Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests on northern Vancouver Island

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Biomass and C, N, P, and K contents of woody debris and the forest floor were surveyed in adjacent stands of old-growth western red cedar (*Thuja plicata* Donn) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (CH type), and 85-year-old, windstorm-derived, second-growth western hemlock – amabilis fir (*Abies amabilis* (Dougl.) Forbes) (HA type) at three sites on northern Vancouver Island. Carbon concentrations were relatively constant across all detrital categories (mean = 556.8 mg/g); concentrations of N and P generally increased, and K generally decreased, with increasing degree of decomposition. The mean mass of woody debris was 363 Mg/ha in the CH and 226 Mg/ha in the HA type. The mean forest floor mass was 280 Mg/ha in the CH and 211 Mg/ha in the HA stands. Approximately 60% of the forest floor mass in each forest type was decaying wood. Dead woody material above and within the forest floor represented a significant store of biomass and nutrients in both forest types, containing 82% of the aboveground detrital biomass, 51–59% of the N, and 58–61% of the detrital P. Forest floors in the CH and HA types contained similar total quantities of N, suggesting that the lower N availability in CH forests is not caused by greater immobilization in detritus. The large accumulation of forest floor and woody debris in this region is attributed to slow decomposition in the cool, wet climate, high rates of detrital input following windstorms, and the large size and decay resistance of western red cedar boles.

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La biomasse et le contenu en C, N, P et K des débris ligneux et de la couverture morte ont été inventoriés dans de vieux peuplements adjacents de thuya géant (*Thuja plicata* Donn) – pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) (type CH) et dans des peuplements de seconde venue de pruche de l'Ouest – sapin gracieux (*Abies amabilis* (Dougl.) Forbes) âgés de 85 ans et originant de tempêtes de vent (type HA) dans trois stations du nord de l'île de Vancouver. La concentration de C était relativement constante pour toutes les catégories de détritus (moyenne = 556,8 mg/g); généralement, la concentration de N et P augmentait tandis que celle de K diminuait avec l'augmentation du degré de décomposition. La masse moyenne des débris ligneux était respectivement de 363 et 226 Mg/ha dans les types CH et HA tandis que la masse moyenne de la couverture morte pour les mêmes types était de 280 et 211 Mg/ha. Le bois en décomposition représentait ~60% de la masse de la couverture morte dans chaque type forestier. Le matériel ligneux mort au-dessus et dans la couverture morte représentait un pool significatif de biomasse et de nutriments dans les deux types forestiers, contenant 82% de la biomasse détritique épigée, de 51 à 59% de N et de 58 à 61% du P détritique. Les couvertures mortes dans les types CH et HA contenaient des quantités totales similaires de N, ce qui suggère que la plus faible disponibilité de N dans les forêts de type CH n'est pas causée par une plus grande immobilisation dans les détritus. La forte accumulation de la couverture morte et de débris ligneux dans cette région est attribuée à la lente décomposition dans ce climat frais et humide, aux hauts taux d'apport de détritus par les tempêtes de vent, et aux troncs de grande taille ainsi qu'à la résistance à la décomposition du thuya géant.

[Traduit par la rédaction]

Introduction

Woody debris and forest floor organic matter are important components of many forest ecosystems (Harmon et al. 1986). Coarse woody debris (dead trees and fallen logs with a diameter greater than about 15 cm) is a major element of structural diversity in old-growth forests (Franklin et al. 1981), and an important component of nutrient and organic matter dynamics that has often been overlooked in studies of carbon storage and nutrient cycling in forests (Harmon et al. 1990; Harmon and Hua 1991). Downed logs can be important sites for seedling establishment (Scott and Murphy 1987; Harmon and Franklin 1989) and are habitat for insects, fungi, and microorganisms that have a role in many aspects of ecosystem functioning (Maser and Trappe 1984).

Accumulated woody debris is an obvious component of the massive old-growth forests of the Pacific Northwest region of the United States, and several studies have quantified the biomass and nutrient content of woody debris and forest floor in these forests (e.g., Graham and Cromack 1982; Harmon et al. 1987; Spies et al. 1988; Bingham and Sawyer 1988). Recent studies have also documented the quantities of these materials in smaller statured forests in other parts of continental North America (Arthur and Fahey 1990; Muller and Lui 1991).

Forests of similar structure to those of the Pacific Northwest are found along coastal British Columbia. However, few studies have estimated the biomass contained in woody debris or the forest floor in these forests. This paper provides information on the biomass and chemistry of these components in two forest types occupying large areas on the northern end of Vancouver Island: the old-growth western red cedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) type; and the windstorm-derived, second-growth type consisting of western hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes).

The objectives were to (*i*) quantify the biomass of standing dead and downed logs by decay class, and the forest floor material by woody and nonwoody L, F, and H layers; (*ii*) determine the concentrations and total amounts of C, N, P, and K in this material.

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The study is part of a larger project aimed at improving our understanding of the causes of lower nutrient (particularly N) availability in the forest floors of the old-growth, cedar–hemlock stands. Weetman et al. (1989*a*, 1989*b*) found in studies of fertiliser trials that growth of planted and naturally regenerated conifer seedlings on these sites was limited by low availability of N and P.

Study area

The study area is a gently undulating coastal plain generally less than 300 m in elevation situated on the northern part of Vancouver Island, British Columbia, near the town of Port McNeill, at a latitude of 50°60′N. Administratively, this plain is the major part of Block 4, Tree Farm Licence 25, operated by Western Forest Products Ltd. The vegetation in this locality has been described by Lewis (1982). The forests lie within the very wet maritime subzone of the Coastal Western Hemlock (CWH) biogeoclimatic zone (Pojar et al. 1991). This zone occupies the lower and middle elevations of Vancouver Island and the coastal mainland of British Columbia. Forests in the locality occurring in well or moderately well drained situations (around 60% of Block 4) are a mixture of old-growth and even-aged stands originating after a major windstorm around 1906 (see Table 1). The old-growth (CH) stands are structurally diverse and dominated by western red cedar and western hemlock with a wide age range. Cedar attains diameters at breast height (DBH) of over 200 cm, ages of up to 1000 years, and heights of 40–45 m. The understory in these stands is dominated by salal (*Gaultheria shallon* Pursh). The second-growth (HA) stands are densely stocked hemlock and amabilis fir with maximum diameters of about 80 cm, dominant heights of 45 m, and an understory of mosses and ferns. The transition between these types is very abrupt, with no evidence that the even-aged stands were occupied by cedar prior to the 1906 windstorm. Poorly drained areas are occupied by cedar, lodgepole pine (*Pinus contorta* var. *contorta* Loud.), and *Sphagnum* and *Myrica* spp.

Climatic data from the weather station at Port Hardy airport, 15 km from the study area, show that mean annual precipitation is approximately 1700 mm, 65% of which occurs between October and February. The summer months experience less rainfall than the winter months, but rainfall during the growing season is thought to be sufficient to prevent any soil moisture deficit (Lewis 1982). Hours of sunshine range from an average of 6.4 h/day in July to 1.5 h/day in December, reflecting the frequent occurrence of fog in the summer and frontal clouds in the winter. 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 the relatively wet, cloudy summers, wildfire is uncommon in this locality, and the predominant source of disturbance is windstorms. The surface geological material consists of deep (>1 m in many places) unconsolidated morainal and fluvial outwash material overlying sedimentary and volcanic bedrock. The predominantly well drained to somewhat imperfectly drained mineral soils are medium-textured, Humo-Ferric Podzols overtopped by mor forest floors varying in depth from 10 cm to 1 m (Lewis 1982).

Methods

Field measurements

Three sites considered representative of the forests on better drained situations were selected for investigation. They were situated around 20 km west of Port McNeill and within 5 km of each other. Each site was located on gently undulating topography with the CH and HA types in close proximity, and a 50 × 50 m (0.25 ha) plot was located in a representative portion of each type. All downed logs greater than 1 m in diameter at midpoint, and all dead standing trees and stumps, were surveyed on the entire plot. The length and midpoint diameter of each large downed log, the height and DBH of each dead standing tree, and the height and midpoint diameter of each stump were recorded.

Fallen boles and branches between 1 cm and 1 m in diameter were sampled using the line intersect method (Brown 1974). In each plot 16 points were systematically located on a grid pattern and used as midpoints for 32 randomly oriented lines (one line at each point was 10 m long for pieces from 15 to 100 cm in diameter, and the other was 4 m long for pieces from 1 to 15 cm in diameter). The diameter over bark of each piece at the point of intersection with the line and the angle between the ground and the log (used to correct the volume calculation for logs not parallel with the ground) were recorded.

Each dead standing tree, stump, and downed log was classified into a decay class using a modified version of the five-class system of Sollins (1982). Decay classes were distinguished by structural integrity, wood texture, and the presence of twigs, roots, and other vegetation. Modifications related to the presence and condition of bark, which in the species surveyed during this study, was often the portion of the bole most resistant to decay. Decay class I wood was intact material with no decay, whereas decay class V material had little structure and a mushy (when wet) or powdery (when dry) texture. Where possible, species was also recorded, but this was not usually feasible beyond decay class III.

A section of wood (around 1000 cm^3) from a subsample of logs in each decay class was taken at two of the sites using a chainsaw to estimate density and nutrient content. Bark was included when present on the sampled log, so the values for these parameters reflect the overall makeup of the sampled boles. For decay classes I and II, four to six logs were selected from each decay class – species combination; for decay classes III, IV, and V, five logs were selected at each site without any identification of species.

Samples of the forest floor (30 × 30 cm) were extracted at eight systematically located points in each plot. These samples were sorted in the field into L (foliar litter), L_w (twigs less than 1 cm diameter), F (nonwoody), F_w (from wood), H (nonwoody), and H_w (from wood). Five samples of each forest floor component from each plot were analysed for nutrient concentrations.

Laboratory measurements and calculations

The sample of wood (and bark, if present) cut from each log was divided in two. One part was weighed, dipped in melted paraffin wax, weighed again, and immersed in water; the volume was measured by displacement (American Society for the Testing of Materials 1978). The volume of the wax was calculated from its weight and specific gravity and subtracted to obtain the volume of the wood sample. The other part of the sample was weighed, dried at 70°C for 3 days, and weighed again to determine the moisture content. Density of each sample was calculated as dry weights divided by wet volumes.

These dried samples and those of the forest floor were ground and digested using a modification of the method of Parkinson and Allen (1975). Percent N and P were determined colorimetrically with a Technicon AutoAnalyzer, and percent K, by atomic absorption spectrophotometry. Percent organic C was determined by the titrimetric method of Walkley–Black (Nelson and Sommers 1982).

The volumes of dead standing trees, downed logs, and woody debris were calculated for each plot in the following way. Volume of downed logs greater than 1 m diameter was estimated by using midpoint diameter and the length in Huber's formula (Wenger 1984). Under-bark bole volumes of dead standing trees were estimated from equations in British Columbia Forest Service (1976). No allowance was added for bark or branches. These were present on recently dead trees, and because of this the biomass of dead standing trees was probably slightly underestimated. For broken-topped stems the volume was adjusted using a regression equation developed between diameter and height from live trees in each plot. Predicted volume was calculated using the predicted height from this equation, and this predicted volume was reduced by the ratio actual height/predicted height. Stumps were assumed to be a cylinder, and volumes were calculated from the height and midpoint diameter measurements. The values for each dead tree, large bole, and stump were summed, and the totals for each plot were multiplied by four to give volumes on a per-hectare basis.

TABLE 1. Stand density and basal area of the forests at the three study sites in old-growth western red cedar – western hemlock and second-growth western hemlock – amabilis fir forests on northern Vancouver Island

	Cedar–hemlock				Hemlock–fir			
	BL	RU	SC	Mean	BL	RU	SC	Mean
Density (stems/ha)								
Cedar	104	124	128	119	—	—	—	—
Hemlock	424	348	388	387	352	596	452	467
Fir	88	80	8	59	156	108	32	99
Total	616	552	524	564	508	704	484	565
Basal area (m^2/ha)								
Cedar	63.7	67.6	121.5	84.2	—	—	—	—
Hemlock	21.9	19.9	22.5	21.4	53.8	65.2	69.9	63.0
Fir	1.9	5.3	0.2	2.5	21.7	15.8	4.2	13.9
Total	87.5	92.8	144.2	108.2	75.5	81.0	74.1	76.8

NOTE: BL, Beaver Lake; SC, SCHIRP experimental area; RU, Rupert.

The estimated mean volume per hectare of logs between 0.15 and 1 m was calculated for each decay class using the volume calculation formula in DeVries (1986), with the 16 lines per plot treated as independent samples. Volume of branches and twigs less than 0.15 m was calculated in the same way, but not separated into decay class. Mass was estimated by multiplying the volume of each class by the mean density of that class. For the material less than 0.15 m the mean of decay classes I and II was used.

All roots greater than 0.5 mm diameter were removed from the forest floor samples, and the forest floor material weighed wet. Both components were then dried at 70°C for 48 h and reweighed. When the wet mass of forest floor material exceeded 1 kg a subsample was used to estimate water content.

The quantity of C, N, and K contained in woody debris was estimated by multiplying the mean mass in each decay class by the mean nutrient concentration for each decay class. The concentrations of P obtained in this study were below the detection limits of the chemical analysis, and P concentrations contained in the decaying boles of similar species by Sollins et al. (1987) were used to calculate P content in woody debris. For the forest floor material the mean mass of each layer at each site was multiplied by the mean nutrient concentration.

Differences between the forest types in density and mass of woody debris and nutrient content of woody debris and forest floor were investigated using Student's *t*-test (Sokal and Rohlf 1981). If the variances were not homogeneous the test was done on log-transformed data. Differences in the total mass, and in the mass of the different layers of the forest floor, were investigated using a two-way ANOVA, with the eight replicates in each plot used to test the significance of differences between sites and the forest type – site interaction. All analyses were performed using SYSTAT (Wilkinson 1990).

Results and discussion

Density and nutrient concentrations

Values for the density of different decay classes of logs are shown in Table 2. Density of decay class I hemlock wood was higher in the CH than the HA type, which may be due to a higher proportion of denser late (summer) wood to early (spring) wood. Undecayed cedar wood was less dense than hemlock, which is consistent with the known timber characteristics of these species (Jessome 1977). The density of decay class V logs was about 50% of the density of decay class I in both forest types. The pattern and magnitude of the decline in density with increasing decay generally concur with other studies that used a similar system of decay classification (Sollins 1982; Sollins et al. 1987; Arthur and Fahey 1990).

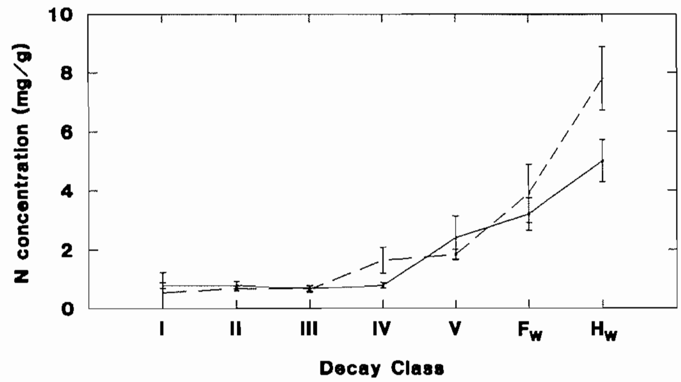

FIG. 1. Nitrogen concentrations in decaying boles (decay classes I–V) and woody material in the L and F layers of the forest floor (F_w, H_w) in samples taken from old-growth, western red cedar – western hemlock (solid line) stands and second-growth western hemlock – amabilis fir (broken line) stands on northern Vancouver Island. Bars indicate standard errors.

The exception was the value of 0.23 g/cm^3 for decay class V wood in the CH type, which was higher than the values reported in a study of the same species by Sollins et al. (1987). This was probably due to presence of less-decayed wood within some samples of logs that were classified into class V because the external wood was in a highly decayed condition.

Nutrient concentrations in samples of downed logs are shown in Table 2, those in the forest floor layers are shown in Table 3, and the N concentrations for woody material in both types are shown in Fig. 1. Carbon concentrations were reasonably consistent in all materials, with an overall mean of 556.8 mg/g (SE 6.51 mg/g), indicating that C was generally being lost at the same rate as mass during the decay process. Nitrogen concentrations generally increased with increasing decay of logs in both forest types, and this trend was also evident in the woody forest floor material (Figure 1). Phosphorus concentrations were generally very low (<0.1 mg/g) in the log samples, and this was beyond the detection limits of the analytical method used. There were slightly higher, and therefore measurable, concentrations in decay class V logs and in the woody forest floor material. The trend in this latter component was for P concentration to increase with

TABLE 2. Mean density and nutrient concentrations of wood samples of each species from old-growth western red cedar – western hemlock and second-growth western hemlock – amabilis fir forests on northern Vancouver Island

Decay class	Species	n	Density (g/cm^3)	C (mg/g)	N (mg/g)	P (mg/g)	K (mg/g)
			Cedar–hemlock				
I	Cedar	6	0.36	561.0	0.92	nd	0.16
			(0.039)	(10.03)	(0.11)		(0.05)
	Hemlock	8	0.44	524.0	0.68	nd	0.35
			(0.021)	(8.57)	(0.09)		(0.08)
II	Cedar	5	0.31	568.1	0.88	nd	0.35
			(0.046)	(15.3)	(0.07)		(0.08)
	Hemlock	9	0.42	492.9	0.71	nd	0.29
			(0.067)	(9.38)	(0.18)		(0.20)
III		11	0.33	572.6	0.70	nd	0.15
			(0.036)	(16.61)	(0.1)		(0.03)
IV		10	0.25	575.2	0.80	nd	0.11
			(0.028)	(15.55)	(0.09)		(0.01)
V		10	0.23	577.4	2.41	0.14	0.17
			(0.034)	(10.40)	(0.72)	(0.03)	(0.04)
			Hemlock–fir				
I	Hemlock	9	0.34	563.7	0.58	nd	0.36
			(0.034)	(8.36)	(0.08)		(0.12)
	Fir	7	0.34	576.2	0.50	nd	0.17
			(0.036)	(13.87)	(0.06)		(0.04)
II	Hemlock	9	0.34	544.3	0.72	nd	0.31
			(0.031)	(6.13)	(0.10)		(0.15)
	Fir	8	0.32	575.3	0.66	nd	0.19
			(0.021)	(18.98)	(0.06)		(0.06)
III		10	0.35	553.9	0.67	nd	0.09
			(0.030)	(14.89)	(0.11)		(0.0)
IV		10	0.22	579.3	1.65	0.12	0.12
			(0.032)	(9.13)	(0.44)	(0.02)	(0.01)
V		10	0.18	571.3	1.84	nd	0.13
			(0.018)	(12.50)	(0.18)		(0.02)

NOTE: Values in parentheses are standard errors. nd, Not detected; i.e., below the measurement limits of the instrumentation used for analysis.

TABLE 3. Mean nutrient concentrations (mg/g) of forest floor layers in old-growth western red cedar – western hemlock and second-growth western hemlock – amabilis fir forests on northern Vancouver Island

	Cedar–hemlock				Hemlock–fir			
Layer	C	N	P	K	C	N	P	K
Nonwoody								
L	541.4	6.7	0.6	0.6	534.3	8.3	0.8	0.8
	(7.96)	(0.14)	(0.00)	(0.02)	(7.36)	(0.13)	(0.04)	(0.01)
F	530.4	9.0	0.6	0.7	530.6	9.9	0.7	0.6
	(9.83)	(0.65)	(0.03)	(0.15)	(6.61)	(0.18)	(0.03)	(0.05)
H	522.6	9.7	0.5	0.6	518.7	11.8	0.5	0.3
	(6.07)	(0.24)	(0.02)	(0.09)	(5.10)	(0.58)	(0.03)	(0.02)
Woody								
Fw	625.8	3.2	0.2	0.2	630.3	3.9	0.3	0.1
	(9.53)	(0.55)	(0.03)	(0.03)	(17.62)	(0.98)	(0.04)	(0.05)
Hw	534.3	5.0	0.3	0.3	559.9	7.8	0.4	0.2
	(6.2)	(0.72)	(0.03)	(0.08)	(7.8)	(1.08)	(0.04)	(0.02)

NOTE: Means are the averages from three sites. Values in parentheses represent standard errors.

decomposition. Concentrations of P in nonwoody forest floor were considerably higher than in the woody forest floor and, in contrast with the woody material, the trend was for the concentration to decrease during decomposition.

Several studies have shown increases in nutrient concentration of wood, particularly N, with stage of decay (Lambert et al. 1980; Graham and Cromack 1982; Arthur and Fahey 1990). These increases have been attributed to (*i*) the trans-

TABLE 4. Mass (Mg/ha) of dead standing trees, downed logs, and small woody debris in old-growth western red cedar – western hemlock and second-growth western hemlock – amabilis fir forests at three sites on northern Vancouver Island

	Cedar–hemlock				Hemlock–fir				
	BL	RU	SC	Mean	BL	RU	SC	Mean	p*
Dead standing	19.6	56.4	164.3	80.1	16.2	24.1	22.5	20.9	0.182
Downed logs (>0.15 m)									
Decay class I	7.5	10.0	6.6	8.0	17.6	9.4	6.8	11.3	0.397
Decay class II	1.3	27.2	11.1	13.2	8.3	17.2	5.0	10.2	0.736
Decay class III	206.9	139.9	83.2	143.1	43.5	16.1	49.7	36.4	0.046
Decay class IV	166.2	43.9	44.3	84.8	42.9	144.5	86.9	91.4	0.898
Decay class V	15.6	33.2	29.9	26.2	16.1	44.6	56.0	38.9	0.386
Small woody debris (0.01–0.15 m)	2.1	13.2	6.4	7.2	17.0	21.3	11.0	16.4	0.105
Total downed wood	399.6	267.4	181.5	282.5	145.4	253.1	215.4	204.6	0.268
Total	419.2	323.8	345.8	362.6	161.6	277.2	237.9	225.5	0.037

NOTE: BL, Beaver Lake; SC, SCHIRP experimental area; RU, Rupert.

*Level of significance of between forest type differences using Student's t-test; for dead standing category the test was done on log-transformed data.

location of nutrients into the wood from throughfall, litter fall, and the adjacent forest floor by fungal hyphae (Grier 1978) and (*ii*) N-fixation by bacteria (Hendrickson 1991).

Potassium concentrations declined with the stage of decomposition in both woody and nonwoody substrates, indicating that it is being lost more rapidly than mass. A similar trend has been observed in other studies (Lambert et al. 1980; Arthur and Fahey 1990), and this is consistent with the relatively high mobility of this ion.

Woody debris mass

The mass of each type of woody debris in each forest type is shown in Table 4. The total mass of dead standing trees and downed logs and branches averaged 363 Mg/ha in the CH, significantly higher than the 226 Mg/ha measured in the HA stands. Much of this difference was due to the higher quantity of dead standing trees in the CH stands (80 versus 20 Mg/ha). The mean mass of downed wood in the CH type was 283 Mg/ha, not significantly higher ($p = 0.268$) than the 205 Mg/ha found in the HA stands.

These values for woody debris mass are among the highest reported in the literature. Agee and Huff (1987) estimated that the mass of dead standing trees and downed logs was 550 Mg/ha in an old-growth *Pseudotsuga–Tsuga* stand of taller stature in the Olympic Mountains of Washington, United States; Harmon et al. (1987) estimated a mass of 400 Mg/ha in a riparian *Sequoiadendron giganteum* (Lindl.) Buchh. stand in California. A comparable figure of 200 Mg/ha of only downed logs was reported by Bingham and Sawyer (1988) for a Californian *Sequoia–Pseudotsuga–Tsuga* forest.

Within the CH type, there were quite large differences in the mass of different categories of material between sites. At the SCHIRP site, the quantity of dead standing trees (mainly cedar) was large, while that of downed logs was quite small. At the Beaver Lake site, on the other hand, the mass of dead standing material was small but the mass of downed logs was very large. The remaining site, Rupert, was intermediate between these two. These differences may reflect differences in the way the catastrophic windstorm that created the HA stands affected the adjacent old-growth forest. Variability in quantity of woody debris in the HA stands suggests that the structure of pre-1906 windstorm stands was quite variable.

Although it was a small proportion of the total woody debris, the mass of small woody debris (<0.15 m) was higher ($p = 0.105$) in the HA than in the CH type. This is indicative of the greater input of this size of material through branch mortality and stand self-thinning in the HA type. This is also reflected in the significantly ($p = 0.001$) higher quantity of small woody material (<1 cm) in the HA type measured in the L layer as part of the forest floor material (Table 5).

Forest floor mass

Mass of the different layers of forest floor is shown in Table 5. The mean mass of the nonwoody L, F, and H layers was significantly higher ($p = 0.012$) in the CH stands (113.7 Mg/ha) than in the HA stands (77.2 Mg/ha). Woody material was the major component of the forest floor: 166 Mg/ha in the CH stands and 134 Mg/ha in the HA stands (63% in both types). The overall (woody + nonwoody) mass of forest floor in the CH stands (280 Mg/ha) was not significantly higher ($p = 0.264$) than that in the HA stands (211 Mg/ha).

There have been few studies on the biomass of forest floor in similar forest types with which to compare these figures. Gessel and Balci (1965) reported an average value of 157 Mg/ha for the LFH of five old-growth coniferous stands in Washington state, United States. Vogt et al. (1983) reported a forest floor mass of 149.5 Mg/ha in an amabilis fir stand in western Washington, which is probably comparable to the second-growth HA stand in this study. In a broad survey of coniferous forest floor biomass in Oregon and Washington undertaken by Little and Ohmann (1988), the highest values, ranging from 181 to 277 Mg/ha, were found at three sites in the Olympic National Forest in western Washington, and were comparable with those in this study. Decaying wood accounted for 5 to 70% of the forest floor biomass at the full range of sites in that study, indicating that the value of 63% found in this area is at the upper end of the range for that geographic region.

TABLE 5. Mean mass (Mg/ha) of forest floor layers in old-growth western red cedar – western hemlock and second-growth western hemlock – amabilis fir forests at three sites on northern Vancouver Island

	Cedar–hemlock				Hemlock–fir				
	BL	RU	SC	Mean	BL	RU	SC	Mean	p*
n	8	8	8	3	8	8	8	3	
Nonwoody									
L	4.3	4.3	4.3	4.3	4.4	4.3	3.7	4.1	0.677
F	13.2	19.1	22.0	18.1	21.3	32.5	36.6	30.1	0.001
H	90.0	114.3	69.7	91.3	33.3	56.2	39.6	43.0	0.013
Sum	107.5	137.7	96.0	113.7	59.0	93.0	79.9	77.2	0.012
Woody									
Lw	1.1	1.5	2.7	1.7	3.6	3.0	4.6	3.7	0.001
Fw	0.3	88.9	0	29.7	7.7	19.3	50.6	25.9	0.847
Hw	177.4	91.6	134.9	134.6	125.8	84.1	102.4	104.1	0.451
Sum	178.8	182.0	137.6	166.1	137.1	106.4	157.6	133.7	0.682
Total	286.3	319.7	233.6	279.8	196.1	199.4	237.5	210.9	0.264

NOTE: BL, Beaver Lake; SC, SCHIRP experimental area; RU, Rupert.
*Level of significance of differences between forest types using two-way ANOVA (Wilkinson 1990).

TABLE 6. Mean mass and nutrient content of four detrital pools in old-growth western red cedar – western hemlock and second-growth western hemlock – amabilis fir forests on northern Vancouver Island

	Cedar–hemlock					Hemlock–fir				
Detrital pool	Mass (Mg/ha)	C (Mg/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Mass (Mg/ha)	C (Mg/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)
Dead standing and stumps	80.1	45.2	78.0	8.3	20.0	20.9	11.7	23.4	2.2	3.2
Logs and woody debris	282.5	161.1	253.9	27.9	43.9	204.6	116.6	271.3	20.7	28.9
Forest floor										
Woody	166.1	91.4	769.4	46.4	46.8	133.7	76.7	915.3	49.5	27.9
Nonwoody	113.7	59.6	1077.3	59.1	70.0	77.2	40.5	839.4	45.9	34.2
Total	642.4	357.3	2178.6	141.7	180.7	436.4	245.5	2049.4	118.3	94.2

Detrital pool sizes

The total mass and nutrient content of detritus in each forest type is shown in Table 6 and Fig. 2. Both forest types had large amounts of biomass in detrital pools: 644 Mg/ha in the old-growth CH stands and 436 Mg/ha in the second-growth HA stands. Most of the detritus was woody (531 Mg/ha in the CH stands and 359 Mg/ha in the HA stands). These large accumulations of wood in both forest types may be due to the prevalence of windstorms, which result in a large number of tree boles being deposited on the forest floor. In the cool, wet climate these logs rarely dry out, and this can lead to a low rate of decay (Harmon et al. 1987). The wood of western red cedar has high concentrations of extractives and secondary compounds that make it highly resistant to decomposition until they are leached out (Minore 1983). Early and late successional stages also generally have greater quantities of woody debris than intermediate stands (Spies et al. 1988). Both of these factors may explain the higher quantities of woody forest floor in the CH stands.

The nutrient content of this detrital biomass was high: 2178 kg/ha of N in the CH stands and 2049 kg/ha in the HA stands. These values are comparable to the reported values of 2040 kg/ha of N in the old-growth coniferous stands in Washington (Gessel and Balci 1965) and 2260 kg/ha of N in a 115-year-old *Picea* stand in Germany (Cole and Rapp 1980).

Material of woody origin contained 82% of the measured detrital biomass in both types, with 52–56% contained in logs and dead standing trees above the forest floor. These logs and trees contained a small proportion of the nutrients in detritus (15% of the N, and 19–25% of the P), but all the woody material in and above the forest floor contained 51–59% of the N, and 58–61% of the P. Arthur and Fahey (1990) suggested that the role of dead wood in forest nutrition may be less significant than expected simply on the basis of the total mass of this component. However, when the nutrients accumulated in woody forest floor material are included, decaying wood is a major component of the nutrients stored in detritus in these ecosystems.

This study is part of a larger project aimed at improving understanding of the causes of lower available N in the forest floors of the old-growth CH stands compared with the HA stands (Prescott et al. 1993). Our data indicate that the total amount of N in detrital pools in the two forest types is similar, and therefore differences in N availability between the forests are probably not caused by differences in the amounts of N accumulated in the forest floor. However, nutrient availability is generally related to nutrient concentration rather than

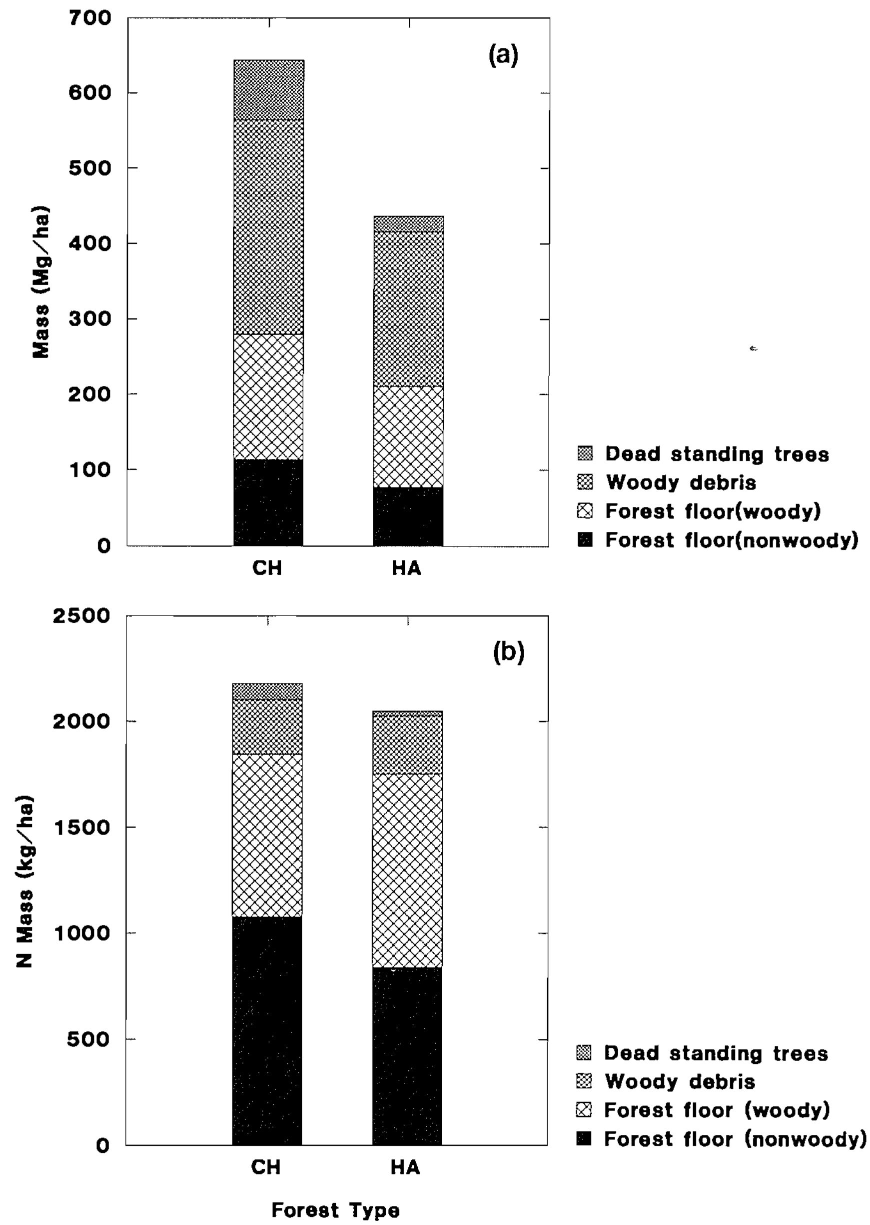

FIG. 2. Mean biomass and N content of four detrital pools in old-growth western red cedar – western hemlock (CH) and second-growth western hemlock – amabilis fir (HA) stands on northern Vancouver Island.

content and the rate at which nutrients are released through decomposition and mineralization. There is a higher accumulation of woody material in the CH type (Table 6, Fig. 2*a*), and this may be indicative of greater inputs and (or) slower turnover of this material. This could produce a higher forest floor C/N ratio and a lower rate of N mineralization.

The detritus measured was a considerable C sink, with 357 Mg/ha in the CH and 246 Mg/ha in the HA stands. Biomass accumulation and storage of C in forest floor pools generally increases from the tropics to the boreal regions, with intermediate values from intermediate latitudes, in a pattern largely determined by variation in global temperature (Vogt et al. 1986; Schlesinger 1991). The larger than expected accumulation in this area may result from the combination of windstorms depositing large amounts of wood to decay on the forest floor, the cool, wet climate resulting in slow decomposition, and the large size and decay resistance of western red cedar boles.

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