Availability of N and P in the forest floors of adjacent stands of western red cedar – western hemlock and western hemlock – amabilis fir on northern Vancouver Island

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Availability of N and P was compared in the forest floors of old-growth forests of western red cedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (CH forests), and second-growth forests of western hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes) (HA forests) of windthrow origin. Five samples of each forest floor layer (litter, fermentation (woody and nonwoody), and humus (woody and nonwoody)) were collected from three forests of each type (CH and HA). All layers of CH forest floors had smaller concentrations of total and extractable N and mineralized less N during 40-day aerobic incubations in the laboratory. Total and extractable P was lower in the litter layer of CH forest floors. Seedlings of western red cedar, Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock, and amabilis fir grown from seed in forest floor material from CH forests grew more slowly and took up less N and P than did seedlings grown in HA forest floor material. The low supply of N and P in CH forest floors may contribute to the nutrient supply problems encountered by regenerating trees on cutovers of this forest type.

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La disponibilité de N et P a été comparée pour les couvertures mortes de vieilles forêts de cèdre rouge occidental (*Thuja plicata* Donn) et de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) (forêts de type CH), et des forêts de seconde venue de pruche de l'Ouest et de sapin gracieux (*Abies amabilis* (Dougl.) Forbes) (forêts de type HA) originant de chablis. Cinq échantillons de chaque couche de la couverture morte (la litière, l'horizon de fermentation (avec ou sans bois) et l'horizon d'humification (avec ou sans bois) ont été collectés dans trois forêts de chaque type (CH et HA). Toutes les couches des couvertures mortes de type CH avaient les concentrations de N total et de N extractible les plus faibles et ont minéralisé moins de N durant les 40 jours d'incubation aérobique effectuée au laboratoire. Le P total et le P extractible étaient plus faibles dans la couche de litière des couvertures mortes de type CH. Les semis de cèdre rouge occidental, d'épinette de Sitka (*Picea sitchensis* (Bong.) Carr.), de pruche de l'Ouest et de sapin gracieux cultivés à partir de semences dans le matériel de la couverture morte des forêts de type CH ont cru plus lentement et ont prélevé moins de N et de P que les semis cultivés dans le matériel de la couverture morte des forêts de type HA. Le faible apport de N et P dans les couvertures mortes des forêts de type CH peut contribuer aux problèmes d'apport de nutriments rencontrés par les arbres en régénération dans les coupes des forêts CH.

[Traduit par la rédaction]

Introduction

Poor regeneration, with associated slow growth and chlorosis, has been reported in cutovers of old-growth forests of western red cedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (CH forests) on northern Vancouver Island (Weetman *et al.* 1989*a*). Fertilization experiments have identified N and P deficiencies as the cause of poor growth of planted Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and naturally regenerating western hemlock and western red cedar (Weetman *et al.* 1989*a*, 1989*b*). Adjacent cutovers of second-growth stands of western hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes) (HA forests) did not show symptoms of nutrient deficiencies. The role of the ericaceous shrub salal (*Gaultheria shallon* Pursh) in contributing to the nutritional difficulties of regeneration on CH cutovers through competition or allelopathy has been addressed in related studies (Messier and Kimmins 1990; deMontigny 1992). Our objective was to determine whether there was less N and P available in CH forest floors prior to clear-cutting, which might contribute to the nutrient supply problems encountered on CH cutovers. We compare amounts of total and extractable N and P, rates of net N mineralization, and biomass production by seedlings grown in forest floors from adjacent CH and HA forests.

Study area

The study area is in the wetter Coastal Western Hemlock biogeoclimatic zone (CHWb) (Pojar *et al.* 1987) between the towns of Port McNeill and Port Hardy, B.C. (50°60′N, 127°35′W). The climate at the Port Hardy airport, 15 km from the study area, is very wet maritime with an annual average precipitation of 1700 mm. Mean daily temperatures range from 3.0°C in January to 13.7°C in July. Topography is gently undulating, and elevations are all less than 300 m. Soils are well to imperfectly drained Ferro-Humic Podzols on deep unconsolidated morainal and fluvial outwash material.

Three study sites were established within a 20-km^2 area in Block 4 of Tree Farm Licence 25 operated by Western Forest Products Ltd. Each study site has adjacent stands of uncut HA and CH, with a transitional area of approximately 10 m between the two forest types. The HA stands are even aged, originating from a catastrophic windstorm in 1908. They are very dense with small amounts of mosses and ferns in the understory. The average mass of forest floors in HA stands is 211 Mg/ha (Keenan *et al.* 1993). The CH forests are uneven

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TABLE 1. Concentrations (%) of N, P, and C, and pH, of each forest floor layer from adjacent hemlock – amabilis fir (HA) and cedar–hemlock (CH) forests

Layer[a]	Forest	N	P	C	C:N	pH
L	HA	0.83 (0.05)	0.08 (0.01)	53.4 (2.3)	64	3.96 (0.11)
	CH	0.67 (0.05)*	0.06 (0.01)*	54.3 (1.9)	81	4.75 (0.28)*
F	HA	0.99 (0.10)	0.07 (0.01)	53.1 (1.8)	54	3.45 (0.20)
	CH	0.90 (0.11)*	0.06 (0.01)	52.9 (2.8)	59	4.21 (0.31)*
Fw	HA	0.40 (0.21)	0.03 (0.01)	62.8 (4.5)	157	3.58 (0.02)
	CH	0.32 (0.16)	0.02 (0.01)	62.6 (3.5)	196	3.57 (0.15)
H	HA	1.17 (0.18)	0.06 (0.01)	51.7 (2.3)	44	3.19 (0.14)
	CH	0.97 (0.12)*	0.05 (0.01)	52.3 (1.7)	54	3.65 (0.24)*
Hw	HA	0.80 (0.33)	0.04 (0.01)	55.8 (3.6)	70	3.23 (0.14)
	CH	0.50 (0.15)*	0.02 (0.01)*	53.4 (4.3)	107	3.41 (0.23)

NOTE: The mean and standard deviation of 15 samples are presented; asterisks indicate significant differences ($p < 0.05$) between the two forest types based on two-factor ANOVA.
[a]L, litter; F, fermentation; H, humus; w, woody.

aged and contain cedars more than 500 years old, and hemlocks up to 400 years old. These stands have open canopies and a dense understory of salal. CH forest floors have an average mass of 280 Mg/ha (Keenan *et al.* 1993).

Methods

Forest floor sampling

Samples of the forest floor were collected from five randomly selected locations within each of the six plots (3 CH and 3 HA) in July 1990. Each forest floor layer (litter (L), fermentation (F), and humus (H)) was collected separately, as was woody material in the F and H layers (Fw and Hw, respectively). The 150 samples were kept refrigerated at 5°C while being processed during a 3-week period. Samples were passed through a 2 cm mesh sieve to remove large pieces of wood, coarse roots, and shoots. Samples of Fw greater than 2 cm in diameter were broken up by hand.

Total and extractable N and P

A 20-g fresh-weight portion of each field-moist sample was extracted with 50 mL of 2 M KCl (Page *et al.* 1982) and analyzed for concentrations of NH_4-N and NO_3-N on an Alpkem RFA 300 autoanalyzer. A second subsample was oven-dried at 70°C to determine moisture content. The remainder of each sample was then air dried and extracted with Bray's solution (McKeague 1978) and analyzed for extractable PO_4-P on the same autoanalyzer. Concentrations of total N and P were measured on the autoanalyzer following sulphuric acid – hydrogen peroxide digestion of ovendried (70°C) samples (Parkinson and Allen 1975). Total C was measured by the titration method of Walkley (1947). The pH of 5-g samples mixed with 20 mL of distilled water was measured (Fisher Accumet model 750 pH meter). All analyses were done at the MacMillan Bloedel Woodland Services Laboratory in Nanaimo, B.C.

Net N mineralization

Five-gram (dry weight equivalent) samples of each fresh forest floor sample collected in July 1990 were incubated in canning jars (Kerr wide mouth, 1 pint (0.6 dm^3)) and opened to outside air for 30 min at weekly intervals. After 40 days, the contents of the jars were extracted with 50 mL of 2 M KCl and concentrations of extractable NH_4-N and NO_3-N were determined on the autoanalyzer. Differences between the amounts of KCl-extractable N before and after incubation were used to estimate the rates of net mineralization (if positive) or net immobilization (if negative), of N in each forest floor layer.

Seedling growth

The capacity of the forest floors to provide available nutrients was measured by growing seedlings in material from the F layer at each site, which had the majority of fine roots and fungal mycelia. In January 1990, five samples of F layer material from each of the six sites were collected and kept refrigerated until April 1990. Four 60-g portions (dry-weight equivalent) of each sample were mixed with perlite (4:1 (v/v)) and put in 15 cm diameter plastic pots. Ten seeds of western red cedar, Sitka spruce, western hemlock, or amabilis fir (locally collected by Western Forest Products) were planted in each of the pots in April and May (one species per week) and thinned to three seedlings in August. All 120 pots received a layer of granite grit to prevent moss growth, and daily watering for 1 year in a greenhouse on the University of British Columbia campus. Roots and shoots from the three seedlings per pot were harvested in April and May 1991 (one species per week), oven-dried at 70°C, and weighed separately. One bulked sample of shoot material from the five pots in each species × site combination was analyzed for total N and P, as described earlier; root material was similarly bulked and analyzed. The mass of N and P in each pot was calculated to estimate the capacity of each forest floor to supply available nutrients to seedlings.

Statistical analysis

Differences in the mean values for each parameter were tested using two-factor analysis of variance, assessing the effects of forest types and sites, and interactions between the two factors (Zar 1974). Differences between the two forest types (CH and HA) that were significant at $p < 0.05$ are noted. All analyses were done with SPSS[x] (Norusis 1988).

Results

Total and extractable N and P

Concentrations of total N in each forest floor layer were less in CH forests than in HA forests (Table 1). Nitrogen concentrations were highest in H layers (1.17 and 0.97% in HA and CH, respectively) and lowest in Fw (0.40 and 0.32%). Significantly lower concentrations of total P were found in the L and Hw layers of CH forest floors (Table 1). Phosphorus concentrations were highest in L layers (0.08 and 0.06%) and lowest in Fw (0.03 and 0.02%). Carbon concentrations ranged from 52% in H material to 63% in Fw and were similar in the two forest types. C:N ratios of every forest floor layer were greater in CH forests, and decreased in the order Fw > Hw > L > F > H. The pH of all layers except Fw and Hw was significantly higher in CH forests (Table 1). The pH of the forest floor was between 3.2 and 4.0 in HA forests and 3.4 and 4.8 in CH forests.

Concentrations of KCl-extractable N were significantly less in CH forests in all layers except Fw (Fig. 1*a*). Most of the N was present as NH_4-N, but some NO_3-N was detected in all forest floor layers. Concentrations of Bray-extractable PO_4-P

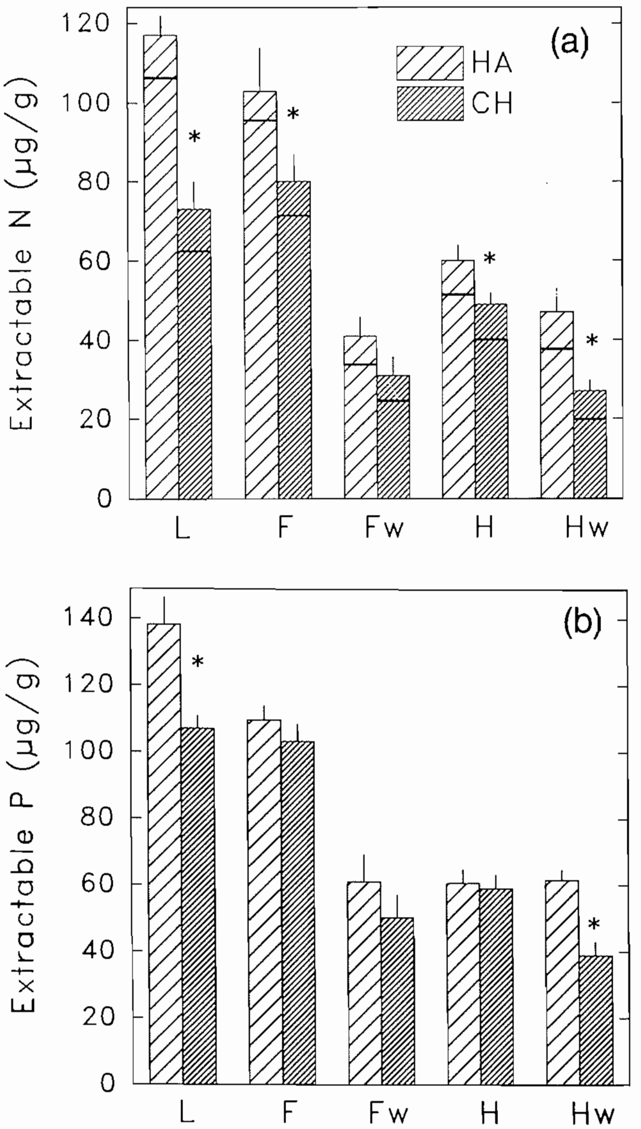

FIG. 1. Concentrations of KCl-extractable N and Bray-extractable P in each forest floor layer of adjacent hemlock – amabilis fir (HA) and cedar–hemlock (CH) forests. Each value represents the mean (+1 SE) of 15 samples; asterisks indicate significant differences ($p < 0.05$) between the two forest types based on two-factor ANOVA. Abbreviations for forest floor layers are defined in Table 1. Horizontal lines in Fig. 1*a* separate values for NO_3-N (above) and NH_4-N (below).

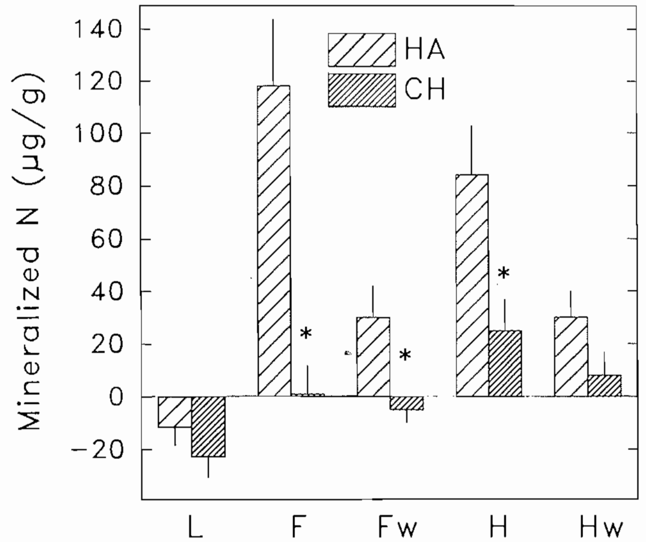

FIG. 2. Amounts of N mineralized during a 40-day aerobic incubation of each forest floor layer of adjacent hemlock – amabilis fir (HA) and cedar–hemlock (CH) forests. Each value represents the mean (+1 SE) of 15 samples; asterisks indicate significant differences ($p < 0.05$) between the two forest types based on two-factor ANOVA. Abbreviations for forest floor layers are defined in Table 1.

were significantly lower in the L and Hw layers of CH forests (Fig. 1*b*). Concentrations of extractable N and P were highest in the L and F layers of the forest floors in both forest types.

Net N mineralization

The amount of N mineralized during the 40-day aerobic incubation was significantly less in the F, Fw, and H layers of CH forest floors (Fig. 2). Net immobilization of N occurred in L material from both forests. Almost all of the mineralized N was NH_4-N; the changes in NO_3-N concentrations during the 40-day incubation were between -2.6 and 1.2 µg/g.

Seedling growth

Seedlings of all four species grown in F material from the CH forests produced significantly less biomass during the year than those grown in F material from the HA forests (Fig. 3). Shoot biomass values of all four species were significantly different between sites; root biomass values were significantly different for all species except hemlock. Concentrations of N and P in root and shoot material of each species did not differ between pots containing F material from CH and HA forests (Table 2). Thus, the total amount of N and P taken up by seedlings (concentration × biomass) was significantly lower in forest floor material from CH forests than in that from HA forests.

Discussion

The concentrations we found of C, N, and P in the L, F, and H layers of the CH and HA forest floors are similar to those found by Quesnel and Lavkulich (1980) in similar forests, but the pH levels of the L and F layers of the CH forests in the present study are greater than their estimates. Nitrogen concentrations in each layer of these forest floors are greater than those reported by Fyles *et al.* (1991). Material referred to as F in this study corresponds to their Fr, and our H is the same as their Hr. We found Hd material only in CH forests, and it had a chemical composition similar to that of Hr material, and so was not reported here. Our differences in both total and mineralizable N among forest floor layers are also consistent with those of Fyles *et al.* (1991), being highest in F layers and lowest in woody materials. Increases in N concentrations with increasing decay of wood (Fw to Hw) are also consistent with the findings of Fyles *et al.* (1991) in coastal British Columbia and Sidle and Shaw (1983) in coastal Alaska.

The various measurements of N availability (total, extractable, mineralized, and plant-available N) were consistent in demonstrating lower availability of N in CH forests than in HA forests. Good correlations among techniques for assessing N availability have also been reported by Fyles *et al.* (1991) and Prescott *et al.* (1992). Nevertheless, as discussed at length

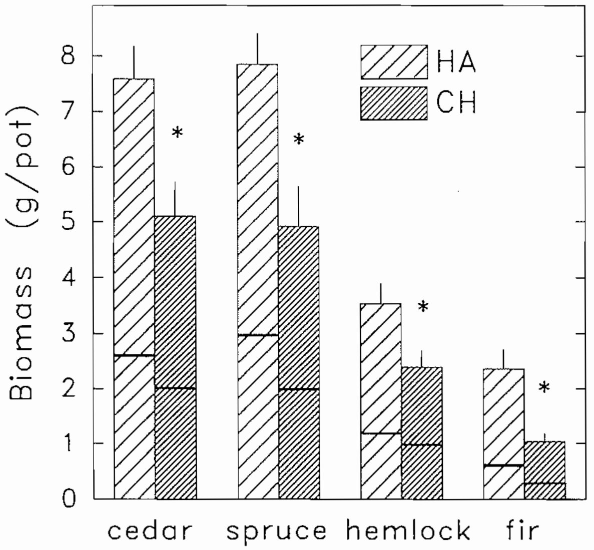

FIG. 3. Biomass production by seedlings of four species grown for 1 year in F layer material from adjacent hemlock – amabilis fir (HA) and cedar–hemlock (CH) forests. Each value represents the mean (+1 SE) of 15 samples; asterisks indicate significant differences ($p < 0.05$) between the two forest types based on two-factor ANOVA. Horizontal lines separate values for shoots (above) and roots (below).

TABLE 2. Nutrient concentrations (mg/g) of shoot and root material of seedlings grown in F layer material from adjacent hemlock – amabilis fir (HA) and cedar–hemlock (CH) forests

	N		P	
	HA	CH	HA	CH
	Shoots			
Cedar	6.23 (2.66)	6.07 (0.47)	0.40 (0.10)	0.47 (0.06)
Hemlock	9.00 (0.56)	9.37 (1.21)	0.47 (0.06)	0.53 (0.15)
Spruce	4.92 (0.77)	5.43 (0.81)	0.43 (0.06)	0.43 (0.06)
Fir	9.53 (1.11)	10.67 (0.15)	0.60 (0.10)	0.63 (0.12)
	Roots			
Cedar	6.33 (1.32)	5.37 (0.25)	0.63 (0.05)	0.63 (0.06)
Hemlock	9.09 (1.12)	8.67 (0.70)	0.70 (0.10)	0.77 (0.15)
Spruce	5.67 (0.31)	6.17 (0.58)	0.60 (0.00)	0.63 (0.06)
Fir	11.80 (0.87)	10.77 (1.00)	0.87 (0.06)	0.80 (0.00)

NOTE: The mean and standard deviation of three bulked samples are presented; there were no significant differences ($p < 0.05$) between the two forest types based on two-factor ANOVA.

by Binkley (1986), each technique measures a somewhat different pool of N, so several estimates are necessary for a thorough assessment of N availability.

The consistently lower concentrations of N and P in the forest floors of CH forests suggest that the nutrient supply problems on CH cutovers are at least partly the result of poorer quality organic matter in these forests. The importance of organic matter quality (in particular the concentrations of lignin, N, and polyphenols) in determining nutrient availability has been demonstrated by Flanagan and Van Cleve (1983) in taiga forests of Alaska. In their study, organic matter quality was more important than site factors in determining rates of decomposition and nutrient supply. They also demonstrated that seedlings grown in poor quality organic matter contained more tannins and less N in their tissues than those grown in higher quality organic matter, and that trees on increasingly N poor sites produced increasingly N poor litter. Tannins appear to be more prevalent in CH than in HA forest floors (deMontigny *et al.* 1993), in addition to the smaller N supply.

The occurrence of smaller N and P concentrations in the L layer of CH forest floors suggests that differences in the nutritional quality of the litter produced by the two forests could be responsible for differences in nutrient availabilities in the forest floors. Concentrations of N and P in foliar litter in CH forests are one-half and two-thirds, respectively, of those in HA forests (Keenan *et al.* 1992). Relationships between the amount of N circulating in litter fall and rates of N mineralization have been demonstrated by Vitousek *et al.* (1982) and Van Cleve *et al.* (1983). As described by Gosz (1981), this could establish a negative feedback loop, because low-quality litter on N-poor sites releases less N during decomposition, exacerbating the existing low availability of N in the forest floor.

Differences in litter quality between CH and HA forests could arise by two mechanisms: directly as a result of the species involved or indirectly through a reduction in litter quality of each species in response to lower nutrient availability (Gosz 1981). Foliar litter from cedar is low in N relative to other conifers (Beaton *et al.* 1965; Daubenmire 1953) and decomposes more slowly (Harmon *et al.* 1990), which could lead to nutrient supply problems in the forest floors under cedar. However, Harmer and Alexander (1986) found that the forest floors under plantations of western red cedar were rich in N relative to those under other species, indicating that the lower quality litter does not necessarily reduce N availability in the forest floor.

Nutrient availability in old-growth CH forests might also be inhibited by the ericaceous shrub salal, which is much more abundant in CH forests than in neighbouring HA forests. Salal leaves and roots contain large amounts of phenolic compounds (deMontigny 1992), which could inhibit decomposition and N mineralization (deMontigny and Weetman 1990). Damman (1971) reported slow rates of organic matter decomposition and accumulations of N in humus in heath areas of Newfoundland dominated by the ericaceous shrub *Kalmia angustifolia* L.

Low rates of nutrient supply in CH forests could also be the indirect result of immobilization of nutrients in the forest floor. Immobilization of N in large accumulations of organic matter have been implicated in the poor nutritional conditions in black spruce (*Picea mariana* (Mill.) B.S.P.) forests (Van Cleve *et al.* 1983; Roberge *et al.* 1968). Keenan *et al.* (1993) found similar amounts of N in the forest floors and woody debris in these CH and HA forests (2207 and 1984 kg N/ha, respectively) and suggested that immobilization of N in the forest floor was not responsible for the lower nutrient supply in CH forests.

CH forests might experience greater rates of N loss that could leave less available in the forest floor. There is growing evidence that both nitrification and denitrification are more prevalent in north temperate forests than previously recognized (Groffman and Tiedje 1989; Hart *et al.* 1991). Forest floors under cedar have been found to have much higher rates of nitrification than those under other conifers (Harmer and Alexander 1986; Krajina *et al.* 1973), perhaps as a result of the associated higher pH, cation exchange capacity, and base saturation (Alban 1969; Turner and Franz 1985). We did not detect any differences in NO_3-N concentrations in CH and HA forest floors, despite the higher pH.

The task now is to determine the influence of each of these factors possibly contributing to the lower nutrient supply in CH forest floors (i.e., litter quality and decomposition, tannins and phenolic compounds, immobilization and losses of nutrients). The interplay of the many factors that control nutrient availability in forest ecosystems makes it difficult to identify cause–effect relationships. Van Cleve *et al.* (1991) have suggested the state factor approach of Jenny (1980) as a useful framework for studying controls of element cycling in forests. This approach involves analysis of the five factors that control ecosystem structure and function: microclimate, topography (elevation, slope, and aspect), soil, vegetation, and successional phenomena. The ecosystems on northern Vancouver Island satisfy the three criteria necessary for state factor analysis as outlined by Van Cleve *et al.* (1991): relatively undisturbed by man, small number of tree species (three), and clear and repeatable patterns of distribution across the landscape. State-factor analysis may provide the framework for testing the many hypotheses presently being addressed to explain the peculiar phenomenon of distinctly different nutritional conditions in two forests growing side by side on the same parent material on northern Vancouver Island.

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