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NUTRIENT CYCLING IN 37- AND 450-YEAR-OLD DOUGLAS-FIR ECOSYSTEMS[1]

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ABSTRACT

Biomass and nitrogen, phosphorus, potassium, and calcium distribution, and biogeochemical and stand nitrogen, phosphorus, potassium, and calcium budgets were determined for 37- and 450-year-old *Pseudotsuga menziesii* (Mirb.) Franco stands in the U.S. Pacific Northwest. Biomass of the 450-year-old stand is greater, but annual growth is less than that of the 37-year-old stand. About 50% of the annual growth and over 50% of the nutrient uptake and return in the 450-year-old stand occurs in subordinate vegetation compared with less than 15% in the 37-year-old stand. Chemical differences in soil parent material between the two stands are reflected in both the biogeochemical and stand nutrient cycles.

INTRODUCTION

Coniferous forests of the U.S. Pacific Northwest are among the most productive forests in the world. In the Douglas-fir region, for example, stands often reach 1000 metric tons ha^{-1} of standing biomass in 100 years. Because nutrients are involved in almost all ecosystem processes, studies of nutrient movement and accumulation yield a great deal of information about factors affecting productivity of these forests. Further, studies of nutrient cycling contribute much to understanding overall behavior of coniferous forest ecosystems.

In general terms, the objectives of nutrient cycling research of the Coniferous Forest Biome are: (1) to study the role of nutrients in ecosystem function; (2) to develop conceptual and simulation models representing our understanding of nutrient cycling; and (3) to use those models both to extend our understanding of ecosystems and to evaluate the effects of various perturbations on ecosystem processes and entire ecosystems.

This paper is intended as an overview of current nutrient cycling research in the Coniferous Forest Biome. The discussion here emphasizes research directed toward meeting the first two of the above objectives with the research reported by comparing nutrient cycling between two intensive research sites. A comparison of nutrient cycling rates and processes between the 37- and 450-year-old stands on these sites should increase our understanding of some of the broader aspects of ecosystem behavior.

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[1]This is contribution no. 61 from the Coniferous Forest Biome.

RESEARCH AREAS

Thompson Research Center, Washington

The Allan E. Thompson Research Center is a research area developed for study of nutrient cycling in second-growth Douglas-fir stands. It is located about 64 km southeast of Seattle, Washington, at an elevation of 215 m in the foothills of the Washington Cascades. A full description of the geology, soils, vegetation, and climate is given by Cole and Gessel (1968).

The study site is located on a glacial outwash terrace along the Cedar River. This outwash terrace was formed during the recessing of the Puget lobe of the Fraser ice sheet about 12,000 years ago.

The soil underlying the research plot described in this paper is classified as a Typic Haplorthod (U.S. Department of Agriculture 1960, 1972) and is mapped as Everett gravelly sand loam. This soil contains less than 5% silt plus clay and normally contains gravel amounting to 50%-80% of the soil volume. The forest floor is classified as a duff-mull (Hoover and Lunt 1952) and ranges from 1 cm to 3 cm thick. This forest floor represents the accumulation since 1931 when the present stand was established following logging (around 1915) and repeated fires.

The present overstory vegetation is a planted stand of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) which was established about 1931. Currently, the trees average about 19 m high with a crown density of about 85%.

The principal understory species are salal (*Gaultheria shallon* Pursh.), Oregon grape (*Berberis nervosa* [Pursh] Nutt.), red huckleberry (*Vaccinium parvifolium* Smith), and twinflower (*Linnaea borealis* L. ssp. *americana* [Forbes] Rehder). Various mosses are the principal understory vegetation beneath the denser portions of the canopy.

The climate is typical of foothill conditions in the Puget Sound basin. Temperatures have ranged from -18°C to 38°C, but these extremes are seldom reached. The average temperature for July is 16.7°C and for January is 2.8°C. The average annual precipitation is 136 cm, almost all falling as rain. Precipitation rates are generally less than 0.25 cm hr^{-1} and over 70% of precipitation falls between October and March.

Watershed 10, H. J. Andrews Experimental Forest, Oregon

Watershed 10 is a 10.24-ha watershed located in the western Cascade Range about 70 km east of Eugene, Oregon. Elevations on the watershed range from 430 m at the stream gaging station to about 670 m at the highest point. Slopes on the watershed average about 45% but frequently exceed 100%.

The study site is located in an area underlain by volcanic tuff and breccia. Soils of the watershed are derived from these materials. Soils of the watershed are classified as Typic Dystrochrepts (Inceptisol, U.S. Department of Agriculture, 1960, 1972) and range from gravelly, silty clay loam to very gravelly clay loam. The <2-mm fraction of these soils ranges from 20% to 50% clay and contains gravel amounting to 30%-50% of the soil volume. The forest floor ranges from 3 to 5 cm thick and is classified as a duff-mull (Hoover and Lunt 1952).

The present overstory vegetation is dominated by a 60- to 80-m-tall, 450-year-old stand of Douglas-fir (*Pseudotsuga menziesii*) containing small islands of younger age classes. Distribution of understory vegetation reflects topography and slope-aspect on this watershed. Dry ridgetops and south-facing slopes have an understory composed primarily of chinkapin (*Castanopsis chrysophylla*), Pacific rhododendron (*Rhododendron macrophyllum*), and salal. More mesic parts of the watershed support an understory of vine maple (*Acer circinatum*), rhododendron, and Oregon grape, with a well developed intermediate canopy of *Tsuga heterophylla*. Subordinate vegetation of the moist areas along the stream and on north-facing slopes is primarily vine maple and sword fern (*Polystichum munitum*).

The climate of watershed 10 is typical for the western Oregon Cascades. Average annual precipitation is 230 mm per year with over 75% of the precipitation falling as rain between October and March. Snow accumulations on the watershed are not uncommon, but seldom last more than two weeks. Based on two years' data, the average daytime temperature for July is 21°C and for January is 0°C. Observed extremes have ranged from a high of 41°C in August to a low of -20°C in December.

METHODS

Mapping of Watershed 10

A 25-m by 25-m grid system, corrected to horizontal distance, was established on watershed 10. All mapping used this grid system for reference. Soils were mapped on the basis of depth, stone and gravel content, and water storage in the upper 100 cm of profile. Subordinate vegetation was mapped using methods outlined by G. M. Hawk (pers. commun., 1973). Diameter, species, and location of all living and standing dead trees on the watershed greater than 15 cm dbh (diameter breast height) were mapped. These data were punched on computer cards. Trees less than 15 cm dbh were considered to be understory vegetation.

Organic Matter and Nutrient Distribution

Biomass, nutrient capital, and productivity of the overstory vegetation of the Thompson site were estimated from destructive analysis of trees from that area (Dice 1970). Overstory biomass and nutrient distribution on watershed 10 were estimated from regression equations using diameter and species data compiled for the stem map. The regression equations were based on data from destructive analysis of the major overstory species on the watershed based on a modification of the fixed-internal stratification method outlined by Monsi and Saeki (1953). The modification used consisted of dividing both the branchless stem and the canopy of each felled sample tree into three equal segments and weighing and sampling component mass in each of these segments.

Annual growth of stands on watershed 10 was estimated as follows: Average diameter increment over the past five years was determined for 10-cm-diameter classes for each species on the watershed. This increment was added to recorded tree diameters according to species and diameter class and overstory biomass was recomputed using the new diameters. Productivity was then estimated as the difference between the first and second biomass estimates. Nutrient distribution in overstory biomass and nutrients incorporated in new growth were estimated by sampling and analyzing new growth and older plant components during the sampling for biomass estimation.

Understory biomass and nutrient distribution on watershed 10 were estimated by regression methods based on destructive sampling for larger understory species, while the mass of smaller shrubs and herbs was determined by total harvest. Methods used in understory biomass estimates are described by Russel (1973). Understory biomass and nutrient capital of the Thompson site was determined by harvest of small plots.

Litter layer mass on watershed 10 was determined by sampling the litter layer in two areas representative of the entire watershed. Total and exchangeable nutrients; water storage; depth of L, F, and H layers; and litter mass were determined using methods outlined by Youngberg (1966). Litter layer mass and nutrient capital at the Thompson site were determined using methods reported by Grier and McColl (1971).

The mass of standing and down dead trees on watershed 10 was estimated from data gathered during stem mapping. Heights of standing dead trees were estimated and diameters were measured. Length and diameter of all recognizable fallen trees were measured. Similar methods were used for the Thompson site. Mass of standing and down dead was computed from the Smalian volume of logs and standing dead, assuming a density of 0.3 and a uniform taper of 2%.

Soil nutrient and organic matter content of watershed 10 were determined by sampling of soil in the areas where litter mass was determined. Total and exchangeable nutrients and organic matter were determined by methods outlined by R. B. Brown and R. B. Parsons (pers. commun., 1973). Methods used for soil analysis at the Thompson site are outlined by Grier and Cole (1972).

Epiphyte standing crop and nitrogen content in the overstory of watershed 10 were determined by methods reported by Pike et al. (1972). Epiphytes are a negligible component of the stand at the Thompson site.

Organic Matter and Nutrient Fluxes

Litterfall at both sites is collected on screens placed approximately 15 cm above the soil surface. Eight 0.21-m^2 screens are used in the plot at the Thompson site. On watershed 10, litter is collected from 75 0.26-m^2 screens located randomly within each of the 15 soil-vegetation units with approximately the same area sampled in each unit. Total area sampled is 0.41% for the Thomson site and 0.02% on watershed 10. Litter is collected monthly, dried at 70°C, and sorted into the following categories: conifer foliage, hardwood foliage, woody material, reproductive parts, living foliage and twigs, and "other material." Nutrient content of each of these categories is determined.

Throughfall at both sites is collected in 20-cm-diameter polyethylene funnels having a neck screen of the same mesh as the litter screens. The funnels are inserted in 20-liter polyethylene bottles and the assembly is placed immediately adjacent to each litter screen. Eight collectors are used at the Thompson site and 75 are used on watershed 10. Litter is allowed to collect in the funnels so that nutrients leached from the litter are collected in throughfall. Collections are made monthly and analyses are performed on unfiltered samples. Chloroform is added to the collectors to retard microbial effects on water chemistry.

Stemflow on watershed 10 is collected on fifteen 10-m by 10-m plots in which all trees >5 cm dbh are fitted with polyurethane foam collars at breast height (Likens and Eaton 1970). On each plot, water is piped from the sampled trees to a group of opaque 125-liter polyethylene trash cans fitted with tight lids. Collections are made as necessary to avoid overflow, with a maximum interval of one month. At the Thompson site, stemflow is diverted from six representative trees into opaque 160-liter trash cans by rubber collars at breast height (130 cm).

Litter decomposition studies based on litterbags filled with specific substrates are in progress on watershed 10. Methods used are reported by Cromack (1973). Mineralization and leaching of nutrients from the litter layer are directly measured at both sites using tension lysimeters (Cole 1968).

Nutrient leaching in the soil profile at the Thompson site is measured with tension lysimeters placed at the lower boundaries of the A1 and B2 horizons and at 1 m in the C horizon to collect percolating soil water. On watershed 10, Soiltest soil solution extractors are placed at the base of the rooting zone (1 m) and at different depths in the subsoil to determine nutrient concentrations in the subsoil water.

Incorporation of nutrients into growth by overstory and understory vegetation was estimated by sampling and analysis of new growth at the end of the growing season and using nutrient concentrations and annual growth estimates to compute nutrient content of new growth.

Annual biogeochemical nutrient budgets for watershed 10 were prepared from measurements of quantity and chemistry of input and outflow water. Methods used are reported by Fredriksen (1972). Annual budgets for the Thompson site are based on data from the lysimeter installation (Cole et al. 1968). Chemical analyses of plant tissue and water were done using methods outlined by Grier and Cole (1972) and Fredriksen (1972).

RESULTS AND DISCUSSION

As would be expected, there are large differences in distribution of organic matter, nitrogen, phosphorus, potassium, and calcium between the 37-year-old stand of the Thompson site and 450-year-old stand on watershed 10 (Tables 1 and 2). These differences reflect not only the age difference between the stands but also differences in soil and soil parent material. In terms of biomass and nutrient distribution, age differences between these two ecosystems are best illustrated by the larger accumulation of stem biomass, subordinate vegetation, and woody litter on watershed 10.

The stem mass on watershed 10 is about 3.4 times greater than that of the Thompson site. In contrast, the proportional difference in nutrients in boles on the two sites is smaller with N, 1.5; P, 0.63; K, 1.3; and Ca, 2.4 times greater on watershed 10 than on the Thompson site. These differences reflect a changed proportion of relatively high-nutrient-content sapwood between young and old stands. Sapwood normally has higher nutrient concentrations than heartwood (Kramer and Kozlowski 1960). Since sapwood basal area is directly proportional to foliage mass in Douglas-fir (Grier and Waring 1974) and the foliage mass of the two sites is about the same, the differences are due to the higher proportion of heartwood on watershed 10.

Overstory foliage mass of the two stands is essentially the same. This supports numerous observations regarding stabilization of overstory foliage mass early in stand growth (Marks and Bormann 1972) with only minor fluctuations later, largely because of mortality and breakage. On watershed 10, however, overstory foliage is concentrated on a relatively few large trees leaving numerous gaps in the canopy. These light gaps are responsible for a much greater mass of understory vegetation on watershed 10 than beneath the denser canopy of the Thompson site (Tables 1 and 2).

Table 1. Organic matter, nitrogen, phosphorus, potassium, and calcium distribution in vegetation, soil, and litter in a second-growth Douglas-fir ecosystem, watershed 10, Andrews Forest, Oregon.

System component	Organic matter ($kg\ ha^{-1}$)	Nutrient content ($kg\ ha^{-1}$) N	P	K	Ca
Overstory					
Foliage	8,906	75	20	70	93
Branches	48,543	49	10	49	243
Bole	472,593	189	12	123	284
Understory					
Large shrubs and small trees					
Foliage	1,604	17	2	5	10
Stems	4,834	8	3	7	21
Small shrubs					
Foliage	1,991	17	2	9	11
Stems	270	1		1	1
Herb layer	65	1		1	1
Epiphytes	1,100	14	ND	ND	ND
Roots (all plants)	74,328	62	5	21	97
Total vegetation	614,234	433	54	286	761
Litter layer					
01 + 02[a]	43,350	434	61	50	363
Logs	55,200	132	9	20	80
Soil (0-100 cm)	79,250[b]	4300	29[c]	1200[d]	5500[d]
TOTAL ECOSYSTEM	792,034	5300	153	1556	6704

[a]01 = fresh litter; 02 = litter in various stages of decomposition. [b]Walkley-Black carbon. [c]Exchangeable phosphorus. [d]Ammonium acetate extracted. ND = not determined.

Table 2. Organic matter, nitrogen, phosphorus, potassium, and calcium distribution in vegetation, soil, and litter in a second-growth Douglas-fir ecosystem, Thompson Research Center, Washington (from Cole et al. 1968).

System component	Organic matter ($kg\ ha^{-1}$)	Nutrient content ($kg\ ha^{-1}$) N	P	K	Ca
Overstory					
Foliage					
Current	1,990	24	5	16	7
Older	7,107	78	24	46	66
Branches					
Current	513	4	1	3	[illegible]
Older	13,373	40	9	32	65
Dead	8,145	17	2	3	39
Wood					
Current	7,485	10	2	10	4
Older	114,202	67	7	42	43
Bark	18,728	48	10	44	[illegible]
Roots	32,986	32	6	24	[illegible]
Total tree	204,529	320	66	220	333
Understory	1,010	6	1	7	[illegible]
Litter layer					
01 + 02	16,427	161	24	24	[illegible]
Logs	6,345	14	2	8	17
Total forest floor	22,772	175	26	32	[illegible]
Soil (0-60 cm)	111,552[a]	2,809	3,871[b]	234[c]	[illegible]
TOTAL ECOSYSTEM	339,863	3,310	3,971	493	[illegible]

[a]Total carbon times 2. [b]Total phosphorus. [c]Ammonium acetate extracted.

The large mass of understory vegetation on watershed 10, relative to the Thompson site, implies major differences in nutrient cycling pathways between young- and old-growth stands. Calculations, based on average foliage turnover rates for understory and overstory species of the two sites, indicate that between 40% and 60% of leaf litterfall on watershed 10 is contributed by understory compared with about 15% for the Thompson site. The large litter input from understory vegetation on watershed 10 is confirmed by litterfall data indicating that from 10% to 70% of annual leaf litter input on individual litter screens is hardwood foliage (C. C. Grier, unpublished data).

Generally, nutrient return by foliage of understory vegetation should be proportionally greater than overstory foliage return because of the generally higher nutrient content of hardwood foliage. For example, hardwood litter from watershed 10 has 15%, 28%, 32%, and 55% higher respective N, K, Ca, and Mg concentrations than does conifer litter, while P concentrations in understory litterfall are 22% lower than in overstory litter (Abee and Lavender 1972).

These data indicate that in the 450-year-old stand of watershed 10, a major portion of the nutrient cycling is taking place through subordinate vegetation. In contrast, the major nutrient pathway in the young stand of the Thompson site is through the overstory.

Litter layer mass and nutrient capital also reflect the large age difference between these two stands (Tables 1 and 2). Standing crop of the 01 and 02 layers of the forest floor is 2.6 times greater on watershed 10 than at the Thompson site. This difference reflects in part the large input of woody material from the decadent overstory vegetation of watershed 10. Abee and Lavender (1972) found that 47% of litterfall in two plots on watershed 10 was woody material. This is in contrast to the approximately 30% reported by Bray and Gorham (1964) for cool-temperate forests of the world and the 33% woody material in litterfall of the Thompson site.

Mass of standing and down dead trees is substantially greater on watershed 10 than at the Thompson site. The stand at the Thompson site has had little mortality since it was established in 1931 and forest floor logs here are remnants of the former stand. In contrast, tree mortality in the stand of watershed 10 is high, estimated at 2% per year currently. In addition, much of the mortality on watershed 10 is of larger trees.

The litter layer, including logs, of both sites constitutes a substantial pool of potentially available nutrients. About 11% N, 4.5% K, and 6.6% Ca are in the litter out of the total amounts of these elements in the watershed 10 ecosystem, in comparison with 5.2% N, 6% K, and 11% Ca in the litter layer of the Thompson site. Phosphorus values for the two sites (Tables 1 and 2) are not directly comparable because of the different extraction procedures used for soil phosphorus.

Soil parent material differences between the two sites may be reflected in the higher total concentrations of Ca and K in the watershed 10 ecosystem. Total ecosystem Ca and K (Table 1), expressed as percentages of total ecosystem organic matter, are 0.85% Ca and 0.2% K for watershed 10 and 0.36% Ca and 0.14% K for the Thompson site. On the other hand, calcium and potassium concentrations in the total vegetation component of the two systems are reversed, with the stand of the Thompson site having 0.16% Ca and 0.11% K compared with 0.12% Ca and 0.05% K for watershed 10.

Higher Ca and K concentrations in the total watershed 10 ecosystem probably reflect the relatively high concentration of these elements in the andesite and andesitic-tuff soil parent material of this ecosystem. In contrast, soil parent material at the Thompson site is primarily granitic and acid metamorphic rocks. Contributions of these different parent materials to nutrient cycles of the two ecosystems will be discussed later in this paper.

An unexpected difference between the old-growth forest of watershed 10 and the second-growth stand of the Thompson site is the difference in overstory foliar nutrient concentrations. Average nutrient concentrations in the overstory foliage mass are 1.12% N, 0.32% P, 0.68% K, and 0.80% Ca for the Thompson site, and 0.84% N, 0.22% P, 0.78% K, and 1.04% Ca for watershed 10. New foliage N concentrations for overstory Douglas-fir average <1%.

Considering the large differences in distribution of organic matter and nutrients, the large age difference and the different soil parent material in these two stands, the overall N, P, and K budgets of the sites are remarkably similar (Table 3). Similarities are especially marked when compared with nutrient budgets of stands in other regions of the United States. For example, Likens and Bormann (1972) report a nitrogen increment of 3.5 kg ha^{-1} yr^{-1} for an undisturbed hardwood forest at Hubbard Brook, New Hampshire, while W. T. Swank (pers. commun., 1972) reports an annual accumulation of 3.34 kg ha^{-1} for an undisturbed hardwood forest of the Coweeta Experimental Forest, North Carolina.

Table 3. A comparison of annual inputs, losses, and balances of nitrogen, phosphorus, potassium, and calcium at the Thompson site, Washington and watershed 10, H. J. Andrews Experimental Forest, Oregon (kg ha^{-1}).

Location	N	P	K	Ca
Thompson site[a]				
Input (precipitation)	1.1	trace	0.8	[illegible]
Loss (leached beyond rooting zone)	0.6	0.02	1.0	[illegible]
Forest stand balance	+0.5	-0.02	-0.2	[illegible]
Watershed 10[b]				
Input (precipitation)	0.90	0.27	0.11	[illegible]
Loss (runoff)	0.38	0.52	2.25	[illegible]
Unit watershed balance	+0.52	-0.25	-2.14	[illegible]

[a]Measured in 1964-1965 measurement year (Cole et al. 1968). [b]Measured from 1 October 1970 to 1 October 1971 (Fredriksen 1972).

The larger input of phosphorus to watershed 10 may be because of fallout of phosphorus fertilizer dust from grass-seed fields in the Willamette Valley. Prevailing winds across watershed 10 are usually from the direction of the Willamette Valley.

Cation balances of the two study sites probably reflect differences in the chemical composition of the subsoil. As previously noted, soil and subsoil of watershed 10 are derived primarily from andesite and andesitic tuffs, while those of the Thompson site are derived from ice- and water-transported, granitic and acid metamorphic rock. Andesite has a higher proportion of hornblende, olivine, and plagioclase feldspars than granitic and acid metamorphic rocks, which are high in quartz and orthoclase feldspars (Longwell and Flint 1955). Calcium is a major cation in hornblende and plagioclase feldspars (Hurl[illegible]

1959). Weathering of these minerals in the soil and subsoil probably contributes much of the calcium and potassium lost from watershed 10. Similar calcium losses have been observed from watersheds on limestone-derived soil-subsoil. For example, W. T. Swank and J. W. Elwood (unpublished document, 1971) report an annual loss of 58.6 kg ha^{-1} from a watershed on limestone near Oak Ridge, Tennessee.

Within the overall nutrient budgets of these two stands, considerable differences in pathways of nutrient cycling can be observed. For example, the relative importance of litterfall, throughfall, and stemflow in returning nutrients to the soil surface are quite different in these two stands.

At the Thompson site, stemflow contributes about 0.9% N, 14% P, 12.5% K, and 17% Ca of the total quantity of these elements returned to the soil (Table 4). These quantities are transferred by stemflow amounting to 5%-10% of total precipitation. In contrast, stemflow in old-growth Douglas-fir is reported to be only 0.27% of total precipitation (Rothacher 1963), suggesting this to be a minor source of nutrient input on watershed 10. Rothacher's study, however, was done in a more uniform old-growth stand than watershed 10 and included only trees >28 cm dbh. Our preliminary results from the more heterogeneous stands of watershed 10 and based on trees 5 cm dbh and larger indicate that 2%-4% of total precipitation returns to the soil as stemflow. This suggests that small stems carry a disproportionate share of total stemflow in old-growth stands and further indicates that stemflow volume estimates based strictly on tree basal area may be inaccurate.

Nutrient return by throughfall is greater on watershed 10 than for the Thompson site for all elements except calcium (Table 4). Throughfall return of N, P, K, and Ca on watershed 10 is 130%, 800%, 205%, and 65%, respectively, of the return of these elements at the Thompson site.

Table 4. Annual nutrient return by litterfall, throughfall, and stemflow[a] in 43- and 450-year-old stands at the Thompson site, Washington, and watershed 10, H. J. Andrews Experimental Forest, Oregon (kg ha^{-1} yr^{-1}).

Location	N	P	K	Ca
Thompson site				
Litterfall	21.0	0.3	0.5	1.8
Throughfall	1.5	0.3	10.7	3.5
Stemflow	0.2	0.1	1.6	1.1
Total	22.7	0.7	12.8	6.4
Watershed 10				
Litterfall	27.3	4.7	8.0	67.3
Throughfall[b]	2.0	2.5	22.0	2.3
Total	29.3	7.2	20.0	29.6

[a]Stemflow at Thompson site only. [b]Average for two watershed 10 plots from Abee and Lavender 1972.

A variety of factors have been shown to contribute to the quantity of nutrients leached from plants (Tukey 1970) including: (1) plant species involved (hardwoods tend to have larger amounts leached than conifers); (2) nutrient elements (potassium is leached in greater amounts than calcium); (3) age of foliage (older foliage is leached more readily than young foliage); (4) intensity and volume of precipitation (more nutrients are leached by long, low-intensity precipitation than by short intense storms).

Most of the above factors probably contribute in some part to the differences observed between throughfall on watershed 10 and the Thompson site. Watershed 10 has a much higher proportion of hardwoods (Tables 1 and 2), and a greater proportion of older foliage. Additionally, watershed 10 has 170% greater precipitation, which falls at about the same rate as at the Thompson site, and greater total foliage and branch mass exposed to leaching (Tables 1 and 2).

In combination, these factors probably account for the major differences observed in leaching of N, K, and Ca. The factors responsible for the 800% greater return of P on watershed 10 cannot be satisfactorily explained at present, especially since P is usually leached from plants in relatively small amounts (Tukey 1970). Further research is proposed to examine this phenomenon.

Organic matter and nutrient transfers by litterfall also reflect the differences between the two sites. Annual litterfall in the 37-year-old stand of the Thompson site is currently about 2900 kg ha^{-1} compared with 5900 ka ha^{-1} on watershed 10. Annual foliage litterfall, however, is similar for the two sites, with 2200 kg ha^{-1} and 2800 kg ha^{-1} for the Thompson site and watershed 10, respectively. The larger amount for watershed 10 is due to the large mass of hardwoods in the understory.

Of total nutrients returned in litterfall for the two research sites (Table 4), about 90% are returned in the foliage component of the litter at the Thompson site. In contrast, 48% N, 69% P, 61% K, and 70% Ca are returned annually in foliage litter on watershed 10; the remaining nutrients are returned in woody material, reproductive parts, epiphytes, microlitter, and other minor categories.

Nutrients returned in epiphyte- and microlitter make a measurable contribution to the annual nutrient cycle on watershed 10. In this old-growth stand, epiphytes on branches alone amount to a dry weight of 800-1600 kg ha^{-1} and contain about 13.5 kg ha^{-1} N (Pike et al. 1972). Many lichens fix atmospheric N and, because of this and their possible role in adsorbing and desorbing nutrients in precipitation and throughfall, further studies of the role of epiphytes in nutrient cycling are planned. Annual nutrient by epiphyte-fall on watershed 10 is 6.7% N, 3.6% P, 5.6% K, and 0.7% Ca of total nutrients in litterfall (Abee and Lavender 1972). Epiphytes are a negligible component of litterfall at the Thompson site.

A portion of nutrient return by litterfall is in the form of fine organic matter such as insect frass, spores, pollen, and dust. This material is overlooked in many nutrient cycling studies in spite of nutrient concentrations such as 2% N in pollen and 7.8% N in some insect bodies (Stark 1973). This microlitter is a strongly seasonal input to the litter layer. Studies of microlitter input and turnover are currently in progress on watershed 10.

As previously mentioned, over 80% N, 30% P, 20% K, and 70% Ca reaching the soil surface of these two research sites do so by litterfall. Research is currently in progress at both sites to determine factors involved in making nutrients returned by litterfall available for plant uptake, including studies of the relation between climate and litter decomposition, the relation between decomposition and mineralization, and ion leaching in the soil.

Data on nutrient mineralization during decomposition are being provided for both sites from two sources, tension lysimetry (Cole 1968) and analysis of litterbags (Cromack 1973). Tension lysimetry provides integrated mineralization data for the total litter mass and data of nutrient flux in the soil, while litterbag studies provide mineralization data for specific organic substrates. Preliminary results of litterbag studies indicate that in the first six months of decomposition, weight loss of green needle litter was 17%, while potassium, magnesium, and calcium concentrations decreased by 75%, 75%, and 15% respectively, and nitrogen and phosphorus concentration showed no change (K. Cromack and R. Fogel, unpublished). Similar data are now available for a wide variety of substrates. For example, weight loss of fallen conifer needles and moss (*Isothecium stoloniferum*) is 10% in the first year (K. Cromack and R. Fogel, unpublished), while nitrogen-rich lichens lose 50% to 60% of their weight in one year (Rossman, unpublished).

Overstory vegetation of the Thompson site is currently over four times more productive than that of watershed 10 (Table 5). Over 40% of annual growth on watershed 10 is in the understory vegetation, however, so total production on watershed 10 is actually about one-half that of the Thompson site. The values given in Table 5 do not include mortality; doing so would probably reduce the overstory growth value for watershed 10 considerably. Nutrient utilization by understory of watershed 10 should nearly equal that of the overstory because of higher nutrient concentrations in new hardwood growth (Russel 1973). Onsite observations indicate mortality is high for watershed 10 and negligible for the Thompson site, but long-term data will be needed to establish mortality at both sites.

Table 5. Net[a] annual organic matter and nutrient accumulation by vegetation of 37- and 450-year-old Douglas-fir stands[b] on the Thompson site, Washington, and the H. J. Andrews Experimental Forest, Oregon ($kg\ ha^{-1}$).

Location	Organic matter	N	P	K	Ca
Thompson site (43 years old)					
Total all vegetation	9988	23.6	6.6	14.4	8.7
Watershed 10 (450 years old)					
overstory	2362	5.0	1.1	4.4	4.3
understory[c]	1840	d	d	d	d
Total all vegetation	4202				

[a] Mortality not deducted from above figures. [b] Does not include root production. [c] From Russel 1973. [d] Not available at time of writing.

Nutrient accumulation in new growth in the overstory is low for both sites compared with stands in other parts of the world. For example, Nelson et al. (1970) report 34.3 kg/ha N, 4.7 kg ha^{-1} P, 18.9 kg ha^{-1} K, and 22.0 kg ha^{-1} Ca accumulated by 5-year-old loblolly pine (*Pinus taeda* L.) in producing 9400 kg ha^{-1} of organic matter during one year. Annual nutrient accumulations in new tissue of the old-growth forest are substantially below those of the 37-year-old stand of the Thompson intensive site in spite of the threefold greater biomass accumulation on watershed 10. The lower demand for nutrients by the old-growth forest may indicate a successional pattern of reduced nutrient utilization that will be continued into climax *Tsuga heterophylla* stands typical of this area.

SUMMARY

Biomass and nutrient distribution and nutrient cycling process in 37- and 450-year-old Douglas-fir stands of the Thompson site in Washington and watershed 10 in Oregon reflect both the differences in age and soil and soil parent material. total biomass of the older stand is greater. Overstory foliage mass of the two sites is the same. In the 450-year-old stand, foliage is concentrated on fewer stems causing light gaps in the canopy. The greater light penetration through the older canopy promotes dense understory vegetation. Litter accumulation is fourfold greater in the older stand because of larger input of slowly decomposing woody material. Nutrient concentrations are generally lower in the less physiologically active 450-year-old overstory.

Input-output nutrient budgets for the two stands are relatively similar except for calcium. The large calcium output from watershed 10 is probably due to subsoil weathering.

Annual return of nutrients to the litter layer is greater in the 450-year-old stand, with approximately half this annual return contributed by understory vegetation. In contrast, less than 15% of annual return is contributed by understory in the 37-year-old stand.

The greater nutrient return by throughfall on watershed 10 is probably explained by the greater precipitation, larger amounts of older foliage, greater foliage and branch mass, and the larger mass of hardwoods in this stand. Nutrient return by stemflow is significant in the 43-year-old stand of the Thompson site. Stemflow is less important in the older stand but comparable data are not yet available.

Annual incorporation of nutrients in overstory growth is 4.7, 6, 3.3, and 2 times greater for N, P, K, and Ca, respectively, in the 43-year-old stand. Including the understory, nutrient incorporation in growth should be at least twice the above figures, since understory production is nearly equal that of the overstory.

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