, however, hydrolyzes to ammonium bicarbonate through an enzymatic reaction involving urease, an enzyme common in soils. As the ammonium bicarbonate solution moves through the soil profile, NH_4^+ displaces native cations such as K^+, Ca^{2+}, Mg^{2+}, and H^+ from the exchange sites by mass action. Thus urea fertilization makes many cation nutrients available for uptake in addition to NH_4^+. Displaced H^+ combines with HCO_3^- to form H_2CO_3, so

bicarbonate as well as ammonium concentrations decrease as solutions pass deeper into the soil.

Johnson (1979) found rapid immobilization of fertilizer-applied NH_4^+ by microorganisms. He also found that NH_4^+ levels dropped to near those of unfertilized plots within four months of urea fertilization in soils similar to those studied by Crane and Cole (Figure 7.12). At four months most fertilizer nitrogen could be accounted for in the humus fraction of soil nitrogen, but there was evidence for a continual re-release of fertilizer nitrogen during the growing season for up to seven years (Johnson 1979).

Nitrification did not occur following urea fertilization in any of these studies. This is fortunate in terms of nitrogen retention, since nitrate is a mobile anion in the soil and readily leaches from the rooting zone. Laboratory experiments conducted by Heilman (1974) indicated that some forest soils produced considerable nitrate, and that urea treatment increased nitrate production in most cases. Further work is needed to determine the effects of widespread urea application on nitrification in a variety of forest soils.

Douglas-fir has a remarkable array of internal mechanisms that allow it to respond rapidly to changes in soil nitrogen availability. In a nitrogen manipulation study Turner (1977) found that the rate of nitrogen uptake was related to apparent soil nitrogen availability (Figure 7.13). Uptake was high when soil-available nitrogen was high, allowing the trees to increase foliar nitrogen reserves (Figure 7.14). On the other hand, when soil nitrogen availability was reduced by carbohydrate additions, uptake was low (Figure 7.12) and the trees were forced to rely heavily on internal translocation to meet growth requirements (Figure 7.14). As a result, foliar biomass increased and litterfall decreased in urea-treated stands, whereas foliar biomass decreased and litterfall increased in carbohydrate-treated stands. Thus, even though soil nitrogen availability may decrease rapidly after fertilization, trees may continue to benefit from enhanced nitrogen status and grow more rapidly for many years by conserving the fertilizer nitrogen they have stored internally.

Acid Rainfall and Sulfate Deposition

Acid rainfall resulting from increased sulfur dioxide and nitrous oxides from industrial sources has caused concern in recent years in terms of potential effects on both terrestrial and aquatic ecosystems (Dochinger and Seliga 1976). With respect to forest nutrition, it is feared that sulfuric or nitric acid precipitation may leach soil nutrient cations over and above rates occurring in natural systems. This has been observed particularly in Norway (Abrahamsen et al. 1976) and in the eastern United States (Likens and Bormann 1974). Records at the Thompson site show that this area has been subject to acid rainfall for the last ten years, since records of rainfall pH were begun. Analysis shows that sulfuric acid is responsible for the acidity though nitric acid is occasionally
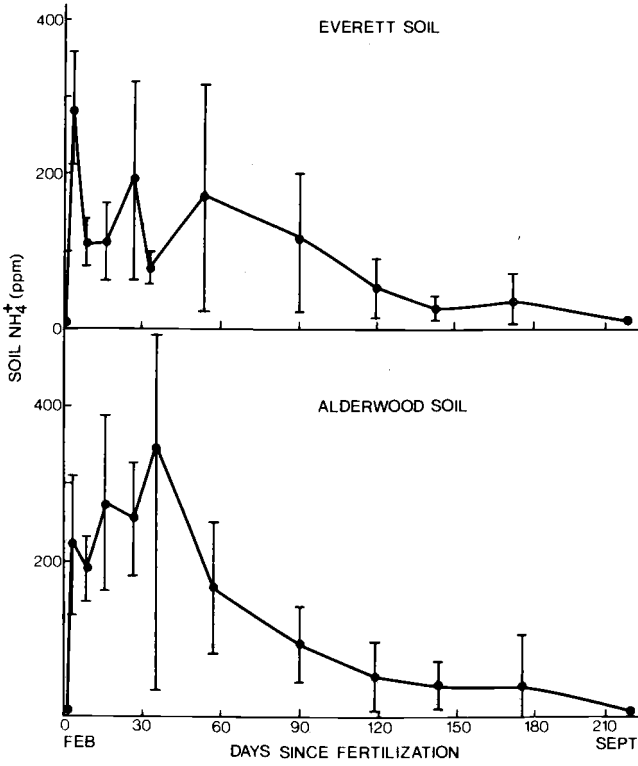
FIGURE 7.12 *Soil NH$_4^+$ levels after fertilization with 200 kg/ha urea-N (from Johnson 1979). Bars represent standard errors of the mean.*
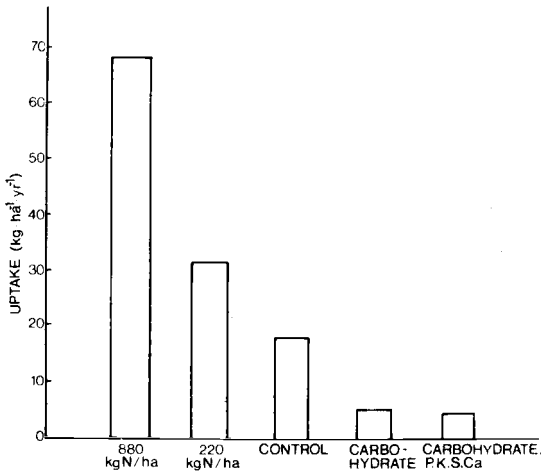

FIGURE 7.13 *Nitrogen uptake as a function of soil N availability (after Turner 1977).*
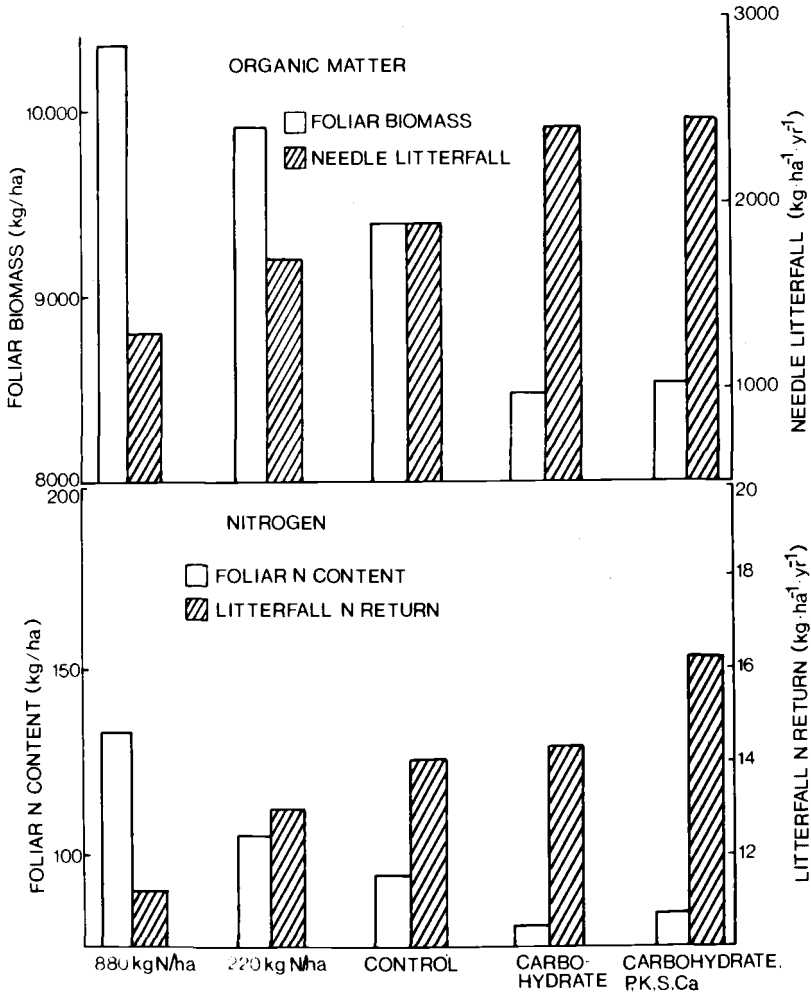
FIGURE 7.14   *Foliar biomass, N content, litterfall, and N return in Douglas-fir stands subjected to different soil N availabilities (after Turner 1977).*

present. At present levels, acid rainfall and sulfate deposition are responsible for about 20 percent of the cations removed from the rooting zone at this site (Table 7.10; Cole and Johnson 1977). This loss may not be critical to maintenance or productivity. However, should sulfuric acid in rainfall increase as anticipated use of high-sulfur coal or large quantities of low-sulfur coal (that is, Great Plains coal) increases, the situation may change.

In order for increased sulfuric acid addition to take a toll on nutrient reserves, the sulfate anion must be mobile in the soil, as is the bicarbonate anion. Two simple experiments have shown that the mobility of sulfate is

TABLE 7.10 *Annual transfers of water (cm), H^+, SO_4^{2-}, HCO_3^-, and cations (eq/ha) at the Thompson Research Center, Washington[a]*

Sample station	Water	H^+	SO_4^{2-}	HCO_3^-	Cations
Precipitation	140	240	260	420	1070
Throughfall	110	70	320	570	1080
Forest floor	90	10	1000	990	2370
A horizon	80	0	400	950	1760
B horizon	70	0	380	840	1570

Note: Average of two years from February 1973 to February 1975 calculated by converting volume fluxes at each station to a per-hectare basis. All measures except those for cations are rounded to the nearest ten units.
[a]Cole and Johnson 1977.

TABLE 7.11 *H^+, SO_4^{2-}, and total cation budgets (eq/ha) after sulfuric acid application to the soil at the Thompson Research Center, Washington.[a]*

Horizon	Input			Output			Storage		
	H^+	SO_4^{2-}	Total cations[b]	H^+	SO_4^{2-}	Total cations	H^+	SO_4^{2-}	Total cations
Forest floor	17,760	17,760	0	0.2	16,000	10,000	17,760	1,760	−10,000
Forest floor +A	35,520	35,520	0	0.2	15,000	11,200	35,520	20,000	−11,200
B (50 cm)	0.2	15,000	11,200	0.0	200	200	0.2	14,800	11,000

[a]Johnson and Cole 1977.
[b]Ca^{2+}, Mg^{2+}, Mn^{2+}, Na^+, and K^+ only.

limited in the Everett soil at the Thompson site (Johnson and Cole 1977). Applications of sulfuric acid ranging from 10^{-3} to 10^{-1} normal resulted in almost no change in cation-sulfate leaching past 50 cm in the soil (Table 7.11). Soil extractions with potassium phosphate solutions showed that the input sulfate was accounted for as absorbed sulfate. Laboratory studies confirmed that the Everett soil has a strong sulfate adsorption capacity, as do many other soils with appreciable sesquioxide contents (Howard and Reisenauer 1966).

This study showed that the Everett series soil at the Thompson site has appreciable sulfur adsorption capacity and temporarily buffers out high acid inputs. Mobility of sulfur in these systems over long periods is now known. It should be recalled that sulfate is an essential nutrient and elimination of the sources of its input may cause sulfur deficiencies (Tabatabai and Bremner 1972). In fact, Turner et al. (1977) have shown that some stands in the northwest that did not respond to nitrogen fertilization have very low foliar sulfate concentrations, implying that they are sulfur-deficient.

CONCLUSIONS

Nutrient cycling research in the coniferous biome program has unquestionably made a large contribution to the body of knowledge on this subject. Coniferous forests of this region contain efficient mechanisms for capitalizing on and conserving critical nutrients, especially nitrogen. Nutrients influence forest productivity because many nutrient cycling pathways are intertwined with carbon pathways.

Although some studies during the biome program suggested actual or potential deficiencies in potassium, magnesium, calcium, or sulfur, the overriding importance of nitrogen is clearly evident. The fact that nitrogen is the most critically limiting nutrient in forests of the northwest is not new, but biome research has illuminated various coupled mechanisms that allow these forests to efficiently utilize and conserve this critical nutrient.

Atmospheric inputs, nitrogen fixation, soil weathering, internal translocation, litterfall and crownwash, litter decomposition, uptake, and soil leaching are the key processes regulating nutrient cycling. Particulate deposition plays a role in nutrient inputs close to the coast; however, foliage leaching tends to modify atmospheric inputs such that soluble inputs to the forest floor are similar no matter where stands are located.

Nitrogen fixation is obviously the most important source of nitrogen input into coniferous forests. The principal nitrogen fixers in the biome, at least in terms of biomass, are red alder *(Alnus rubra)* and snowbush *(Ceanothus velutinus)*. In old-growth stands, the canopy dwelling foliose lichen *(Lobaria oregana)* is also important. Another site of fixation is downed logs, and estimates of greater than 5 $kg \cdot ha^{-1} \cdot yr^{-1}$ have been made. Estimates of nitrogen fixation by red alder range from 15 to 321 $kg \cdot ha^{-1} \cdot yr^{-1}$ with a maximum at about age 20. Snowbush has fixation rates ranging from 72 to 108 kg $\cdot ha^{-1} \cdot yr^{-1}$. Canopy fixation by lichens is relatively small (approximately 5 $kg \cdot hg^{-1} \cdot yr^{-1}$).

Very little accurate information is available on elemental inputs from weathering. It appears, however, that weathering rates for elements at the Thompson site may be unable to keep pace with cation removal by uptake or leaching, and the assumption of steady state in soil-exchangeable cations may not be justifiable.

Internal translocation or withdrawal of nutrients from foliage prior to abscission is an important mechanism of nutrient conservation, particularly for nitrogen. The litterfall/decomposition cycle can be short-circuited in this manner. There appears to be an increase in internal translocation of nitrogen in Douglas-fir stands as they age, particularly in nitrogen-limited ecosystems. On the other hand, potassium and calcium are not internally translocated to the degree noted for nitrogen. Nitrogen transfers via litterfall and internal translocation are very much attuned to available nitrogen in the soil such that in urea-treated stands foliar biomass increases and litterfall decreases.

Litter decomposition is limited more by moisture than temperature in the biome, particularly in lowland ecosystems, and is more pronounced in southern than in northern areas. Temperature plays a more important role in high-altitude ecosystems although considerable decomposition occurs under snowpacks. Decomposition rates generally decrease along age and altitudinal gradients. Litter fungi, both decomposers and mycorrhizae, play an important role in nitrogen conservation and immobilization.

Once nitrogen is released as a result of decomposition it is available to the trees. Studies with Douglas-fir seedlings indicate that the form of nitrogen available influences nitrogen uptake in that NH_4^+-N is taken up more rapidly than NO_3^--N. Interestingly, although seedlings grown in NH_4^+-N in solution culture accumulate considerably more N than those grown in NO_3^--N, the accumulation of cations in the latter is lower, probably because of a charge balance problem. In general, nitrogen is taken up more rapidly than other nutrients.

On a stand basis, uptake of nutrients changes significantly with stand age. For example, in Douglas-fir the maximum annual uptake of nitrogen, calcium, and potassium closely corresponds to maximum crown development, which is also the time of maximum decomposition. This is between twenty and thirty years, depending on stand density.

Cations are leached through soil in many temperate forest ecosystems by the carbonic acid or bicarbonate mechanism where H^+ ions associated with bicarbonate ions displace cations from the soil exchange sites. This mechanism, however, does not operate in all forest ecosystems. Although it dominates in tropical and lowland temperate ecosystems, organic acids dominate in subalpine and more northerly sites. For example, in Alaska organic acids dominate, mainly because of low soil pH values and the fact that carbonic acid does not dissociate appreciably below pH 4.5. Cold forest ecosystems thus conserve nutrients by suppressing carbonic acid leaching within the rooting zone. This is important because CO_2 pressures build to very high levels beneath melting snowpacks, and if pH conditions allowed it, carbonic acid leaching would be great. Erosion is also an important process in terms of nutrient output; however, it is episodic in nature. Nitrogen accumulation is a direct expression of the various inputs and outputs during the total age of the ecosystem. In the geologically young Puget Sound lowland soils, only 3000 to 5000 kg nitrogen/ha have accumulated since the glaciers receded approximately 12,000 years ago. This represents an accumulation rate of 0.2 to 0.4 $kg \cdot ha^{-1}$. This seems to be a very low average rate; however, if a site were occupied by red alder, nitrogen accumulation could be as high as $320 \cdot ha^{-1} \cdot yr^{-1}$. Such large inputs are partially balanced by fire and more recently by logging. A fire in a second-growth forest, for example, could consume up to 400 kg/ha of nitrogen. Fire thus plays an important ecological and nutritional role in western coniferous forests.

There are many similarities between organic matter and nutrient accumulation patterns during Douglas-fir stand development. Accumulation of nitrogen and potassium within foliage follows that of foliar biomass (that is, near steady state after canopy closure) but for different reasons. Nitrogen is translocated from older to current foliage while potassium is leached from foliage. Calcium accumulates at least for the first seventy-five years, largely because needle retention time increases as stands age.

Accumulation patterns for nitrogen, potassium, and calcium within the understory closely follow that for understory biomass, reaching a maximum between ten and twenty years in age and then decreasing. A second period of understory nutrient accumulation may occur as the canopy begins to break up in old-growth ecosystems.

Nitrogen and calcium accumulate in the forest floor as stand age increases and nitrogen deficiency can be induced with time because of this accumulation. On the other hand, the accumulation rate for potassium is markedly lower because its retention is not totally dependent on litter decomposition.

Ecosystems with slow nitrogen litter mineralization apparently keep larger foliar reserves; however, some evidence suggests that foliar biomass may not be determined by nutrient status but rather by site water balance, since trees on drier sites retain less foliage. Analysis of MRT of nitrogen in foliage and the forest floor shows that as MRT of the forest floor increases so does foliage retention time, suggesting that nutrient status does control the amount of foliar biomass.

There are large gaps in our knowledge of nitrogen cycling, however. The processes of nitrogen fixation, nitrification, and denitrification are poorly understood and each deserves further study. As nitrogen fertilization becomes more widespread in these forests, information on potential deficiencies of other nutrients and the interactions of nitrogen with them will become increasingly necessary. Biome research has set a direction for future research in this area in terms of weathering release of cations and the relations between acid rain, soil sulfur status, and stand sulfur deficiencies.

In a more general vein, these biome studies have demonstrated the value of a systems approach to the study of nutrient cycling, which integrates long-term budget studies with short-term process studies. Comparisons of state variables such as nutrient content of the soil and foliage are of limited value without complementary information on nutrient transfer processes. State variables such as nutrient pool sizes are no more than a result of several transfer processes integrated over time. We are not yet able to develop a model that numerically integrates all the short-term processes into long-term nutrient accumulations, but we can conceptualize this, as in Figure 7.1. Of the processes depicted in Figure 7.1, biome research has dealt with each at various levels of intensity, but more information is needed, especially for belowground processes. It is to be hoped that post-IBP research will address some of these needs.

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