

Chapter 2

Nutrient Cycling: Effects on Productivity of Northwest Forests

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ABSTRACT

Nutrient availability—the quantity of nutrients available for uptake by trees—limits forest productivity. In the U.S. Pacific Northwest and British Columbia (the Northwest), nitrogen is the major growth-limiting nutrient element, although sulfur potentially may be limiting in southern Oregon, potassium in gravelly outwash soils, phosphorus in coastal Washington, and boron and zinc in southwest British Columbia. This chapter examines, with particular reference to the Northwest: (1) characteristics of nutrient-limited stands, (2) the concept of nutrient availability in relation to nutrient cycling, (3) specific challenges facing forest managers, such as restoring nutrients after harvest, and (4) management options for maintaining long-term productivity. The theory of “optimum nutrition”—providing all necessary elements at a rate determined by tree growth—is discussed. Nutrient-rich sites are generally more robust than nutrient-poor sites, but the nutrient capital even on productive sites should be conserved by using fire carefully and minimizing soil disturbance during site preparation. Weed control generally increases nutrient availability. Maintaining woody debris could be important in managed plantations. Foresters are encouraged to install “low-intensity” nutrient experiments to test ideas on maintaining productivity.

INTRODUCTION

The productivity of many forests is limited by nutrient availability, as seen from plant growth responses to fertilization (Axelsson 1985). But to understand nutrient availability—the quantity of nutrients available for uptake by trees—we must understand nutrient cycling. It is only when we consider how nutrients cycle through an entire ecosystem that we can judge the impact of forest management operations on long-term productivity. Information on nutrient cycling, tree nutrition, and soil chemistry all have some meaning in terms of productivity, but none should be considered in isolation (McColl and Grigal 1979).

The elements commonly limiting tree growth are nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), sulfur (S), zinc (Zn), and boron (B) (Lavender and Walker 1979, Tamm 1979). Other elements such as iron (Fe), manganese (Mn), copper (Cu), molybdenum (Mo), and chloride (Cl) are required but are rarely limiting. In a classic example of how nutrient availability affects long-term productivity, Ebermayer (1876) as quoted by Tamm (1979) demonstrated that removing litter, and thus nutrients, from middle European forests for use in cow stables adversely affected site quality. Forest growth declined, particularly on infertile sites. In another example, productivity of second-rotation radiata (or Monterey) pine (*Pinus radiata* D. Don) plantations declined in South Australia (Keeves 1966, Woods 1980) and in New Zealand (Stone and Will 1965). In South Australia, the affected plantations were growing in infertile, sandy soils, where slash (harvest residues) from the previous rotation had been burned (Woods 1980). This situation, still of concern in Australia, can be corrected with fertilizers or organic matter management (Farrell et al. 1986). Windrowing also tends to impact long-term productivity (Ballard 1978). Although we have few examples of the effects of management practices on nutrients, and therefore forest productivity in the Northwest, Perry and Rose (1989) suggest that windrowing and broadcast burns are likely to reduce long-term productivity. Skeletal soils in southwest Oregon may be susceptible to harsh site-preparation disturbances (Lewis and Abee 1981).

It is the intent of this chapter to examine—with particular reference to the U.S. Pacific Northwest and British Columbia (the Northwest)—(1) characteristics of nutrient-limited stands, (2) the concept of nutrient availability and its relationship to nutrient cycles in different ecosystems, (3) specific challenges, such as restoring nutrient levels after harvesting, facing forest managers, and (4) management options for maintaining

long-term productivity. Productivity may be expressed in two ways—as the total amount of biomass or as merchantable wood volume produced annually. Commercial forest managers are more interested in the latter, most productivity researchers in the former.

NUTRIENTS OF CONCERN IN THE NORTHWEST

Nitrogen is the major growth-limiting nutrient element in the Northwest and is the only one that Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] responds to consistently (Heilman 1979, Peterson and Gessel 1983). Sitka spruce [*Picea sitchensis* (Bong.) Carr.] also appears to benefit from N fertilization (Webster et al. 1976, Farr et al. 1977). Response of western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] has been inconsistent (Webster et al. 1976), but recent work suggests that it will respond better to combined N and P fertilizers (Radwan and Shumway 1983) or to P fertilizer alone on some coastal soils in Washington (Porada 1987). We are just beginning to understand possible effects of nutrient interactions (Radwan and Brix 1986). Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in interior British Columbia has also been inconsistent in its response to N fertilization (Weetman and Fournier 1982). However, N fixers such as red alder (*Alnus rubra* Bong.) are unlikely to respond to N fertilization.

In the case of Douglas-fir, field experiments with the entire range of essential elements have failed to demonstrate widespread deficiencies of any other element than N (Gessel et al. 1979, Heilman 1979). However, S may be limiting in southern Oregon (Blake 1985, Edmonds and Hsiang 1987), K in gravelly outwash soils (Johnson et al. 1982), and B and Zn in some Douglas-fir, as well as in some western hemlock and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), plantations in southwestern British Columbia (Carter et al. 1984, 1986).

Concentrations of N, P, K, Calcium (Ca), and Mg as they relate to deficiency in foliage of five western coniferous species are given in Table 2.1; general interpretations (not species specific) are given in Table 2.2 for Mn, Fe, Zn, Cu, B, and Mo. Van den Driessche (1979) determined "adequate" levels of nutrients in current-year needles of Douglas-fir to be 1.8% for N, 0.22% for P, 0.80% for K, 0.20% for Ca, 0.12% for Mg, and 0.18% for S. However, it is difficult to interpret nutrient deficiencies from foliar levels alone because levels in foliage of different ages vary. The New Zealanders have had some success in determining nutrient deficiency levels with radiata pine (Will 1985). The N:S ratio in foliage may also indicate whether N fertilization is likely to induce S deficiency (Turner et al. 1977). Because of the widespread nature and dominance of N deficiency in Pacific Northwest forests, this chapter focuses largely on this element.

CHARACTERISTICS OF NUTRIENT-LIMITED STANDS

Most forest stands are nutrient limited to one degree or another, so trees are well adapted to this type of stress. One way to examine the characteristics of nutrient-limited sites is to contrast the characteristics of a single species in ecosystems which are relatively high and relatively low in nutrients. Douglas-fir is a good test species. Douglas-fir ecosystems with low site quality and relatively moist conditions in northern Oregon, Washington, and British Columbia generally have the following features, compared to those with high site quality (Johnson et al. 1982, Peterson 1982, Vogt and Edmonds 1982, Feller et al. 1983b, Vogt et al. 1983b):

- (1) Lower aboveground production and wood biomass.
- (2) Longer needle retention time.
- (3) Lower photosynthesis rates.
- (4) Lower canopy leaf areas.
- (5) Lower foliar N concentrations.
- (6) Greater translocation of N from old foliage to living tree tissues before litterfall.
- (7) Less litterfall and lower litterfall N concentrations.
- (8) Lower litterfall lignin concentrations.
- (9) Thicker forest floors with well-developed humus layers, perhaps because of more fine-root biomass.
- (10) Roughly the same decomposition rates.
- (11) Higher forest-floor C:N (carbon:nitrogen) ratios.
- (12) More fine-root, but less total live-root, biomass.
- (13) More mycorrhizae.
- (14) Less total soil N.
- (15) Less available soil N (ammonium, NH_4^+ , and nitrate, NO_3^- forms).

Values for many of these features are contrasted in Table 2.3. However, some of these may not apply to drier sites in southern Oregon or California. For example, forest floors are thinner in hot, dry areas.

TABLE 2.1. Interpretation of foliar nutrient concentrations for five coniferous species (adapted from Ballard and Carter 1985).

Element ¹	Foliar concentration, % (dry-mass basis)					Interpretation of deficiency
	Douglas-fir	Lodgepole pine	Western hemlock	White spruce ²	Western redcedar ³	
N	0.00	0.00	0.00	0.00	0.00	Very severe
	1.05	1.05	0.95	1.05	1.15	Severe
	1.30	1.20	1.20	1.30	1.50	Slight-moderate
	1.45	1.55	1.45	1.55	1.65	Adequate
P	0.00	0.00	0.00	0.00	0.00	Severe
	0.08	0.09	0.11	0.10	0.10	Moderate
	0.10	0.12	0.15	0.14	0.13	Slight
	0.15	0.15	0.35 ⁴	0.16	0.16	Adequate
K	0.00	0.00	0.00	0.00	0.00	Very severe
	0.35	0.35	0.40	0.25	0.35	Moderate-severe
	0.45	0.40	0.45	0.30	0.40	Adequate
Ca	0.00	0.00	0.00	0.00	0.00	Severe
	0.10	0.05	0.05	0.07	0.07	Moderate-severe
	0.15	0.06	0.06	0.10	0.10	Slight-moderate possible
	0.20	0.08	0.08	0.15	0.20	Little, if any
	0.25	0.10	0.10	0.20	0.25	Adequate
Mg	0.00	0.00	0.00	0.00	0.00	Severe
	0.06	0.06	0.06	0.05	0.05	Moderate-severe
	0.08	0.07	0.07	0.06	0.06	Slight-moderate possible
	0.10	0.09	0.09	0.10	0.12	Little, if any
	0.12	0.10	0.10	0.12	0.14	Adequate

¹N = nitrogen, P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium.

²*Picea glauca* (Moench) Voss.

³*Thuja plicata* Donn ex D. Don.

⁴Based on a single sample (Everard 1973) and perhaps not representative.

TABLE 2.2. Interpretation of foliar nutrient concentrations not yet species specific (adapted from Ballard and Carter 1985).

<i>Element¹</i>	<i>Foliar concentration, ppm (dry-mass basis)</i>	<i>Interpretation of deficiency</i>
Mn	0	Severe
	4	Probable
	15	Possible or near
	25	Adequate
Fe	0	Likely
	25	Possible
	50	Unlikely
Active Fe	0	Likely
	30	Unlikely
Zn	0	Probable
	10	Possible
	15	None
Cu	0	Probable
	1	Possible
	2	Possibly somewhat
	2.6	Possible slight
	4	None
B	0	Deficiency likely
	10	Possible; NID ²
	15	Unlikely; N < 1.5 ³ , NID possible; if N > 1.5, NID unlikely
	20	None
Mo	0	Possible
	0.1	None

¹Mn = manganese, Fe = iron, Zn = zinc, Cu = copper, b = boron, Mo = molybdenum.²NID = deficiency inducible by N fertilizer application.³N = percent N concentration.

TABLE 2.3. Features (mean \pm standard deviation) of Douglas-fir stands with differing site quality.

Feature	High site quality	Low site quality
Foliar N, % ¹	1.40	1.23
Litterfall N, % ²	0.63 \pm 0.05	0.60 \pm 0.07
Litterfall lignin, % ²	45.6 \pm 6.7	43.2 \pm 6.6
Forest-floor depth, cm ³	3.3 \pm 1.5	5.2 \pm 1.6
Needle weight loss after 2 years' decomposition, % ⁴	43.5 \pm 5.0	43.0 \pm 0.6
N remaining in needles after 2 years' decomposition, % ⁴	109 \pm 15	133 \pm 19
Forest-floor C:N ⁴	36 \pm 8	51 \pm 17
Total live roots, kg/ha ⁴	68,000	12,000
Total live fine roots, kg/ha ⁴	433 \pm 508	1,544 \pm 1,295
Mycorrhizal live roots, kg/ha ³	149 \pm 199	426 \pm 337
Total fine roots infected by mycorrhizae ³	69 \pm 14	87 \pm 11
Total soil N, kg/ha ⁴	6,227 \pm 3,441	2,895 \pm 1,119
Soil NH ₄ ⁺ , ppm ⁵	21.8 \pm 2.4	14.0 \pm 3.8
Soil NO ₃ ⁻ , ppm ⁵	3.1 \pm 1.5	1.0 \pm 0.2

¹Edmonds and Bigger (1983); stand age 53 years. N = nitrogen.

²R. L. Edmonds, unpublished data, University of Washington, 1987; stand ages range from 11 to 163 years.

³Vogt et al. (1983b); stand ages range from 11 to 163 years.

⁴Feller et al. (1983a); stand age 48 years. C = carbon.

⁵Vogt and Edmonds (1982); stand ages range from 45 to 175 years.

Interestingly, total productivity of Douglas-fir stands in Washington with low site quality is not dramatically less than that of stands with high site quality (Keyes and Grier 1981, Grier et al. 1986). The major difference seems to be how carbon is allocated. Lower nutrient availability apparently requires greater investments of photosynthate in fine-root production and mycorrhizae, leaving less photosynthate for wood production. Fine-root production may not always be greater on poor sites, however; for example, Nadelhoffer et al. (1985) found that it was less.

Nutrient-limited Pacific silver fir stands at high elevation tend to have many of the same features as poor Douglas-fir stands, but the features are exaggerated (see chapter 8, this volume). Fine-root and mycorrhizal biomass is much higher, forest floors are thicker (Vogt et al. 1983a), decomposition rates are lower (Edmonds 1980), foliar is retained longer, and N concentrations in litter are lower (Johnson et al. 1982).

Some of the reported differences in site quality can be attributed to different moisture regimes rather than nutrients. To assess the influence of nutrient limitation alone on forest stands, we can examine stands growing on the same site with the same soil moisture, some of which have been fertilized and others not. Several studies have done this. Foliar biomass in Douglas-fir is greater on urea-fertilized sites (Gessel and Turner 1976, Vogt et al. 1986a) as result of (1) increased needle size, (2) more needles per shoot, and (3) greater number of shoots produced (Tamm 1979, Grier et al. 1986). Brix (1971) also found some increase in photosynthetic capacity (milligrams of carbon fixed per unit surface area or biomass of foliage) of Douglas-fir after N fertilization. A much larger response from fertilization can thus be expected in stands in which canopies are not fully closed and there is room for foliage area to increase.

Litterfall may also be influenced by fertilization. Gessel and Turner (1976) indicated that litterfall decreases after fertilization, then increases for at least 5 years. Yet Vogt et al. (1986a) found little difference in litterfall between fertilized and unfertilized stands 14 years later. Berg and Staaf (1980) noted that fertilization only moderately increased decomposition rates of needle litter.

The proportion of photosynthates allocated to shoots relative to roots increases after fertilization (Waring and Schlesinger 1985, Axelsson 1986). Vogt et al. (1986a) found that fine-root biomass decreased after fertilization in Douglas-fir stands in Washington whereas coarse-root and aboveground biomass increased. Fourteen years after fertilization, fine-root biomass was 1,350 kg/ha, while it was 5,620 kg/ha in an unfertilized stand. Fine-root turnover on the fertilized stand was 50% of that on the unfertilized. Axelsson (1986), however, found no decrease in fine-root biomass in fertilized Scots pine (*Pinus sylvestris* L.) stands in Sweden, but an increase in coarse-root and aboveground biomass.

THE CONCEPT OF NUTRIENT AVAILABILITY

The productivity of many forests appears to be controlled by nutrient availability—that is, the quantity of nutrients available for uptake each year. If the current supply is not sufficient, nutrient deficiencies occur. Nutrient availability can be considered similar to dividends earned on financial investments:

$$\begin{aligned}\text{Dividends} &= \text{capital} \times \text{interest rate} \\ \text{Nutrient availability} &= \text{nutrient capital} \times \text{turnover rate}\end{aligned}$$

The availability of nutrients can be changed either by changing the amount of nutrient capital or by changing the turnover rate—the rate at which nutrients are released from the nutrient capital in the soil. Management can do both. Moreover, the total nutrient capital is a conglomerate of various “pools” with various turnover rates. Nutrient capital is fairly easy to measure, but turnover rate is difficult. Detecting changes in turnover rates may be even more difficult.

Many forest-tree species appear to have different nutritional requirements (Tamm 1979) and different nutrient-use efficiencies—that is, net primary production per unit of nutrient accumulated. Wild plants that are restricted to infertile soils generally have lower maximum potential growth rates and are less responsive to added nutrients than related plants from more fertile sites (Chapin et al. 1986) (Fig. 2.1).

Chapin et al. (1986) have contrasted nutrient limitation in individuals with that in the community. Over the range of a dominant species such as Douglas-fir, individuals on infertile sites are more responsive to fertilization than individuals on more fertile sites (Fig. 2.2). Understory vegetation in Douglas-fir stands, however, may respond differently because the understory species on fertile and infertile sites are usually different. The potential productivity of each community depends on the growth potential of each of its component species. Thus, an understanding of both individual- and ecosystem-level processes is necessary if we are to accurately interpret the results of fertilization experiments (see chapter 11, this volume).

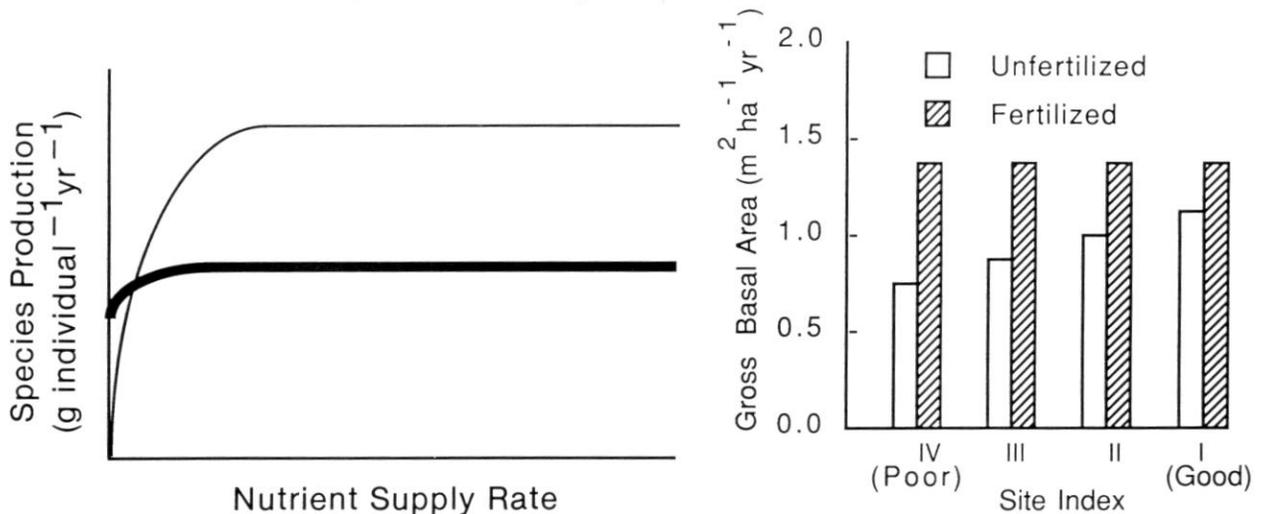


FIG. 2.1. Production by a crop species (light line) and a species adapted to low levels of nutrients (heavy line) in response to variable nutrient supply rate (adapted from Chapin et al. 1986).

FIG. 2.2. Estimated increase in gross basal area over 10 years for unfertilized and heavily fertilized (450 kg/ha of nitrogen) unthinned Douglas-fir in the Northwest growing on sites of variable quality (adapted from Peterson 1982, Chapin et al. 1986).

Indexes of nutrient availability, including soil incubations (both anaerobic and aerobic in the field and laboratory; Strand 1984) and ion-exchange resins (Binkley and Matson 1983) have been developed. These indexes have been used with mixed success in predicting the response of monospecific (one species) forests to fertilization (Chapin et al. 1986), suggesting that our understanding of this concept in forests is incomplete.

Nutrient availability may be reflected in nutrient concentrations in tree foliage which, in turn, are related to tree growth (Fig. 2.3). Thus, as soil nutrient availability increases, foliar nutrient concentrations and tree growth should increase until some optimum beyond which tree growth levels off and then declines as a result of toxic effects.

Ingstad (1974, 1982), however, challenged the concept of an optimum concentration of nutrients in soil

and foliage, suggesting instead that it is the nutrient flux density (amount of nutrients available per unit time) and the total amount of nutrients in the biomass that are important in determining tree growth rates. Ingestad's concept seems to be borne out when relationships between foliar nutrient concentration and stand age are considered. On a site of given productivity, foliar N concentration decreases as trees age (Lavender and Walker 1979). It may be only 0.83% in a 450-year-old Douglas-fir stand with dark green foliage, but 1.2% in a 50-year-old stand with chlorotic foliage. Nutrient availability is adequate to maintain green foliage in the old-growth stand but not in the younger stand despite the presence of higher foliar N concentrations in the latter. Thus, foliar nutrient concentrations alone may not be very useful in characterizing how nutrient limitations affect productivity.

Many conifers, including our western species, have high growth potentials (Axelsson 1985). For example, western hemlock can produce $36 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ aboveground (Fujimori 1971), although this is not often achieved. Most Douglas-fir stands produce less than $20 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (Long 1982). Net biomass production will increase if maximum leaf area is rapidly achieved. There is a strong relationship between total leaf area and net primary production in Douglas-fir and other Northwest species (Fig. 2.4). Although the leaf areas shown in this figure may be overestimates for old-growth forests (Marshall and Waring 1986), the relationship is still strong. The main factor increasing leaf area of conifers is the nutrient flux density, which can be manipulated to a greater extent than other variables controlling growth (Axelsson 1985). Nutrient availability is thus related to the current requirement of trees. In low-elevation Douglas-fir forests, low nutrient availability may prevent a site from supporting the leaf area possible given that site's water balance (Grier et al. 1986).

Thus, manipulating nutrient availability can increase wood production (Binkley 1986). In Sweden, "optimum nutrition" (adding all necessary elements at a rate determined by tree growth and beginning at an early age) could produce a gain in mean annual volume increment of about 300% for pine and 150% for spruce (Axelsson 1985)—a gain 2–3 times greater than that achieved with conventional fertilization throughout a rotation. The theory behind optimum nutrition and maximum growth is that the whole stand-soil system is saturated with nutrients in 10–20 years (Axelsson 1985). The system then cycles the N necessary for high production throughout the rotation, requiring little or no additional fertilization. The necessary maximum dose thus decreases with time while internal N cycling increases. Extremely high productivity can be expected even in stands carrying moderate amounts of foliage if the nitrogen flux density is high.

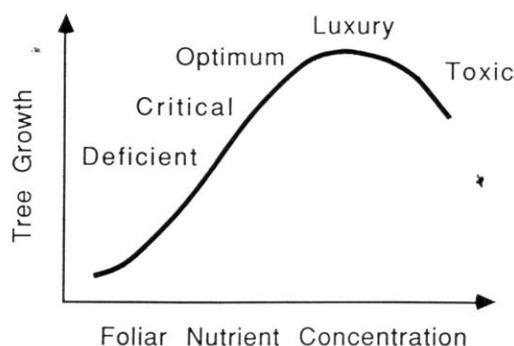


FIG. 2.3. Relationship of tree growth to nutrient concentrations in tree foliage (adapted from Waring and Schlesinger 1985).

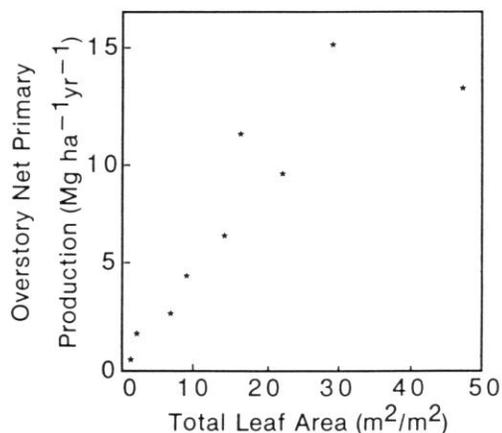


FIG. 2.4. Relations between total leaf area and overstory net primary production in nine Northwest vegetation zones, along a transect from the Pacific coast to the east side of the Cascade Mountains (adapted from Gholz 1982, Grier et al. 1986).

FACTORS INFLUENCING NUTRIENT TURNOVER RATES

Nutrient availability is strongly influenced by nutrient turnover rates, which are generally controlled by the rates of organic matter decomposition. Soil organic matter is extremely complex. The forest floor, for example, contains many different substrates (needles, twigs, cones, bark, branches, and logs), each decomposing and releasing nutrients at different rates. Some substrates (e.g., red alder leaves) decompose quickly and do not immobilize N or any other element (Edmonds 1980). Others (e.g., Pacific silver fir needles and branches)

may immobilize N for more than 5 years (Edmonds 1984, 1987). Still others (e.g., very slowly decomposing logs) may immobilize N and other nutrients for more than 25 years (Grier 1978). Most of the N mineralized (i.e., released from decomposing substrates) in conifer stands appears to come from the forest floor rather than the mineral soil. Using buried incubation bags, McClaugherty et al. (1985) determined that up to 18% of the N mineralized in eastern hemlock [*Tsuga canadensis* (L.) Carr.] and white pine (*Pinus strobus* L.) stands was derived from the mineral soil, the rest from the forest floor; in contrast, 53% of the N mineralized in bigtooth aspen (*Populus grandidentata* Michx.) stands came from the mineral soil.

Litter chemistry (mostly C:N and lignin:N ratios and lignin concentrations), site microenvironment (mostly moisture and temperature), and microbial populations (soil microflora and microfauna) are the dominant factors controlling decomposition and mineralization rates (Fogel and Cromack 1977, Edmonds 1980, 1984, 1987).

Today's management practices—clearcutting, shorter rotations, site preparation (including slash burning and yarding unmerchantable material)—strongly influence the type of organic matter on a site, the populations of soil microbes, and the rate of organic matter decomposition and nutrient release (McCull and Powers 1984). Thus, management practices strongly influence nutrient availability. Some research on the effects of harvesting practices in forests has been conducted (Bormann and Likens 1979, Leaf 1979), with a certain amount in western forests (e.g., Jurgensen et al. 1979, Bigger and Cole 1983, Edmonds and Bigger 1983, Entry et al. 1986, Bigger 1988). Harvesting generally is thought to increase decomposition rates by creating warmer, moister conditions. However, conditions immediately after harvesting may be too warm, and the resulting excess drying may actually retard decomposition. Binkley (1984) found that surface litter decomposition may be retarded in clearcuts, but humus decomposition may be increased. Decomposition may also be greater at forest edges adjacent to clearcuts (Edmonds and Bigger 1983); if so, this could have implications with respect to the size, shape, and configuration of clearcuts (see chapter 6, this volume). Although our knowledge of these processes is far from complete, it appears that maintaining organic matter on a site is important to sustaining site productivity.

NUTRIENT AVAILABILITY IN RELATION TO NUTRIENT CYCLING

Nutrient availability is determined by nutrient cycles. Nutrient cycling in forests is well explained in many publications (Cole and Rapp 1981, Johnson et al. 1982, Miller 1984, Waring and Schlesinger 1985, Binkley 1986), so it will only be briefly described here. Forest nutrient cycles involve annual inputs, internal transfers, and annual outputs (Fig. 2.5). This is further elaborated for N in Figure 2.6. Nitrogen cycling is complex and involves the processes of nitrification (microbial transformation of NH_4^+ to NO_2^- and then to NO_3^- under aerobic conditions) and denitrification (microbial transformation of NO_3^- and NO_2^- to the gases N_2O and N_2 under anaerobic conditions). In many cases, episodic events such as fires and harvest are more important than the sum of the annual fluxes through the rotation. Table 2.4 shows some common rates of N transfers for certain processes in several different types of ecosystems.

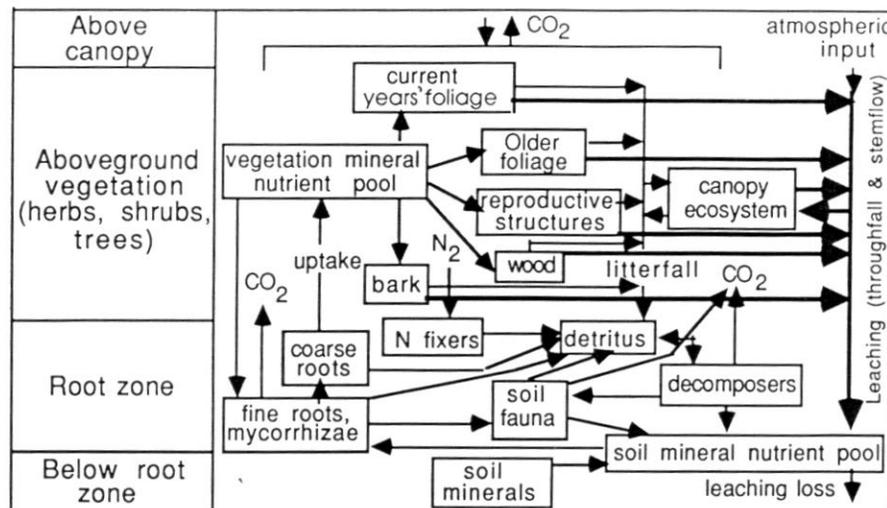


FIG. 2.5. Conceptual model of nutrient cycling in coniferous forests (adapted from Johnson et al. 1982).

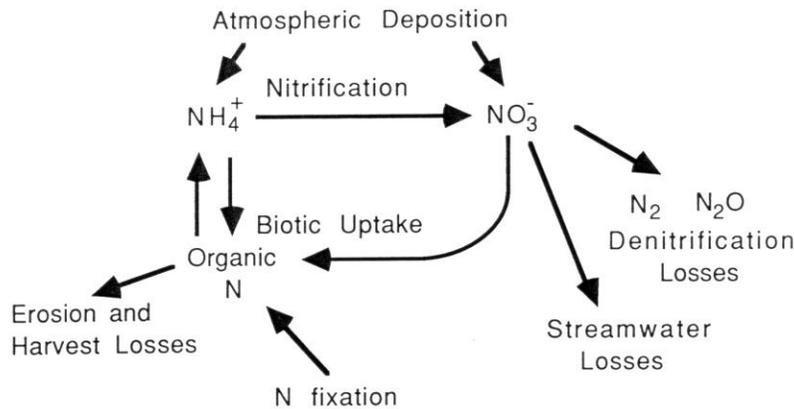


FIG. 2.6. Inputs, internal transfers, and outputs of nitrogen (N) in a forest ecosystem (adapted from Waring and Schlesinger 1985).

TABLE 2.4. Nitrogen transfers (kg ha⁻¹ yr⁻¹) among ecosystem components in young, mature, and old-growth coniferous ecosystems (adapted from Johnson et al. 1982).

Process	42-yr-old Douglas-fir	121-yr-old Pacific silver fir	170-yr-old western hemlock/ Sitka spruce	450-yr-old Douglas-fir
Input (precipitation, dry fall) ¹	1.7	5.5	1.3	2.0
Return to forest floor ²				
Throughfall + stemflow	0.5	—	1.3	3.4
Litterfall	25.4	—	16.3	25.6
Total forest floor	25.9	35.8 ³	17.6	29.0
Within vegetation transfers				
Requirement	45.8	39.9	23.1	33.3
Redistribution	20.7	0.0	12.4	18.5
Uptake	25.1	39.9	10.7	14.8
Soil transfers				
* Forest floor to soil	7.3	—	10.3	4.7
Loss from rooting zone	3.4	2.0	2.7	1.5
Input minus loss from rooting zone	* -1.7	3.5	-1.4	0.5

¹Weathering inputs are negligible for nitrogen (N). N fixation is minimal in western conifer stands (Cushon 1985).

²Throughfall is rain dripping through the canopy; stemflow is water collected at the base of the stem; litterfall is needles, leaves, twigs and other fine material.

³Separate estimates for throughfall, stemflow, and litterfall not available.

Inputs

Atmospheric inputs come dissolved in precipitation, as dry particles deposited on canopies, and, in areas subject to pollution, even as gases (mostly sulfur dioxide and nitrogen oxides). Atmospheric inputs of N in western forests are generally less than 2 kg ha⁻¹ yr⁻¹ but may be slightly higher (near 5 kg ha⁻¹ yr⁻¹) in coastal forests (Table 2.4). Nitrogen fixation, which converts atmospheric N gas into proteins, is an important source of N in forests, particularly those containing large proportions of symbiotic N fixers such as *Ceanothus* spp. and red alder, which can fix up to 100 and 50–200 kg ha⁻¹ yr⁻¹, respectively (Bormann and DeBell 1981, Binkley et al. 1982). Once fixed, the N continues to cycle within the forest. Although free-living (asymbiotic) microbes also can fix N, the rates are generally insignificant compared to those of symbiotic N fixers. Cushon (1985) studied gaseous N fluxes in a mature (approximately 100-year-old) Douglas-fir, western hemlock, and western red-

cedar (*Thuja plicata* Donn ex D. Don) forest in southwestern British Columbia in which no symbiotic N-fixing plants such as alder were present. He found that N fixation added approximately $0.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ while denitrification losses were less than $0.01 \text{ kg ha}^{-1} \text{ yr}^{-1}$, for a net gain of approximately $0.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$. Similar low inputs from free-living N fixers (B. Heath, personal communication, Oregon State University, 1987) and low losses for denitrification (D. Myrold, unpublished data, Oregon State University, 1987) have been found in Oregon. Gaseous inputs and outputs are not included in Table 2.4 because the data are from coniferous forests where such fluxes are very small.

Weathering of soil minerals can release sizable quantities of cation (positively charged) nutrients such as K, Ca, and Mg and sometimes P but usually no N. But such estimates of weathering inputs are difficult to obtain and are not included in Table 2.4. An additional source of nutrients is, of course, fertilization, which has mostly been used to increase productivity. However, future fertilization use might extend to maintaining productivity on sites where natural supplies have been depleted.

Internal Transfers

Organic matter decomposition and subsequent nutrient release are key processes in forest ecosystems, and the rates at which C and nutrients flow through the forest floor can play a large role in regulating ecosystem productivity. Soil microbes are strong competitors for plant nutrients; so when microbes are nutrient limited, trees can become nutrient deficient.

Microbes are also important in nitrogen transformations in forest soils (Fig. 2.5). Highest rates of nitrification are observed in red alder stands. Lower rates are observed in Douglas-fir stands, but rates are higher for sites that are more productive. Little or no nitrification occurs in high-elevation Pacific silver fir stands (Vitousek et al. 1979). The factors controlling nitrification in forest soils are not completely understood, but substrate (ammonium) availability appears to be the most important.

Trees can take up N as ammonium, nitrate, or amino acids. Ammonium is assumed the dominant form taken up, at least by conifers in the Northwest (Johnson et al. 1982). Once absorbed by plants, nutrients move to sites where they are needed. However, some elements are more mobile than others. Potassium, for example, may be leached from needles by rain. Some elements, particularly N and S, and sometimes P, may be translocated back into living tree tissues before needles are lost as litterfall (Johnson et al. 1982). This translocation tends to be greater on more nutrient-limited sites. Other elements, such as Ca, cannot be easily mobilized and are lost with litterfall. Interestingly, a large proportion of the litter (or detritus) is produced belowground through fine-root turnover. In many cases, belowground inputs exceed aboveground (Vogt et al. 1986b). In some ecosystems, woody litter may be an important source of nutrients and could also be an important site for N fixation (Harmon et al. 1986). Of the nutrients taken up annually, on average, roughly 20% are retained and accumulated in tree biomass; the rest are recycled to the soil. Temperate-zone conifers typically take up $47 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of N and return $36 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Cole 1986). If we assume that uptake regulates productivity, $1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of N taken up will, on average, produce $194 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of aboveground biomass (Cole 1986).

Outputs

Most forests are very efficient at retaining nutrients. Not only are outputs usually smaller than inputs, but outputs are a small fraction of the amount cycled annually when forests remain undisturbed.

Leaching and erosion are usually the major pathways for loss. Fires can volatilize both N and S and, through fly ash as well, cause significant nutrient losses. Some N can be lost as a gas through denitrification, but this is usually minor for forests growing on well-drained soils. Cushon (1985) found denitrification outputs to be less than $0.01 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in southwestern British Columbia. Many of the significant outputs are episodic in nature, particularly those involving fire and harvest.

Fire. Hot wildfires may remove greater than 500 kg/ha of N annually (Table 2.5), slash fires from 10 to over $1,000 \text{ kg/ha}$ of N depending on the severity of the fire (Feller et al. 1983b, Little and Klock 1985, Binkley 1986; M. C. Feller, unpublished data, University of British Columbia, 1987). A typical broadcast slash burn in the coastal Northwest appears to remove more than 200 kg/ha of N (Little and Klock 1985; M. C. Feller, unpublished data, University of British Columbia, 1987).

Harvest. Nutrient loss resulting from harvest depends on the quantity of biomass removed. Long rotations often yield large trees, so more biomass is removed at the time of harvest; however, long rotations remove less biomass than short rotations. This is generally a function of tree species and the amount and type of tissue removed. Whole-tree harvests generally remove about twice as much biomass as bole-only harvests (Leaf

1979). Even the most intensive vegetation removal leaves 87.7% of the total ecosystem N on the site; removing boles typically leaves more than 95% (Table 2.6).

However, determining site N capital depends greatly on the soil depth used in the calculations because different depths contain different amounts. For example, mineral soil usually contains the greatest quantities of N. It is uncertain exactly what depth should be used for calculating soil N capital. Furthermore, much of the soil or total ecosystem N is not readily available to trees because it is bound up in organic matter. Thus, although harvesting may remove only 10% of the site N capital, it may remove a much greater proportion of the N that would be readily available for uptake by plant roots. The significance of harvesting losses cannot always be readily assessed from the type of data given in Table 2.6. What we really need to know is the effect of harvesting on the available N pool, and on the short- and long-term rates of replenishment and depletion of this pool. For instance, amounts of N lost through leaching as a result of harvest appear to be slight in western conifer forests (Johnson et al. 1982, Bigger and Cole 1983, Feller and Kimmins 1984, Bigger 1988).

Whole-tree harvesting in Douglas-fir stands at Pack Forest, Washington, strongly reduced height growth in the first 2 years after treatment on poor sites, but had little influence on highly productive sites (Edmonds and Bigger 1983, Bigger 1988). This effect, however, was not so pronounced after 7 years (Bigger 1988). Thus it appears that poor sites like those at Pack Forest, although susceptible to productivity losses, may be fairly resilient with respect to harvesting.

TABLE 2.5. Total annual nitrogen (N) losses and their mechanisms for Douglas-fir ecosystems (Johnson et al. 1982, Feller et al. 1983b).

Condition	Total N loss kg ha ⁻¹ yr ⁻¹	Loss mechanism
Undisturbed	(Gain of 0–10)	(No loss)
Clearcut only	100–300	Stem removal; leaching
Clearcut and slashburned	300–1,200	Volatilization; leaching; stem removal
Burned by hot wildfire	>500	Volatilization; leaching

TABLE 2.6. Nitrogen (N) capital remaining after harvest in forest ecosystems in Washington (WA) and Oregon (OR) (adapted from Johnson et al. 1982).

Tree species	Age, yr	State	Total ecosystem N, kg/ha	% N remaining after removing		
				Boles only ¹	Whole trees ²	Vegetation ³
Douglas-fir	9	WA	3,017	99.6	98.9	97.4
	22	WA	3,281	95.6	93.1	91.0
	30	WA	3,232	95.6	93.2	91.7
	30	WA	3,477	95.1	90.9	90.1
	42	WA	3,366	93.3	89.4	88.3
	49	WA	3,538	95.3	90.6	89.9
	73	WA	3,751	95.4	90.7	90.2
	95	WA	3,686	92.5	87.9	87.7
	95	OR	10,805	97.5	95.2	95.1
	130	OR	8,775	97.9	95.6	95.5
Western hemlock/Sitka spruce	450	OR	5,725	93.9	90.1	89.9
	30	OR	33,781	99.5	98.6	98.6
Noble fir ⁴	121	OR	36,315	98.4	98.0	97.9
	130	OR	15,500	97.5	96.0	96.0
Mountain hemlock ⁴ /Pacific silver fir	130	OR	6,529	97.2	94.0	93.7
Pacific silver fir	23	WA	2,868	99.0	94.1	93.1
Pacific silver fir/mountain and western hemlock	170	WA	4,895	96.9	93.1	92.8

¹To a minimum top diameter inside bark of 10 cm.

²Boles, branches, foliage, and reproductive structures removed from site for all trees greater than 5-cm diameter at breast height (1.4 m above ground).

³All living vegetation removed to surface of litter layer.

⁴Noble fir (*Abies procera* Rehd.); mountain hemlock [*Tsuga mertensiana* (Bong.) Carr.].

NUTRIENT CYCLING PATTERNS THROUGHOUT A ROTATION

Natural forest ecosystems usually have balanced nutrient cycles that allow very little nutrient loss (Vitousek and Reiners 1975, Tamm 1979). The balanced cycle, however, is affected by factors such as successional stage of the forest, water regime, mineralogy and rate of soil weathering, external inputs of nutrients and toxic substances, nitrogen fixation, denitrification and nitrification, and natural or human-caused disturbance (Tamm 1979). Trends for net ecosystem production and nutrient losses during primary successional development are shown in Figure 2.7. In a mature forest, nutrient inputs offset outputs. When net ecosystem production is positive, nutrient outputs in streamwater are less than inputs because of plant uptake. Losses for limiting elements such as N may fall to zero while levels of less essential elements such as K show little change during succession (Vitousek and Reiners 1975).

Little is known about N availability, uptake, and limitation in western forest ecosystems. We have, however, hypothesized trends for these three factors in relation to time (Fig. 2.8). We believe that N availability increases dramatically after harvest and then falls back to original levels. If atmospheric inputs are high, N availability may continue to be higher than before harvest; if harvesting was intensive, N availability may decline below original levels. N uptake initially declines after harvest, increases once vegetation is reestablished, and then declines after canopy closure. Nutrients become limiting when availability cannot meet uptake requirements. Broadcast fertilization immediately after clearcutting may actually result in losses of N because uptake is low. However, before canopy closure heavy demands are made on the soil, and fertilizers may increase growth because N availability is declining. Because demands on soil nutrient supplies drop dramatically after canopy closure, Miller (1981) suggested that fertilizers are likely to be of limited value at this stage. However, this is certainly not the view in the Northwest, where fertilizers are applied after canopy closure with good results (Miller et al. 1986). Different management strategies could alter the differences between the two curves shown in Figure 2.8c. Although these hypothesized trends are appealing, data are needed to test them and to apply them on a site-specific basis.

The major problem involved in testing and applying the concept outlined in Figure 2.8 seems to be determining values for N availability, which are difficult to obtain directly. Mineralizable N has been used to index N availability (Shumway and Atkinson 1978, Powers 1980, Shumway 1984) but does not always reflect availability of N to trees.

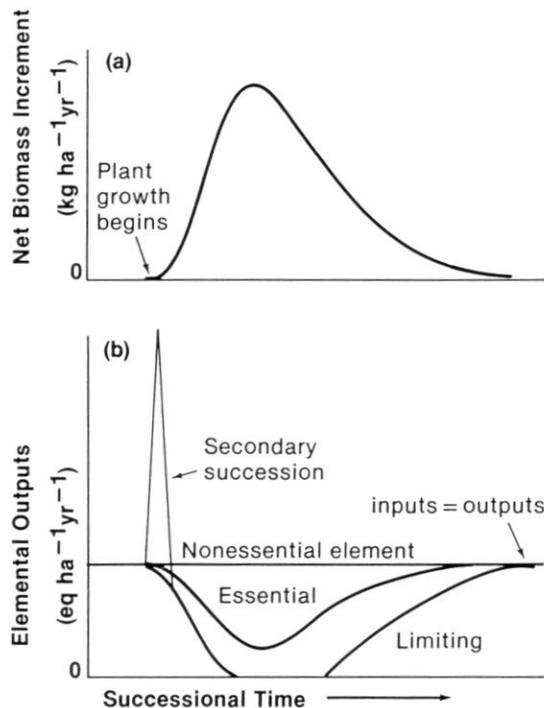


FIG. 2.7. Variation in (a) net biomass increment and (b) nutrient loss of nonessential, essential, and limiting elements (e.g., nitrogen) during plant succession. In (b), the sharply peaked thin line represents a high rate of nutrient loss immediately after disturbance, such as harvesting, during secondary succession; over this period, total ecosystem biomass would decrease (adapted from Vitousek and Reiners 1975).

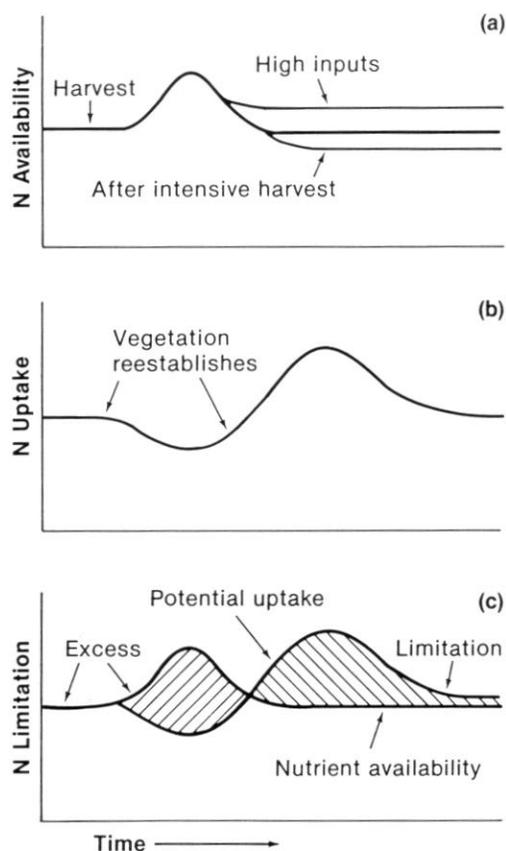


FIG. 2.8. Hypothesized trends for nitrogen (N) (a) availability, (b) uptake, and (c) limitation over time in a Douglas-fir forest.

SPECIFIC CHALLENGES FACING FOREST MANAGERS

The most important of the many challenges facing forest managers with respect to nutrients as they relate to long-term productivity are listed below.

- (1) Precisely determining long-term trends in forest productivity.
- (2) Determining an "ecological" rotation with natural input rates of nutrients and then decreasing this rotation length through management by, for example, using N-fixing species or less intensive harvesting.
- (3) Manipulating nutrient cycling processes by species selection. Stands of mixed tree species would be expected to behave differently from stands of an individual species. The effects of understory species need to be considered, both as nutrient competitors and as producers of readily decomposed litter.
- (4) Increasing nutrient availability by increasing the turnover rate of nutrients already on a site by, for example, reconfiguring cutting units.
- (5) Understanding the importance of woody debris.
- (6) Understanding the relationships between nutrient cycling, water regimes, and soil compaction.
- (7) Determining what is required to restore site productivity if management degrades it by removing nutrients.
- (8) Determining the nutrient implications of genetically selected trees. Will their nutritional needs be greater? There seems to be some potential for manipulating the efficiency of nutrient uptake by genetic means (Nambiar 1985).

RECOMMENDATIONS AND CONCLUSIONS

Nutrient cycling has been studied in the Northwest for more than 2 decades, and we still have much to learn about the effects of forest management on specific processes and, ultimately, long-term productivity. On the basis of our current knowledge and some "best guesses," we feel we can make the following recommendations to managers:

- (1) Conserve the nutrient capital on a site by using fire carefully and minimizing soil disturbance during site preparation. Fires should be hot enough to meet management objectives but no hotter. Make sure that benefits from fire (e.g., reduced brush competition) are not offset by costs (e.g., reduced nutrient availability). Avoid windrowing if possible, and otherwise minimize disturbance of the forest floor. If a chosen management regime entails substantial nutrient losses, consider writing the cost of replacing nutrients into timber-sale calculations. Organic matter losses, however, cannot be easily or cheaply replaced. Nutrient-rich sites, generally more robust than nutrient-poor sites, have greater nutrient capital and faster turnover rates. However, a 10% reduction in growth on a rich site is more costly in terms of wood production than a 10% reduction on a poor site. On nutrient-poor sites, grow trees over longer rotations, lessen harvest intensity, limb where trees fall, and minimize the use of fire.

Fertilization can restore lost productivity in Douglas-fir stands on poor sites after intensive harvest, as observed at Washington's Pack Forest (Bigger 1988) and from the South Australian experience (Farrell et al. 1986). Maintenance of woody debris could be important in managed plantations, particularly on poor sites, but we have little evidence for this as yet.

- (2) Aim at "relieving" vegetative competition in young plantations, rather than removing every single noncrop plant. Weed control generally increases nutrient availability. Although too many alders definitely suppress conifers, as few as 50 red alder/ha (20/acre) can substantially increase site N status because the alders fix nitrogen.
- (3) Take the opportunity to install "low-intensity" experiments. Instead of applying one treatment to an entire management unit, be creative—burn only three-quarters of a unit, or put a species mixture on one-tenth of a unit. With some careful recordkeeping, useful information can be collected without big investments in research.
- (4) Tie fertilizer applications to nutrient availability during a rotation—that is, apply the "optimum nutrition" concept. Try adding small amounts of fertilizer to individual trees at planting.
- (5) Communicate with specialists and researchers as much as possible.

QUESTIONS FROM THE SYMPOSIUM FLOOR

- Q: Can you critique the use of raw sewage sludge to increase nutrients to soil?
- A: Raw sewage is not applied to soils in the U.S.; only treated sewage is applied. It is a source of organic matter, N, P, and many other nutrient elements. Many tree species respond favorably to added sludge, including Douglas-fir, but there are some problems, including nitrate leaching, pathogens, heavy metals, and unwanted organic chemicals (see Cole et al. 1986).
- Q: You speculated that it may be possible to increase nutrient availability rather than applying fertilizers. Do you have any suggestions as to how this could be done?
- A: Opportunities for increasing wood production through manipulating nutrient availability are possible. What I was referring to was the Swedish "optimum nutrition" idea—adding all necessary elements at a rate determined by tree growth and beginning at an early age. This involves fertilization. Otherwise you would have to use N-fixing plants or increase the rate of decomposition (the latter is difficult to manage).
- Q: How significant is large woody debris in long-term nutrient availability? On a good site, would maximum utilization of the stand (removal of all woody debris) have any long-term impact, or would inputs from fine woody debris, foliage, and precipitation be sufficient to maintain long-term productivity?
- A: Large woody debris provides organic matter to the soil over a long period and thus is important to consider for maintaining long-term productivity. Woody debris is a site for N fixation but only provides a small fraction of the annual nutrient needs of trees. Needles and fine woody debris provide most of the readily available nutrients. Thus, from a nutrient point of view, maintenance of coarse woody debris may not be all that important for wood production on a good site. However, it may be important for a variety of other reasons, for example, animal habitats.
- Q: Is height growth or diameter growth the better measure of tree performance?

- A: In the early growth stages, height growth is probably a better measure. However, diameter growth is as good as or perhaps better than height once trees are out of their juvenile phase (e.g., older than 10 years).
- Q: On a moist site, where water is not limiting growth, how feasible would it be to accelerate tree height growth beyond that of brush by fertilizing heavily rather than controlling brush to reduce competition?
- A: I think it would be feasible as long as you applied the fertilizer so that the trees obtained most of it, e.g., in the planting hole.
- Q: Approximately when does nitrogen become deficient in relation to time (see the time axis in Figure 2.8)?
- A: Sometime near canopy closure.
- Q: How are N-fixation inputs measured? Indirectly, by assessing the presence of symbiotic N-fixing plants (e.g., alder), or directly, by studying actual N-fixation rates of free-living microflora (asymbiotic N fixation in soil and litter)?
- A: It has been done both ways in the Pacific Northwest. Nitrogen accretion with time has been determined with red alder and ceanothus. Acetylene reduction techniques have been used for free-living bacteria in litter, logs, and so forth.
- Q: Have you considered that some of the "weed" species—such as herbaceous species with rapid turnover of organic matter—may have a long-term benefit?
- A: These species are no doubt very important in the early stages of stand development, but their importance probably declines after canopy closure. Some understory species, however, such as Oregon grape (*Berberis aquifolium* Pursh), have sclerophyllous (tough) leaves and probably do not decompose very rapidly.
- Q: On sites where nutrients have been reduced by burning and/or whole-tree harvesting, can application of N following harvest return a site to its original level without further treatments?
- A: Average N losses by burning can be replaced through operational fertilization at 200 kg/ha of urea N. Thus, provided volatilization and leaching losses are not great, applying N following harvest could bring site N back to original levels. However, not all of the N will be taken up by the trees.
- Q: In the Pacific Northwest, is weed competition really a problem? I have planted thousands of trees on my place and they always seem to grow better in the brush. Early in the rotation when nutrients are in excess, weeds capture nutrients for release later in the rotation. Please expand on this.
- A: Weed competition is not a problem everywhere in the Pacific Northwest. It is more of a problem on stressed sites, particularly dry sites. It also appears to be a problem in moist areas in British Columbia where weeds establish very rapidly, resulting in inadequate tree stocking. In other areas there is no problem.
- Q: You state that "good" sites are more robust than "poor" sites. Don't you think that potential for absolute (not percent) productivity loss is greater on good sites? Similarly, isn't there more opportunity for enhanced productivity (total volume increase) by fertilizing on many good sites?
- A: You could realize greater absolute productivity loss on good sites, but in general there is an excess of nutrients on these sites, with a lot of nutrients in the "bank." The treatment has to be pretty drastic to have a lasting effect. This is why good sites are not as responsive to fertilization as poor sites. However, if the value of a log on a good site is increased by a small diameter increase, then it might be worth doing.
- Q: Would you comment on the cumulative effect—that is, the effect over several rotations—of losses or gains of nitrogen, phosphorus, and other nutrients without fertilization.
- A: Whether or not cumulative effects occur depends on level of utilization, method of site preparation, nutrient replacement rates, and rotation length. Considering only the nutrients removed in logs, there is probably no cumulative effect; sufficient nutrients are added through natural processes over a rotation to balance removals. Whole-tree harvest greatly increases nutrient removals; studies in both western and eastern North America show excessive losses of calcium associated with whole-tree harvest. When clearcuts are broadcast burned, some proportion of the nitrogen and sulfur contained in logging residues and forest floor is volatilized and lost as gas. What proportion depends on the heat of the burn. If N-fixing plants such as alder and ceanothus occupy a site, nitrogen losses even from intense burns are probably replaced within 5–20 years. Without N-fixing plants, annual nitrogen inputs in the Pacific Northwest total 3–5 kg/ha. Over a 60-year rotation, this would amount to 200–300 kg/ha—enough to balance losses from cool burns, but probably not from moderate burns and certainly not from hot ones. Shorter rotations increase the chance of cumulative effects, longer rotations decrease it. Windrowing is a more severe treatment than broadcast burning in that all nutrients in logging residues, forest floor, and frequently topsoil are removed from most of the site and concentrated on a small portion. Much evidence shows that windrowing is bad news.

REFERENCES

- Axelsson, B. 1985. "Increasing forest productivity and value by manipulating nutrient availability." In *Forest potentials—productivity and value*, edited by R. Ballard, P. Farnum, G. A. Ritchie, and J. K. Winjum, 5–38. Tacoma, Wash.: Weyerhaeuser Science Symposium 4.
- _____. 1986. "Difference in yield at different sites: an irrigation-fertilization study of nutrient flux during fast growth." In *Forest site and productivity*, edited by S. P. Gessel, 171–183. Dordrecht/Boston: Martinus Nijhoff Publisher.
- Ballard, R. 1978. Effect of slash and soil removal on the productivity of second rotation radiata pine on a pumice soil. *New Zealand Journal of Forest Science* 8:252–260.
- Ballard, T. M., and R. E. Carter. 1985. *Evaluating forest stand nutrient status*. Land Management Report No. 20. Victoria, B.C.: British Columbia Ministry of Forests.
- Berg, B., and H. Staaf. 1980. Decomposition rate and chemical changes of Scots pine needle litter. II. The influence of chemical composition. *Ecological Bulletin (Stockholm)* 32:373–390.
- Bigger, C. M. 1988. *Effects of harvest intensity on nutrient removal, nutrient leaching, and growth of seedlings in individual stands of high and low productivity red alder and Douglas-fir*. Ph.D. Thesis. Seattle, Wash.: College of Forest Resources, University of Washington.
- Bigger, C. M., and D. W. Cole. 1983. "Effects of harvesting intensity on nutrient losses and future productivity in high and low productivity red alder and Douglas-fir stands." In *Proceedings IUFRO symposium on forest site and continuous productivity*, edited by R. Ballard and S. P. Gessel, 167–178. General Technical Report PNW-163. Portland, Ore.: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service.
- Binkley, D. 1984. Does forest removal increase rates of decomposition and nitrogen release? *Forest Ecology and Management* 8:229–233.
- _____. 1986. *Forest Nutrition Management*. New York: John Wiley.
- Binkley, D., K. Cromack, and R. L. Fredricksen. 1982. Nitrogen accretion and availability in some snowbrush ecosystems. *Forest Science* 28:720–724.
- Binkley, D., and P. Matson. 1983. Ion exchange resin bag method for assessing forest nitrogen availability. *Soil Science Society of America Journal* 47:1050–1052.
- Blake, J. I. 1985. *Characterization of soil nitrogen and sulfur availability in relation to response of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) in western Oregon and Washington*. Ph.D. Thesis. Seattle, Wash.: College of Forest Resources, University of Washington.
- Bormann, B. T., and D. S. DeBell. 1981. Nitrogen content and other soil properties related to age of red alder stands. *Soil Science Society of America Journal* 45:428–432.
- Bormann, F. H., and G. E. Likens. 1979. *Pattern and Process in a forested ecosystem*. New York: Springer Verlag.
- Brix, H. 1971. Effects of nitrogen fertilization on photosynthesis and respiration in Douglas-fir. *Forest Science* 17:407–414.
- Carter, R. E., J. Otchere-Boateng, and K. Klinka. 1984. Dieback of a 30-year-old Douglas-fir plantation in the Brittain River Valley, British Columbia: symptoms and diagnosis. *Forest Ecology and Management* 7:249–263.
- Carter, R. E., A. M. Scagel, and K. Klinka. 1986. Nutritional aspects of distorted growth in immature forest stands in southwestern British Columbia. *Canadian Journal of Forest Research* 16:36–41.
- Chapin, F. S., P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. *American Naturalist* 127:48–58.
- Cole, D. W. 1986. "Nutrient cycling in world forests." In *Forest site and productivity*, edited by S. P. Gessel, 103–115. Dordrecht/Boston: Martinus Nijhoff Publisher.
- Cole, D. W., C. L. Henry, and W. L. Nutter (editors). 1986. *The forest alternative for treatment and utilization of municipal and industrial wastes*. Seattle, Wash.: University of Washington Press.
- Cole, D. W., and M. Rapp. 1981. "Elemental cycling in forest ecosystems." In *Dynamic properties of forest ecosystems*, edited by D. E. Reichle, 341–409. London: Cambridge University Press.
- Cushon, G. H. 1985. *Gaseous nitrogen transformations in a mature forest ecosystem*. M.S. Thesis. Vancouver, B.C.: University of British Columbia.
- Ebermayer, E. 1876. *Die gesamte lehre der waldstreu mit rücksicht auf die chemische statik des waldbaues*. Berlin: Julius Springer Publisher.
- Edmonds, R. L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock and Pacific silver fir ecosystems in western Washington. *Canadian Journal of Forest Research* 10:327–337.
- _____. 1984. Long-term decomposition and nutrient dynamics in Pacific silver fir needles in western Washington. *Canadian Journal of Forest Research* 14:395–400.
- _____. 1987. Decomposition rates and nutrient dynamics in small diameter woody litter in four forest

- ecosystems in Washington, USA. *Canadian Journal of Forest Research* 17:499–509.
- Edmonds, R. L., and C. M. Bigger. 1983. "Decomposition and nitrogen mineralization rates in Douglas-fir needles in relation to whole tree harvesting practices." In *Proceedings of the Society of American Foresters national convention*, 187–192. Washington, D.C.: Society of American Foresters.
- Edmonds, R. L., and T. Hsiang. 1987. Forest floor and soil influence on response of Douglas-fir to urea. *Soil Science Society of America Journal* 51:1332–1337.
- Entry, J. A., N. M. Stark, and H. Loewenstein. 1986. Effect of timber harvesting on microbial biomass fluxes in a northern Rocky Mountain forest soil. *Canadian Journal of Forest Research* 16:1076–1081.
- Everard, J. 1973. Foliar analysis sampling methods interpretation and application of results. *Quarterly Journal of Forestry* 67:51–66.
- Farr, W. A., A. S. Harris, and S. N. Israilson. 1977. *Effects of an aerial application of urea fertilizer on young Sitka spruce and western hemlock at Thomas Bay, Alaska*. Research Paper PNW-219. Portland, Ore.: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service.
- Farrell, P. W., D. W. Flinn, R. O. Squire, and F. G. Craig. 1986. "Maintenance of productivity of radiata pine monocultures on sandy soils in southeastern Australia." In *Forest site and productivity*, edited S. P. Gessel, 127–136. Dordrecht/Boston: Martinus Nijhoff Publisher.
- Feller, M. C., and J. P. Kimmins. 1984. Effects of clearcutting and slashburning on streamwater chemistry and watershed nutrient budgets in southwestern British Columbia. *Water Resources Research* 20:29–40.
- Feller, M. C., J. P. Kimmins, and K. A. Scouler. 1983a. "FORCYTE 10: calibration data and simulation of potential long-term effects of intensive forest management on site productivity, economic performance, and energy cost/benefit ratio." In *Proceedings IUFRO symposium on forest site and continuous productivity*, edited by R. Ballard and S. P. Gessel, 179–200. General Technical Report PNW-163. Portland, Ore.: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service.
- Feller, M. C., J. P. Kimmins, and K. M. Tsze. 1983b. "Nutrient losses to the atmosphere during slashburns in southwestern British Columbia." In *Proceedings of the 7th conference on fire and forest meteorology*, 128–135. Boston, Mass.: American Meteorological Society.
- Fogel, R., and K. Cromack, Jr. 1977. Effect of habitat and substrate quality in Douglas-fir needle decomposition in western Oregon. *Canadian Journal of Botany* 55:1632–1640.
- Fujimori, T. 1971. *Primary productivity of a young Tsuga heterophylla stand and some speculations about biomass of forest communities on the Oregon coast*. Research Paper PNW-123. Portland, Ore.: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service.
- Gessel, S. P., E. C. Steinbrenner, and R. E. Miller. 1979. "Response of Northwest forests to elements other than nitrogen." In *Proceedings of forest fertilization conference*, edited by S. P. Gessel, R. M. Kenady, and W. Atkinson, 140–149. Contribution No. 40. Seattle, Wash.: Institute of Forest Resources, College of Forest Resources, University of Washington.
- Gessel, S. P., and J. Turner. 1976. Litter production in western Washington Douglas-fir stands. *Forestry* 49:63–72.
- Gholz, H. L. 1982. Environmental limits on aboveground net primary production, leaf area and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63:469–487.
- Grier, C. C. 1978. A *Tsuga heterophylla*—*Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Canadian Journal of Forest Research* 8:198–206.
- Grier, C. C., T. M. Hinckley, K. A. Vogt, and S. T. Gower. 1986. "Net primary production in Douglas-fir ecosystems: its relation to moisture and mineral nutrition." In *Douglas-fir: stand management for the future*, edited by C. D. Oliver, D. P. Hanley, and J. A. Johnson, 155–161. Contribution No. 55. Seattle, Wash.: Institute of Forest Resources, College of Forest Resources, University of Washington.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.
- Heilman, P. E. 1979. "Minerals, chemical properties and fertility of forest soils." In *Forest soils of the Douglas-fir Region*, edited by P. E. Heilman, H. W. Anderson, and D. M. Baumgartner, 121–136. Pullman, Wash.: Cooperative Extension Service, Washington State University.
- Ingestad, T. 1974. Towards optimum nutrition. *Ambio* 3:49–54.
- _____. 1982. Addition rate and concentration. Relative addition rate and external concentration; driving variables used in plant nutrition research. *Plant Cell and Environment* 5:443–453.
- Johnson, D. W., D. W. Cole, C. S. Bledsoe, K. Cromack, R. L. Edmonds, S. P. Gessel, C. C. Grier, B. N. Richards, and K. A. Vogt. 1982. "Nutrient cycling in the Pacific Northwest." In *Analysis of coniferous forest ecosystems in the western United States*, edited by R. L. Edmonds, 186–232. Stroudsburg, Pa.: Hutchinson Ross Publishing Company.

- Jurgensen, M. F., M. J. Larsen, and A. E. Harvey. 1979. *Forest soil biology—timber harvesting relationships*. General Technical Report INT-69. Ogden, Utah: Intermountain Forest and Range Experiment Station, USDA Forest Service.
- Keeves, A. 1966. Some evidence of loss of productivity with successive rotations of *Pinus radiata* in the south-east of South Australia. *Australian Forestry* 30:52–63.
- Keyes, M. R., and C. C. Grier. 1981. Above- and below-ground net production in 40 year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research* 11:599–605.
- Lavender, D. P., and R. B. Walker. 1979. "Nitrogen and related elements in nutrition of forest trees." In *Proceedings of forest fertilization conference*, edited by S. P. Gessel, R. M. Kenady, and W. A. Atkinson, 15–22. Contribution No. 40. Seattle, Wash.: Institute of Forest Resources, College of Forest Resources, University of Washington.
- Leaf, A. L. (editor) 1979. *Proceedings of a conference on the impact of intensive harvesting on forest nutrient cycling*. Syracuse, N.Y.: School of Forestry, State University of New York.
- Lewis, R., and A. Abee. 1981. "Site preparation for skeletal soils." In *Reforestation of skeletal soils*, edited by S. D. Hobbs and O. T. Helgerson, 40–49. Corvallis, Ore.: Forest Research Laboratory, Oregon State University.
- Little, S. N., and G. O. Klock. 1985. *The influence of residue removal and prescribed fire on distribution of forest nutrients*. Research Paper PNW-338. Portland, Ore.: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service.
- Long, J. N. 1982. "Productivity of western coniferous forests." In *Analysis of coniferous forest ecosystems in the western United States*, edited by R. L. Edmonds, 89–125. Stroudsburg, Pa.: Hutchinson Ross Publishing Company.
- Marshall, J. D., and R. H. Waring. 1986. Comparison of methods of estimating leaf-area index in old-growth Douglas-fir. *Ecology* 67:975–979.
- McClougherty, C. A., J. Pastor, J. D. Aber, and J. M. Melillo. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology* 66:266–275.
- McCull, J. G., and D. F. Grigal. 1979. "Nutrient losses in leaching and erosion by intensive forest harvesting." In *Proceedings of a conference on the impact of intensive harvesting on forest nutrient cycling*, edited by A. L. Leaf, 231–248. Syracuse, N.Y.: School of Forestry, State University of New York.
- McCull, J. G., and R. F. Powers. 1984. "Consequences of forest management on soil-tree relationships." In *Nutrition of plantation forests*, edited by G. D. Bowen and E. K. S. Nambiar, 379–412. London: Academic Press.
- Miller, H. G. 1981. "Nutrient cycles in forest plantations, their change with age and the consequence for fertilizer practice." In *Proceedings Australian forest nutrition workshop*, edited by N. G. Turvey, 187–199. Canberra: Division of Forest Research, CSIRO.
- _____. 1984. "Dynamics of nutrient cycling in plantation ecosystems." In *Nutrition of plantation forests*, edited by G. D. Bowen and E. K. S. Nambiar, 53–78. London: Academic Press.
- Miller, R. E., P. R. Barker, C. E. Peterson, and S. R. Webster. 1986. "Using nitrogen fertilizers in management of coast Douglas-fir. I. Regional trends of response." In *Douglas-fir stand management for the future*, edited by C. D. Oliver, D. P. Hanley, and J. A. Johnson, 290–303. Contribution No. 55. Seattle, Wash.: Institute of Forest Resources, College of Forest Resources, University of Washington.
- Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. *Ecology* 66:1377–1390.
- Nambiar, E. K. S. 1985. "Increasing forest productivity through genetic improvements of nutritional characteristics." In *Forest potentials—productivity and value*, edited by R. Ballard, P. Farnum, G. A. Ritchie, and J. K. Winjum, 191–215. Tacoma, Wash.: Weyerhaeuser Science Symposium 4.
- Perry, D. A., and S. L. Rose. 1989. "Productivity of forest lands as affected by site preparation." In *Proceedings of the California conference on forest tree nutrition and soil fertility*, edited by R. Powers and T. Robson. Berkeley, Calif.: Pacific Southwest Forest and Range Experiment Station, USDA Forest Service. (In press).
- Peterson, C. E. 1982. "Regional growth and response analysis for unthinned Douglas-fir." In *Regional forest nutrition project biennial report*, 3–25. Seattle, Wash.: College of Forest Resources, University of Washington.
- Peterson, C. E., Jr., and S. P. Gessel. 1983. "Forest fertilization in the Pacific Northwest: results of the regional forest nutrition research project." In *Proceedings IUFRO symposium on forest site and continuous productivity*, edited by R. Ballard and S. P. Gessel, 365–369. General Technical Report PNW-163. Portland, Ore.: Pacific Northwest Forest and Range Experiment Station, USDA Forest Service.
- Porada, H. J. 1987. *The effect of aluminum on the growth and mineral composition of Douglas-fir and western hemlock*. Ph.D. Thesis. Seattle, Wash.: College of Forest Resources, University of Washington.
- Powers, R. F. 1980. Mineralizable soil nitrogen as an index of nitrogen availability to forest trees. *Soil Science Society of America Journal* 44:1314–1320.

- Radwan, M. A., and H. Brix. 1986. "Nutrition of Douglas-fir." In *Douglas-fir stand management for the future*, edited by C. D. Oliver, D. P. Hanley, and J. A. Johnson, 177–188. Contribution No. 55. Seattle, Wash.: Institute of Forest Resources, College of Forest Resources, University of Washington.
- Radwan, M. A., and J. S. Shumway. 1983. Soil nitrogen, sulfur, and phosphorus in relation to growth response of western hemlock to nitrogen fertilization. *Forest Science* 29:469–477.
- Shumway, J. S. 1984. "Total nitrogen, mineralizable nitrogen and site index as guides to fertilization of Douglas-fir." In *Nitrogen assessment workshop*, compiled by R. F. Strand, 57–59. Report No. 2. Seattle, Wash.: Regional Forest Nutrition Project, College of Forest Resources, University of Washington.
- Shumway, J. S., and W. A. Atkinson. 1978. Predicting nitrogen fertilizer response in unthinned stands of Douglas-fir. *Communications in Soil Science and Plant Analysis* 9:529–539.
- Stone, E. L., and G. M. Will. 1965. "Nitrogen deficiency of second generation radiata pine in New Zealand." In *Forest soil relationships in North America*, edited by C. T. Youngberg, 118–139. Corvallis, Ore.: Oregon State University Press.
- Strand, R. F. (compiler). 1984. *Nitrogen assessment workshop*. Report No. 2. Seattle, Wash.: Regional Forest Nutrition Project, College of Forest Resources, University of Washington.
- Tamm, C. O. 1979. "Nutrient cycling and productivity of forest ecosystems." In *Proceedings of a conference on the impact of intensive harvesting on forest nutrient cycling*, edited by A. L. Leaf. Syracuse, 2–21. N.Y.: School of Forestry, State University of New York.
- Turner, J., M. J. Lambert, and S. P. Gessel. 1977. Use of foliage sulfate concentrations to predict response to urea application in Douglas-fir. *Canadian Journal of Forest Research* 7:476–480.
- van den Driessche, R. 1979. "Estimating potential response to fertilizer based on tree tissue and litter analysis." In *Proceedings of forest fertilization conference*, edited by S. P. Gessel, R. M. Kenady, and W. A. Atkinson, 214–220. Contribution No. 40. Seattle, Wash.: Institute of Forest Resources, College of Forest Resources, University of Washington.
- Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, W. A. Reiners, and R. L. Todd. 1979. Nitrate losses from disturbed ecosystems. *Science* 204:469–474.
- Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* 25:376–381.
- Vogt, D. J., and R. L. Edmonds. 1982. Nitrate and ammonium levels in relation to site quality in Douglas-fir soil and litter. *Northwest Science* 56:83–89.
- Vogt, D., K. Vogt, S. Gower, and C. Grier. 1986a. Long-term N fertilization effect on above- and belowground biomass and production for Douglas-fir. Abstract. Syracuse, N.Y.: 71st Annual Meeting, Ecological Society of America.
- Vogt, K. A., C. C. Grier, C. E. Meier, and M. R. Keyes. 1983a. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington as affected by fine root input. *Ecological Monographs* 53:139–157.
- Vogt, K. A., C. C. Grier, and D. J. Vogt. 1986b. Production, turnover, and nutrient dynamics of above and belowground detritus in world forests. *Advances in Ecological Research* 15:303–377.
- Vogt, K. A., E. E. Moore, D. J. Vogt, M. J. Redlin, and R. L. Edmonds. 1983b. Conifer fine root and mycorrhizal biomass within the forest floor of Douglas-fir stands of different ages and site productivities. *Canadian Journal of Forest Research* 13:429–437.
- Waring, R. H., and W. H. Schlesinger. 1985. *Forest Ecosystems—Concepts and Management*. New York: Academic Press.
- Webster, S. R., D. S. DeBell, K. N. Wiley, and W. A. Atkinson. 1976. "Fertilization of western hemlock." In *Western hemlock management*, edited W. A. Atkinson and R. J. Zasoski, 247–252. Contribution No. 34. Seattle, Wash.: Institute of Forest Products, College of Forest Resources, University of Washington.
- Weetman, G. F., and R. Fournier. 1982. Graphical diagnoses of lodgepole pine response to fertilization. *Soil Science Society of America Journal* 46:1280–1289.
- Will, G. 1985. *Nutrient deficiencies and fertilizer use in New Zealand exotic forests*. Forest Research Bulletin 97. Rotorua, New Zealand: Forest Research Institute, N. Z. Forest Service.
- Woods, R. V. 1980. *An investigation into the relationship between fire and nutrient depletion leading to decline in productivity between rotations of Pinus radiata plantations in South Australia*. Miscellaneous Publication 37. Adelaide, South Australia: Woods and Forests Department of South Australia.