

Litter production and nutrient resorption in western red cedar and western hemlock forests on northern Vancouver Island, British Columbia

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Abstract: Fine litter fall and concentrations of N and P in green foliage and foliar litter were measured in three species over 1 year in two forest types at three sites on northern Vancouver Island to explore the hypothesis that differences in nutrient use and cycling between the dominant tree species on each forest type contribute to differences in forest floor nutrient availability. Total annual aboveground fine litter fall was significantly higher in second-growth, windstorm-derived 85-year-old stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and amabilis fir (*Abies amabilis* (Dougl.) Forbes) forests (4137 kg·ha⁻¹) than in adjacent old-growth forests of western red cedar (*Thuja plicata* Donn) and western hemlock (3094 kg·ha⁻¹) occurring on similar sites. Cedar had significantly lower N concentration in green foliage (9.3 mg·g⁻¹) and litter (4.3 mg·g⁻¹) than the other species in each forest type. Hemlock had a higher litter N concentration in the hemlock – amabilis fir type (8.3 mg·g⁻¹) than in the cedar–hemlock type (6.4 mg·g⁻¹). Cedar resorbed a significantly higher percentage of N during leaf senescence (76%), than hemlock in the cedar–hemlock type (64%), hemlock in the hemlock – amabilis fir type (51%), or amabilis fir (18%). Nitrogen-use efficiency (litter-fall mass/litter N) was considerably higher in cedar (235 kg litter/kg N) than in the other species in either forest type (90–156 kg litter/kg N). These results suggest that differences within and between species in the two types in nutrient use and the amount of nutrients cycling through the litter fall and internal redistribution pathways are contributing to lower rates of nutrient cycling and forest floor nutrient availability in the cedar–hemlock type.

Résumé : La masse de litière fine et les concentrations en N et P du feuillage vert et de la litière foliaire de trois espèces ont été mesurées pendant 1 année dans deux types forestiers sur trois sites dans le nord de l'île de Vancouver afin d'explorer l'hypothèse que les différences dans l'utilisation et le cyclage des nutriments entre les espèces d'arbres dominants de chaque type forestier contribuent aux différences de disponibilité des nutriments de la couverture morte. La masse de litière fine épigée annuelle totale était significativement plus élevée dans les peuplements de seconde venue de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et de sapin gracieux (*Abies amabilis* (Dougl.) Forbes) âgés de 85 ans (4137 kg·ha⁻¹) et résultant de chablis que dans une vieille forêt adjacente de thuya géant (*Thuja plicata* Donn) et de pruche de l'Ouest (3094 kg·ha⁻¹) se retrouvant sur des sites similaires. Le thuya avait des concentrations en N dans le feuillage vert (9,3 mg·g⁻¹) et la litière (4,3 mg·g⁻¹) significativement plus faibles que les autres espèces dans chacun des types forestiers. La litière de pruche avait une concentration plus élevée en N dans le type pruche – sapin gracieux (8,3 mg·g⁻¹) que dans le type thuya–pruche (6,4 mg·g⁻¹). Le thuya a résorbé un pourcentage significativement plus élevé de N durant la sénescence foliaire (76%) que la pruche dans le type thuya–pruche (64%), que la pruche dans le type pruche–sapin gracieux (51%) ou que le sapin gracieux (18%). L'efficacité de l'utilisation d'azote (masse (kg) de la litière/kg N de la litière) était considérablement plus élevée chez le thuya (235) que chez les autres espèces dans les différents types forestiers (90–156). Ces résultats suggèrent que les différences à l'intérieure et entre les espèces dans les deux types forestiers dans l'utilisation

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des nutriments et les quantités de nutriments recyclés par la chute des litières ainsi que la redistribution interne contribuent aux plus faibles taux de cyclage et de disponibilité des nutriments dans la couverture morte dans le type forestier thuya-pruche.

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Introduction

The storage and flux of carbon and other nutrients are important components in the functioning of forest ecosystems (Waring and Schlesinger 1985), and carbon and nutrient cycles are often intimately coupled (Attiwill 1986). For example, in temperate forests N generally limits productivity when water is not limiting, and N availability in the soil depends largely on the rate at which it is mineralized during decomposition of organic matter returned to the forest floor in above- and below-ground litter fall. When climatic conditions are constant, this is mainly determined by the chemistry of carbon associated with N in litter fall (Meentmeyer 1978). Litter fall is therefore a major pathway for the transfer of energy and nutrients from aboveground components to the soil surface in most forest ecosystems, and an understanding of the quantity and chemistry of organic matter and nutrients cycling in litter fall can provide valuable insights into a number of aspects of ecosystem functioning. Annual litter fall is an indicator of primary productivity (Bray and Gorham 1964; Vogt et al. 1986), and the inverse of litter nutrient concentration can be used as an index of nutrient-use efficiency (Vitousek 1982).

It has been argued that plants adapted to growing on nutrient-limited sites use nutrients more efficiently than those adapted to nutritionally richer situations (Vitousek 1982). Higher nutrient-use efficiency in plants on nutrient-poor sites is possibly due to higher retranslocation of nutrients at the time of leaf senescence, resulting in lower litter nutrient concentrations. Concentrations of lignin and other secondary compounds can also be higher on nutrient-poor sites (Waterman and Mole 1989). These differences may be mediated through phenotypic changes within a genotype, by genotypic or species replacement, or both (Vitousek 1982). Thus, there are strong feedbacks between the way in which different species store and utilize the carbon fixed in photosynthesis, the rate at which N is released in the forest floor during decomposition and, ultimately, the level of production that the forest sustains (Hobbie 1992). The potential positive feedback between nutrient limitation, litter quality, decomposition, nutrient availability, and forest productivity has been extensively explored (Gosz 1981; Edmonds et al. 1990). Tilman (1988) has further suggested that differences in nutrient-use efficiency and litter quality between plant species and their effect on soil nutrient availability can determine plant competitive hierarchies where nutrients are the major resource limitation.

Nambiar and Fife (1991) suggest that there are two views on nutrient retranslocation from senescing tissues: one emphasizes retranslocation as a mechanism that has evolved as an adaptation to nutrient shortage; the other supports the idea that retranslocation is either not related to nutrient availability or increases with increasing nutrient availability. A number of studies have reported no increase in the

proportion of nutrients retranslocated across gradients in nutrient availability (Staaf 1982; Birk and Vitousek 1986; del Arco et al. 1991; Nambiar and Fife 1991). Where higher amounts or proportions of nutrients have been resorbed on less fertile sites, it has generally been in experiments where fertilizer has been added to increase nutrient availability (e.g., Turner 1977; Flanagan and Van Cleve 1983).

Forests on northern Vancouver Island are largely composed of two types: an old-growth type dominated by western red cedar (*Thuja plicata* Donn), with a lesser component of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (cedar-hemlock type), and more uniform, second-growth stands of western hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes) (hemlock – amabilis fir type). These forest types occur in a mosaic across the landscape, occupying similar topographic situations and occurring on similar mineral soils. However, major differences in the productivity of conifer regeneration on clear-cut sites of the two types have been observed. Planted and naturally regenerated seedlings on the cedar-hemlock type grow considerably more slowly than those on adjacent sites previously occupied by hemlock – amabilis fir forests (Weetman et al. 1989a, 1989b). Poor growth is partly due to the low availability of N in the forest floors of the cedar-hemlock type (Prescott et al. 1993) and partly to competition for these limited nutrients from the ericaceous shrub salal (*Gaultheria shallon* Pursh) that rapidly occupies the cedar-hemlock sites following clear-cutting (Messier and Kimmins 1991).

The amount of N contained in detritus in the two types is similar (Keenan et al. 1993); therefore, the lower forest floor N availability is a product of the lower rate at which N is mineralized in cedar-hemlock forests. A number of hypotheses have been put forward to explain these differences in N availability (Keenan 1993; Prescott and Weetman 1994), including (i) repeated windthrow causing more rapid decomposition in the hemlock – amabilis fir type through a ploughing effect, (ii) a greater accumulation of woody debris in the cedar-hemlock type leading to lower nutrient mineralization because of nutrient immobilization in decaying wood, and (iii) production of tannins by salal that combine with proteins to form substances that are resistant to further decay (de Montigny et al. 1993). The first hypothesis was eliminated in a previously reported study (Keenan et al. 1994). The second has been discounted because similar quantities of woody debris were found in the two forest types (Keenan et al. 1993), and the amount of nutrients cycled through decaying logs are smaller and decay processes in logs happen over considerably longer time scales compared with foliar litter. The extent to which tannins might influence N mineralization rates has not yet been determined.

This paper explores a further hypothesis put forward by Prescott et al. (1993) that differences in nutrient use and cycling between the dominant tree species on each forest type contribute to differences in forest floor nutrient

availability. The objectives were to (i) determine the annual mass of organic matter and nutrients cycling in above-ground litter fall in the two forest types; (ii) determine whether there were differences in the amounts and proportion of N and P resorbed into living tissues at the time of foliar senescence among species growing in the two forest types; and (iii) use information on litter quantity and nutrient content to estimate N-use efficiency for each forest type.

Study area

The study area was a gently undulating coastal plain generally less than 300 m in elevation situated near the town of Port MacNeill on the northern part of Vancouver Island (50°40'N). Administratively, this area is Provincial Forest and the major part of Block 4, Tree Farm Licence 25 operated by Western Forest Products Ltd. It is classified as part of the very wet maritime subzone of the Coastal Western Hemlock (CWH) biogeoclimatic zone (Pojar et al. 1991) that occupies the lower and middle altitudes of Vancouver Island and the coastal mainland of British Columbia. Vegetation has been described by Lewis (1982). Two forest types occupy well-drained to somewhat imperfectly drained situations and Lewis included these in the same ecosystem association, the *Thuja plicata* – *Tsuga heterophylla* – *A. amabilis* – *G. shallon* – *Rhytidiadelphus loreus* (Hewd.) Warnst. (the salal moss, S1 association). Cedar–hemlock stands were relatively open, with large western red cedar up to 260 cm DBH (diameter at breast height over bark at 1.3 m from the ground) and a smaller component, in terms of basal area, of western hemlock, and occasional amabilis fir. The understorey was dominated by salal, an ericaceous shrub that forms a dense cover up to 2 m tall, and forest floors occupied mainly by mosses, including *R. loreus* and *Hylocomnium splendens* (Hewd.) B.S.G., and occasional ferns. Contiguous poorly drained areas were occupied by widely spaced cedar and lodgepole pine (*Pinus contorta* var. *contorta* Dougl. ex Loud.), *Sphagnum*, and *Myrica* spp.

Hemlock – amabilis fir stands were more uniformly sized and densely stocked. The understorey was dominated by advanced growth of both species, with small patches of salal and *Vaccinium* spp. and a ground cover of mosses and ferns. The transition between the two types is quite abrupt. Large cedar trees can occasionally be found in the hemlock – amabilis fir stands along this transition, but there was no evidence of extensive occupation by cedar prior to the 1906 windstorm.

Climate in the area is wet with mild winters and relatively cool summers (Chilton 1981). Mean annual precipitation at Port Hardy airport, 15 km from the study area, is approximately 1700 mm, 65% of which occurs between October and February. There is less rain in summer than in winter, but growing-season precipitation prevents any soil moisture deficit in most years (Lewis 1982). A small amount of snowfall occurs from December to February and usually melts quickly. Hours of sunshine range from an average of 6.4 h·day⁻¹ in July to 1.5 h·day⁻¹ in December, reflecting the frequent occurrence of fog in the summer and frontal clouds in the winter. Extremes in temperature

are rare, and there is a long frost-free period (175 days). Mean annual temperature is 7.9°C, and the daily average ranges from 2.4°C in January to 13.8°C in August. Because of relatively wet, cloudy conditions and morning marine fogs in summer, wildfires are uncommon in this locality and the predominant source of disturbance is windstorms.

Surface geology is deep (>1 m in many places) unconsolidated morainal and fluvial outwash material overlying three types of bedrock: gently dipping sedimentary rocks of the Cretaceous Nanaimo formation, relatively soft volcanics of the Bonanza group, and a small area of harder, Karmutsen formation basalt that protrudes through the morainal cover in the northwest of the basin. Soils are medium-textured, Humo-ferric Podzols overtopped by mor forest floors varying in depth from 10 cm to 1 m (Agriculture Canada Expert Committee on Soil Survey 1987).

Methods

Aboveground litter-fall mass

Three sites were chosen for investigation with representative examples of the cedar–hemlock and hemlock – amabilis fir types in close proximity on the same aspect and in similar topographic positions. A 50 × 50 m (0.25-ha) plot was established in each type. Twenty litter-fall traps were systematically located in each of the six plots. The traps were 50 × 50 cm, with a base of nylon mesh with a pore size of 1 mm surrounded by a 10 cm high wooden frame, and were raised about 10 cm off the ground. They were cleared at approximately monthly intervals for 10 months from the end of January 1990 until the end of November 1990, then at the beginning of February 1991. Twigs smaller than 1 cm diameter were retained and dried for 24 h at 70°C. Dried samples were sorted into the following categories: woody (e.g., twigs, bark, cones), conifer foliage, understorey foliage, and other (e.g., fine bark, flowers), and weighed. Sorting of needles and cedar foliage by species was very time-consuming, and it was beyond the resources of this study to do this for all collections of all litter traps. To obtain an estimate of the proportion of litter in the cedar–hemlock type belonging to each species, foliar litter from five traps at each site was sorted into species. These proportions were averaged for each site and each collection and then applied to the average value of foliar litter fall. In the hemlock – amabilis fir type, litter fall of each species was assumed to be proportional to basal area.

Nutrient concentration and resorption

Samples of live foliage from two branches in the upper third of the crown of 10 trees per plot (about five cedar and five hemlock in the cedar–hemlock type, and five hemlock and five fir in the hemlock – amabilis fir type) were collected in winter (February 1992) by helicopter. Two small branches were clipped about 1 m back from the tip of a main branch. Foliage from each branch was composited to make a single sample for each tree, and dried at 70°C for 24 h. Five of the litter traps (described above) were randomly selected from each plot. The foliar litter fall from each month for each trap was bulked to form an annual sample, and these were sorted into species (cedar and hemlock for the cedar–hemlock type, and hemlock

Table 1. Annual aboveground litter fall ($\text{kg}\cdot\text{ha}^{-1}$) from the beginning of February 1990 to the end of January 1991 for old-growth cedar–hemlock and second-growth hemlock – amabilis fir forests on northern Vancouver Island.

Litter category	Cedar–hemlock	Hemlock – amabilis fir	<i>p</i> *
Conifer foliage	1516 (36.0)	2093 (138.2)	0.016
Understorey leaves	135 (22.3)	5 (1.6)	0.004
Twigs	806 (49.6)	1108 (100.6)	0.054
Cones	160 (16.3)	604 (58.0)	0.002
Others	478 (18.1)	362 (26.0)	0.022
Total	3094 (38.0)	4173 (206.2)	0.007

Note: Values are the mean of three sites (material from about 20 traps at each site was collected and weighed monthly, and monthly mean values were summed to produce an annual total) with SE given in parentheses.

*The *p*-values indicate the level of significance of the difference between the two forest types based on a Student's *t*-test.

and fir for the hemlock – amabilis fir type). Approximately 0.2 g of each green foliage sample and each foliar litter sample was digested using Kjeldahl methods with Se as a catalyst (100 g K_2SO_4 and 1 g of Se in 1 L of concentrated H_2SO_4). The resulting solution was analysed for N and P using the Technicon AutoAnalyzer in the Forest Ecology Laboratory at the University of British Columbia. Litter fall was considered to be the major aboveground pathway for the transfer of the elements of major interest in this study, N and P (Vitousek 1982); element transfer in throughfall leachate was not measured.

It is more appropriate to express resorption on a mass of nutrient per unit of leaf area rather than a weight basis, because the mass per unit area of foliage can change considerably during senescence, but the area does not (Fahey and Birk 1991). A small portion (0.3–1.0 g) of each sample was weighed, the leaf area (cm^2) was determined using a LI-COR 3100 leaf area meter, and the foliar mass per unit area (g/cm^2) was calculated. Nutrient concentration was then calculated on an area basis in milligrams per square centimetre. Percent resorption was calculated on the basis of area using the mean values of green and senesced foliage for each species on each plot using the following formula (Fahey and Birk 1991):

$$\% \text{ resorbed} = 100 \frac{\text{green nutrient concn.} - \text{senesced nutrient concn.}}{\text{green nutrient concn.}}$$

To obtain an indication of the patterns of N use for each species, litter fall was multiplied by N concentration to determine litter-fall N. Green mass equivalent of annual litter fall was calculated by dividing litter fall by the relative mass per unit area of litter versus green foliage, and this value was multiplied by the N concentration of green foliage to calculate its N content. Assuming that the foliar biomass of both forest types is in steady state, this green equivalent of annual litter fall should be equivalent to annual foliar growth, and the N content equivalent to demand for N by this new growth. This was compared with the amount of N resorbed from senescing foliage to estimate the percentage of demand supplied through resorption.

Nitrogen-use efficiency for each species was calculated as litter-fall mass divided by N content (Vitousek 1982).

Statistical analysis

There was substantial damage and disturbance of the litter-fall traps by wildlife, and the full complement of 20 samples was not available for each plot in every collection. Consequently, the mean monthly value of each litter-fall category was calculated for each of the six plots, and these values were summed to calculate an annual total. Forest types were compared using the annual values for each type across the three sites with Student's *t*-test (Sokal and Rohlf 1981).

Resorption for each litter type was compared using values calculated for each of the three sites. The variances of the means of all the species – forest type combinations were not homogeneous. However, variances between the combinations of the greatest interest were homogeneous, and the following pairwise comparisons were made on untransformed data using Student's *t*-test: cedar versus hemlock in the cedar–hemlock type, hemlock versus amabilis fir in the hemlock – amabilis fir type, and hemlock in the cedar–hemlock versus hemlock in the hemlock – amabilis fir type. All analyses were carried out using SYSTAT (Wilkinson 1990).

Results

Aboveground litter-fall mass

There were significant differences ($p \leq 0.05$) between the forest types in the annual amounts of all litter-fall categories except twigs, where *p* was 0.054 (Table 1). Coniferous foliar litter-fall mass was significantly greater in the hemlock – amabilis fir type (about $2100 \text{ kg}\cdot\text{ha}^{-1}$) than in the cedar–hemlock type (about $1500 \text{ kg}\cdot\text{ha}^{-1}$). Small woody litter fall (twigs and cones) was also greater in the hemlock – amabilis fir (about $1700 \text{ kg}\cdot\text{ha}^{-1}$) than in the cedar–hemlock type ($965 \text{ kg}\cdot\text{ha}^{-1}$). Understorey leaves composed about 8% of the foliar litter fall in the cedar–hemlock type but was a very small component in the hemlock – amabilis fir type (0.2%). This was expected, given the greater understorey biomass in the cedar–hemlock type. Total litter-fall mass was about one-third greater in the

Table 2. Mean concentration and resorption of N and P for four types of foliage in western red cedar and western hemlock forests at three sites on northern Vancouver Island.

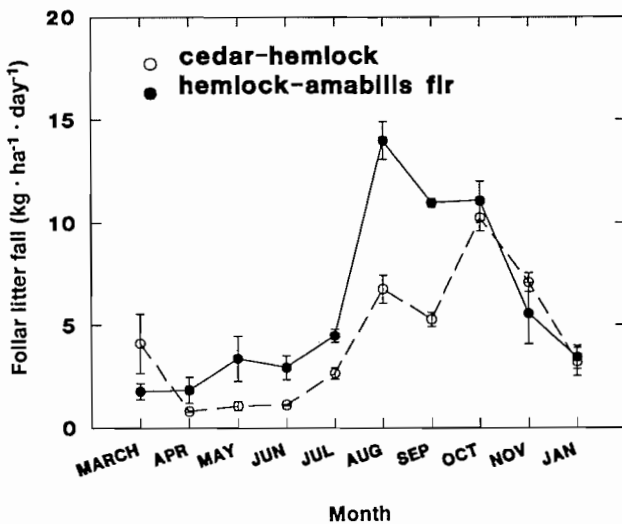
Forest type	Species	Relative MPA*	Nitrogen ($\text{mg}\cdot\text{g}^{-1}$)				Phosphorus ($\text{mg}\cdot\text{g}^{-1}$)			
			Green foliage	Litter	Resorption [†]	Percent	Green foliage	Litter	Resorption [†]	Percent
Cedar-hemlock	Cedar	0.51 (0.007)	9.3a (0.38)	4.3a (0.15)	7.10a (0.315)	76a (0.7)	1.0ab (0.05)	0.4a (0.02)	0.80a (0.050)	80a (0.8)
	Hemlock	0.70 (0.004)	12.6b (0.58)	6.4b (0.17)	8.12a (0.660)	64b (2.4)	0.9a (0.07)	0.4a (0.01)	0.66a (0.08)	70b (3.9)
Hemlock - amabilis fir	Hemlock	0.82 (0.001)	14.0b (0.34)	8.3c (0.08)	7.11a (0.802)	51c (0.9)	1.2ab (0.03)	0.5b (0.01)	0.75a (0.026)	64b (0.8)
	Amabilis fir	0.95 (4.9)	12.9b (0.39)	11.1d (0.22)	2.37b (1.087)	18d (7.8)	1.2b (0.05)	0.6c (0.003)	0.56a (0.082)	47c (5.8)

Note: Values in parentheses under the concentration values are standard errors. Values in different columns followed by the same letter are not significantly different ($p \leq 0.05$).

*Relative mass per unit area of litter versus green foliage.

[†]Concentration of nutrient in green tissue minus concentration of nutrient in litter adjusted for the loss of mass during senescence, i.e., green concentration - (litter concentration \times MPA).

Fig. 1. Mean conifer foliar litter fall from February 1990 to January 1991 from cedar-hemlock and hemlock - amabilis fir forest at three sites on northern Vancouver Island. Mean values for each forest type were estimated by collecting material from about 20 litter traps at three sites. Error bars indicate ± 1 SE across the three sites.



hemlock - amabilis fir type. These differences were consistent across all three sites, and variability in the mean values between the sites was quite low (coefficient of variation was 2.1% for the total in the cedar-hemlock and 8.6% in the hemlock - amabilis fir type). This suggests that the 0.25-ha plot encompassed most of the within-stand variability in litter input in both forest types.

Seasonal pattern of litter fall differed between the two types (Fig. 1). In the hemlock - amabilis fir type, litter fall peaked in the late summer months of August and September. In the cedar-hemlock type, peak litter fall occurred later in the year (in October).

Nutrient concentrations

Cedar had significantly ($p \leq 0.05$) lower N concentration in green foliage ($9.3 \text{ mg}\cdot\text{g}^{-1}$) than the other species in each forest type, which were all statistically equivalent ($12.6\text{--}14.0 \text{ mg}\cdot\text{g}^{-1}$; Table 2). N concentration of foliar litter differed significantly between species on each type. Cedar, again, had the lowest litter N concentration ($4.3 \text{ mg}\cdot\text{g}^{-1}$), while hemlock had a higher litter N concentration in the hemlock - amabilis fir type ($8.3 \text{ mg}\cdot\text{g}^{-1}$) than in the cedar-hemlock type ($6.4 \text{ mg}\cdot\text{g}^{-1}$). P concentrations in green foliage did not differ greatly between species or forest types, but concentrations in cedar and hemlock litter in the cedar-hemlock type ($0.4 \text{ mg}\cdot\text{g}^{-1}$) were significantly lower than in hemlock and fir litter in the hemlock - amabilis fir type (0.5 and $0.6 \text{ mg}\cdot\text{g}^{-1}$, respectively).

Foliar nutrient resorption

All species differed significantly in the proportion of N resorbed at leaf senescence (Table 2). Cedar resorbed the highest percentage (76%), followed by hemlock in the cedar-hemlock type (64%), and hemlock in the hemlock - amabilis fir type (51%). Amabilis fir resorbed a relatively low percentage (18%). This order of resorption rate was the same for P, although the percentage of P resorbed was slightly higher in all cases (47–82%). Cedar and hemlock (in both forest types) resorbed similar amounts of N ($7.10\text{--}8.12 \text{ mg}\cdot\text{g}^{-1}$). Amabilis fir resorbed a significantly lower amount of N than the other species ($2.37 \text{ mg}\cdot\text{g}^{-1}$). Cedar and hemlock resorbed similar amounts of P ($0.66\text{--}0.83 \text{ mg}\cdot\text{g}^{-1}$), and amabilis fir resorbed a lower amount of P than the other species ($0.56 \text{ mg}\cdot\text{g}^{-1}$), but this difference was not statistically significant.

Stand-level N cycling

Annual foliar litter N content was calculated to be $18.4 \text{ kg}\cdot\text{ha}^{-1}$ in the hemlock - amabilis fir type and $8.2 \text{ kg}\cdot\text{ha}^{-1}$ in the cedar-hemlock type (Table 3). N content of the green equivalent of litter-fall mass ("demand") was

Table 3. Foliar litter mass, litter N mass, green foliage mass equivalent, green foliage N content, amount of N resorbed, percentage of green foliage N content, and N-use efficiency (litter fall/litter N) for two forest types on northern Vancouver Island.

	Cedar-hemlock		Hemlock – amabilis fir	
	Cedar	Hemlock	Hemlock	Fir
Foliar litter fall	705 (97.4)	811 (66.2)	1715 (157.4)	378 (138.4)
Litter N	3.0 (0.45)	5.2 (0.32)	14.3 (1.28)	4.14 (1.47)
Green equivalent of litter-fall mass	1370 (176.1)	1154 (79.6)	2089 (196.5)	411 (161.7)
Green N content (demand)	12.9 (2.10)	14.6 (1.01)	29.0 (2.14)	5.4 (2.23)
Amount of N resorbed	9.8 (1.66)	9.4 (0.92)	14.7 (0.89)	1.3 (0.85)
Percent of demand for N satisfied				
by resorption	76 (0.7)	64 (2.4)	51 (0.95)	18 (7.8)
N-use efficiency (kg/kg)	235 (7.93)	156 (5.5)	120 (1.09)	90 (1.8)

Note: Values are means across three sites with SE given in parentheses. All values except N-use efficiency are kilograms per hectare.

12.8 kg·ha⁻¹ for cedar and 14.6 kg·ha⁻¹ for hemlock in cedar-hemlock forests. In hemlock – amabilis fir stands, N demand was 29.0 kg·ha⁻¹ for hemlock and 5.4 kg·ha⁻¹ for amabilis fir. Resorption satisfied 76% of N demand in cedar and 64% in hemlock in the cedar-hemlock type and 51% for hemlock and 18% for amabilis fir in the hemlock – amabilis fir type. Nitrogen-use efficiency was significantly higher for cedar (235 kg litter/kg N) than for hemlock in the cedar-hemlock type (156 kg litter/kg N). Nitrogen-use efficiency of hemlock was significantly lower in the hemlock – amabilis fir type (121 kg litter/kg N) than in the cedar-hemlock type. Nitrogen-use efficiency for amabilis fir (90 kg litter/kg N) was considerably lower than for the other species.

Discussion

Despite their close proximity and their occurrence on similar mineral soils and topographic situations, there were considerable differences between the two forest types in nutrient use and the amount of nutrients cycling through the litter fall and the internal redistribution pathways. Litter-fall mass and N and P content were significantly higher in the hemlock – amabilis fir type than in adjacent stands of the cedar-hemlock type. Nutrient concentrations in both green foliage and foliar litter were within the ranges reported for these species, and the relative arrangement of litter N concentration (fir > hemlock > cedar) is also consistent with that in other studies (Tarrant and Chandler 1951; Daubenmire and Prusso 1963; Beaton et al. 1965; Ovington 1965; Harmon et al. 1990).

Rates of foliar resorption of N (76%) and P (82%) in western red cedar were high, but there were no other studies of this species for comparison of results. Higher rates have been reported for *Larix* spp. (Cole 1981; Tyrrell and Boerner 1987; Gower et al. 1989), and similar rates in Scots pine (*Pinus silvestris* L.; Stachurski and Zimka 1975). Western hemlock in the cedar-hemlock forests had a lower resorption rate than cedar, although values (64% of N and 70% of P) are still relatively high and comparable with many *Pinus* spp. (Miller 1984; Birk and Vitousek 1986; Gower et al.

1989; Prescott et al. 1989). Amabilis fir had relatively low rates of N resorption (18%).

Higher resorption of N in hemlock needles in the cedar-hemlock type (64%) than in those in the hemlock – amabilis fir type (51%) supported the contention that coniferous species can have higher rates of resorption on sites with lower nutrient availability (Gosz 1981; Edmonds et al. 1990). Other studies have indicated that conifers do not generally alter their rates of resorption across gradients of N availability (e.g., Birk and Vitousek 1986); however, these may be restricted to situations where N availability limits tree growth. In situations where N is not limiting, N concentrations in litter fall may be elevated and the rate of resorption may be reduced (Turner 1977). There was little response to N fertilization of conifer seedlings planted on hemlock – amabilis fir sites (Weetman et al. 1990), and this may indicate that N does not limit growth on these sites.

There was a smaller mass of aboveground litter fall in the cedar-hemlock than in the hemlock – amabilis fir type. Combined with low N concentrations in green foliage and the high rate of nutrient resorption prior to senescence, particularly by cedar, this resulted in only 45% as much N returned to the forest floor in litter fall in the cedar-hemlock type compared with the hemlock – amabilis fir type.

While recognising that these results are based on only 1-year's litter-fall data, there is consistent evidence across three sites suggesting that the species in the different forest types investigated in this study have quite different nutrient-use characteristics that can significantly influence the productivity, functioning, and dynamics of these forest ecosystems. Cedar had a high rate of resorption and satisfied a higher proportion of its N demand through resorption compared with the other species, which suggests that it may have adapted to lower nutrient conditions by increasing N-use efficiency. As a result, cedar has litter with lower N concentration, indicating that there may be a positive feedback leading to a lower rate of N cycling and soil N availability in cedar-dominated forests. Cedar seedlings survive and grow better than most other species on N-poor sites in this area (Messier 1993; Weetman et al. 1990),

suggesting that there may be a link between the effect that cedar has on soil properties and the competitive abilities of its progeny, as suggested by Tilman (1988).

Whether low nutrient availability is a general feature of soils under western red cedar is still to be determined. Prescott et al. (1995) investigated nutrient availability under cedar on a range of sites, and found that it had consistently lower litter N concentration and lower forest floor N mineralization than other conifer species planted on adjacent sites. The way that cedar litter may contribute to differences in N availability between the cedar-hemlock and hemlock - amabilis fir forests has been explored further in a study of nutrient dynamics in decomposing litter on these sites. Cedar litter decomposes more slowly than other litter types and, possibly because of its lower N concentration, immobilizes more N in the short term and releases considerably less N at a lower rate in the longer term phases of decomposition (Keenan 1993). Using a computer model of nutrient cycling and forest production, it was found that these factors could result in N mineralization in cedar-hemlock forests being about 60% of those in the hemlock - amabilis fir type (Keenan et al. 1995).

The results of this study, together with those of other studies, support the contention of Prescott et al. (1993) that lower rates and amounts of N cycling through the plant-soil system make a considerable contribution to the differences in forest floor N availability in these two forest types.

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