Nitrogen mineralization and decomposition in forest floors in adjacent plantations of western red cedar, western hemlock, and Douglas-fir

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To determine if western red cedar (*Thuja plicata* Donn) litter contributes to low N availability in cedar–hemlock forests, we measured concentrations of N and rates of net N mineralization in forest floors from single-species plantations of cedar, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) on the same site in coastal British Columbia. Concentrations of total and extractable N and rates of net N mineralization during laboratory incubations were lowest in the cedar forest floor and highest in Douglas-fir. Less C was mineralized in the cedar forest floor during incubation, and the amount of N mineralized per unit C was least in cedar. Rates of mass loss of foliar litter of the three species were similar during the first 50 weeks of a 70-week laboratory incubation, but cedar lost mass more quickly during the final 20 weeks. Rates of net N mineralization in the forest floors were significantly correlated with the initial percent N, C/N, % Klason lignin, and lignin/N of foliar litter. Foliar litter of cedar had lower concentrations of N and greater proportions of alkyl C (based on ^{13}C NMR spectroscopy) than Douglas-fir litter. These characteristics of cedar litter may contribute to low N availability in cedar–hemlock forest floors. Concentrations of alkyl C (waxes and cutin) may be better than lignin for predicting rates of mass loss and N mineralization from litter.

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Afin de déterminer si la litière du cèdre de l'Ouest (*Thuja plicata* Donn) contribue à la faible disponibilité de N dans les forêts de cèdre–pruche, nous avons mesuré les concentrations de N et les taux de minéralisation nette de N dans les couvertures mortes de plantations pures de cèdre, de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et de sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) sur une même station côtière de la Colombie-Britannique. Les concentrations en N total et extractible ainsi que des taux de minéralisation nette durant des incubations en laboratoire étaient les plus faibles dans la couverture morte de cèdre et les plus élevés, dans celle de sapin de Douglas. Moins de C a été minéralisé dans la couverture morte de cèdre durant l'incubation, et la quantité de N minéralisé par unité de C était la plus faible pour le cèdre. Le taux de perte de masse de la litière de feuilles des trois espèces était similaire durant les 50 premières semaines d'une période d'incubation de 70 semaines en laboratoire; la perte de masse de cèdre était plus rapide durant les 20 dernières semaines. Le taux de minéralisation nette de N dans la couverture morte était significativement corrélé avec la teneur initiale en N, le rapport C/N, le taux de lignine (Klason) et le rapport lignine/N de la litière foliaire. La litière foliaire de cèdre avait des concentrations plus faibles en N et des proportions plus élevées en C alkyle (basé sur la spectroscopie de RMN ^{13}C) que la litière de sapin de Douglas. Ces caractéristiques de la litière de cèdre peuvent contribuer à la faible disponibilité de N dans les couvertures mortes des forêts de cèdre–pruche. Les concentrations en C alkyle (les cires et la cutine) peuvent être plus fiables que la lignine pour prédire les pertes de masse et la minéralisation de N dans les litières.

[Traduit par la Rédaction]

Introduction

The species of vegetation occupying a site influences the availability and cycling of nutrients. Although this has been recognized for some time, the specific influence of vegetation, separate from other factors such as climate, soil, time, and topography (Jenny 1980; Van Cleve et al. 1991), has been difficult to assess, because of the propensity for species to grow on different sites. Recent studies of several species on the same site have demonstrated distinct differences in N availability between species, in forests (Harmer and Alexander 1986; Binkley and Valentine 1991; Harris and Riha 1991; Gower and Son 1992), in grasslands (Wedin and Tilman 1990), and in heathlands (Van Vuuren et al. 1992). The extent to which these differences are attributable to differences in litter quality or to other factors mediated by vegetation, such as nutrient uptake, rhizosphere effects, and herbivores, is not well understood (Hobbie 1992). Gower and Son (1992) found a good relationship between the lignin/N concentrations of foliar litter and rates of net N mineralization in soil under five tree species. They suggested that leaf litter fall lignin/N may be an important positive feedback mechanism that influences N availability. Using the ecosystem model LINKAGES, Pastor et al. (1987) demonstrated that spruce needle litter, through its high lignin, low N contents, and slow decomposition, depresses N availability in boreal forests. These studies indicate that species can influence N availability through the quality of the litter that they produce.

In a study on northern Vancouver Island, Prescott et al. (1993) found substantially lower N availability in forest floors of mixed forests of western red cedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.)

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Sarg.) than in adjacent mixed forests of western hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes). Among the suggested causes of the differences in N supply between the two forest types was the presence of cedar in the cedar–hemlock forests. Pure cedar foliar litter from these forests had lower initial concentrations of N and decomposed more slowly than mixed hemlock and fir needle litter (Prescott et al. 1995*a*). Using the computer model LINKAGES, Keenan et al. (1995) demonstrated that the differences in initial litter quality and decomposition rates of cedar and hemlock could, over time, result in lower N availability in the floors of cedar forests. Harmon et al. (1990) also reported lower initial N concentrations and slower decomposition of cedar litter relative to that of other conifers in coastal Washington, which suggests that this may be a characteristic of western red cedar.

In this study, we tested the hypothesis that the presence of cedar results in low N availability by comparing rates of N mineralization in forest floors in single-species plantations of western red cedar, western hemlock, and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) of similar age on the same site. We tested a second hypothesis, that differences in N availability in the forest floors of the three species were related to decomposition rates, by comparing rates of net N mineralization with rates of CO_2 evolution from the forest floors and rates of mass loss of foliar litter of each species in microcosms. We also tested the hypothesis that rates of net N mineralization in the forest floors could be predicted from the initial quality (N and lignin concentrations) of needle litter of each species. The organic composition of foliar litter and forest floors of each species were also characterized using nuclear magnetic resonance spectroscopy (^{13}C NMR).

Study site

The plantations were in the University of British Columbia Research Forest, near Maple Ridge, B.C. (49°17′N, 122°36′W). The site is within the dry maritime subzone of the Coastal Western Hemlock biogeoclimatic zone (CWHdm of Klinka et al. 1991) at 180 m. Average daily temperature is 9°C and average annual precipitation is 2166 mm (Ruekema and Smith 1987). The soil is an Orthic Humo-Ferric Podzol of gravelly to loamy sand, overtop a glacial-fluvial blanket over glacial-marine deposits (Carter et al. 1986). The original old-growth forest consisted of Douglas-fir, western hemlock, and western red cedar. The site index at 100 years was 61 m for Douglas-fir and 40 m for cedar and hemlock (Ruekema and Smith 1987). The original forest was clear-cut in 1955, and the slash was stockpiled and burned. Stumps were left in place, and the entire site was prepared with a bulldozer. There were three contiguous 0.25-ha plots, each containing 10 subplots in which trees were planted at five different spacings from 0.9 to 4.6 m. Nursery stock of Douglas-fir, western red cedar, and western hemlock were planted in the fall of 1957, fall of 1958, and spring of 1959, respectively. Each of the three 0.25-ha plots contained only one species and were within 50 m of one another. There was very little slope. All plots were cleaned and weeded several times to reduce growth of lesser vegetation and hardwoods At the time of sampling in 1992, the stands were 34 years old and had forest floors about 5 cm deep. The humus layers were classified as Leptomoders (Green et al. 1993). Samples of litter and forest floors were taken from random locations throughout each 0.25-ha plot.

Methods

Chemistry of forest floors

Ten samples of the forest floors (FH) in each plot were collected in February 1992, after brushing away the fresh litter that had fallen during the previous autumn. Samples were passed through a 5-mm sieve, and all live plants and large pieces of wood and roots were removed. A portion of each sample was oven-dried at 70°C and digested in sulphuric acid and hydrogen peroxide using a modification of the method of Parkinson and Allen (1975). Concentrations of P in the digest were determined on an Alpkem RFA 300 autoanalyzer, and Ca and Mg concentrations were determined on a Varian Spectra 400 atomic absorption instrument. Concentrations of C, N, and S were determined by combustion in Leco carbon and nitrogen determinators and a Fisher oven, respectively. The pH of 5-g moist samples mixed with 20 mL of distilled water was determined with a Fisher Accumet model 750 pH meter.

N mineralization and respiration in forest floors

Fourteen samples of forest floor FH material were collected from each of the three plots in February 1993. A 10-g (dry-weight equivalent) portion of each sample was extracted with 100 mL of 2 M KCl (Page et al. 1982), and concentrations of NH_4-N and NO_3-N were measured on the autoanalyzer. A second 10-g (dry-weight equivalent) portion of each sample was put in a canning jar (Kerr wide mouth, 1 pint (0.6 dm^3)). Distilled water was sprayed into each sample to bring the moisture contents to 75% (wet-weight basis), and the jars were incubated in the dark at about 20°C. Each lid had an air-tight septum, through which the gas inside each jar was sampled with a syringe at weekly intervals for 28 days. Concentrations of CO_2 in the headspace gas were determined with a Beckman model 215A infrared gas analyzer (Clegg et al. 1978). Immediately after the weekly measurements of CO_2, the jars were opened to outside air for 15 min. After 28 days, each sample was extracted with 100 mL of 2 M KCl, and concentrations of NH_4-N and NO_3-N in the extracts were determined on the autoanalyzer. Differences between the amounts of KCl-extractable N before and after incubation were used to estimate rates of net mineralization of N in each forest floor sample. The concentrations of CO_2 in each sample were converted to milligrams C and summed for the four sampling occasions, to estimate the total amount of C mineralized in each jar during the 28-day incubation.

Litter quality

Needle litter was collected in each of the three plots during October–December 1990 and 1991. In the hemlock and Douglas-fir plots, twenty 0.08-m^2 plastic trays with fibreglass mesh and holes for drainage were distributed throughout each plot and harvested at monthly intervals. Freshly fallen cedar foliar litter was picked up from the forest floor in December of each year. Litter was oven-dried at 70°C and composited into one sample for each species. Concentrations of C, N, P, Ca, Mg, and S in three subsamples of needle litter from each species were determined as described for the forest floors. Concentrations of Klason lignin, cellulose, acid detergent fibre (ADF), and ash content in two subsamples of one bulked sample of litter from each species were determined at the Forest Science Laboratory of Oregon State University, Corvallis, using the method of McClaugherty et al. (1985).

Litter decomposition

Rates of mass loss from needle litter of each of the three species was measured during a 70-week incubation in bags in forest floor material in laboratory microcosms. One-gram samples of ovendried needle litter of each species from the 1990 collection were placed in 10 × 10 cm fibreglass mesh bags with pore size 1.5 mm. Forest floor material (LFH) was collected in August 1991 from a 125-year-old mixed stand of cedar, hemlock, and Douglas-fir near the single-species plots at the University of British Columbia Research Forest. Live plants, roots, and twigs were removed, and the remaining material was remoistened with tap water to 75% moisture content (wet-weight basis). A 100-g (dry-weight equivalent) sample of LFH was added to 50 plastic 1-L tubs. One litterbag of each of the three species

TABLE 1. Nutrient concentrations, pH, and rates of N and C mineralization in forest floors under adjacent plantations of western red cedar, western hemlock, and Douglas-fir

Element	Cedar	Hemlock	Douglas-fir
C (%)	27.39*a* (6.82)	37.3*a* (6.23)	38.85*a* (3.68)
N (%)	1.00*b* (0.12)	1.29*ab* (0.15)	1.49*a* (0.13)
P (%)	0.08*b* (0.01)	0.10*a* (0.02)	0.09*a* (0.01)
S (%)	0.12*b* (0.03)	0.16*a* (0.01)	0.18*a* (0.03)
K (%)	0.09*b* (0.01)	0.10*a* (0.01)	0.09*b* (0.01)
Ca (%)	1.26*a* (0.33)	0.53*b* (0.13)	1.21*a* (0.22)
Mg (%)	0.15*a* (0.03)	0.11*a* (0.05)	0.12*a* (0.03)
pH	5.07*a* (0.31)	4.21*b* (0.36)	5.18*a* (0.20)
Extractable N (mg N / 10 g)	0.27*b* (0.08)	0.36*ab* (0.18)	0.49*a* (0.15)
Net N mineralized ($mg \cdot 10\ g^{-1} \cdot 28\ d^{-1}$)	0.45*b* (0.33)	0.89*ab* (1.02)	1.55*a* (0.70)
C mineralized ($mg\ C \cdot 10\ g^{-1} \cdot 28\ d^{-1}$)	40.45*b* (15.45)	56.58*a* (13.72)	53.28*a* (7.80)
% N mineralized (net N mineralized/ total N)	0.5	0.7	1.0
% C mineralized (C mineralized/ total C)	1.5	1.5	1.4
N mineralized/ C mineralized	0.011	0.016	0.029
% N mineralized/ % C mineralized	0.33	0.47	0.71

NOTE: Values for nutrient concentrations and pH are the mean (and standard deviation) of 10 samples collected in 1992. Values for N and C mineralization are the mean (and standard deviation) of 14 forest floor samples collected in 1993. Values for the three species followed by the same letter are not significantly different ($p < 0.05$) based on one-way ANOVA and Scheffé's multiple range test.

was inserted vertically into each microcosm, such that each bag was surrounded on all sides by forest floor material. Each microcosm was sealed with a polyethylene bag to retain moisture but allow gas exchange (Gordon et al. 1987) and incubated at 15–20°C. At 10-week intervals for 70 weeks, litterbags were removed from five microcosms, and the litter in the bag was dried at 70°C and weighed. The moisture content of the forest floor in each harvested microcosm was determined, and tap water was accordingly sprayed in the remaining microcosms to maintain the moisture content at about 75%.

NMR analysis

The organic composition of foliar litter and forest floors of the three species were characterized using NMR spectroscopy with cross-polarization and magic-angle spinning (CPMAS NMR). This technique, developed to obtain ^{13}C NMR spectra of solid-state samples, has recently been applied to litter and forest floor materials (Baldock and Preston 1995; Norden and Berg 1990; Preston et al. 1994; Zech et al. 1987). One composite sample of foliar litter and two composite samples of the forest floor of each species (each from five samples) were analyzed using a Bruker MSL 100 spectrometer operating at 25.18 MHz for ^{13}C at 2.35 T. Samples were spun at 4 kHz in an aluminum oxide rotor of 7 mm outside diameter. Spectra were acquired with 1 ms contact time, 1.0 s recycle time, and 12 000 – 50 000 scans, and were processed using 25–35 Hz linebroadening and base-line correlation routines from the Bruker software. Chemical shifts were reported relative to tetramethylsilane (TMS) at 0 ppm. All NMR analyses were done at the Department of Chemistry of McMaster University, Hamilton, Ontario. Spectra were divided into chemical shift regions according to chemical types of C, as follows: alkyl 0–50 ppm; *O*-alkyl 50–96 ppm; di-*O*-alkyl 96–110 ppm; aromatic 110–140 ppm; phenolic 140–160 ppm; and carboxyl 160–185 ppm. The areas of each of the chemical shift regions were measured by cutting and weighing and were expressed as proportions of the total area (i.e., relative area). Two additional parameters were derived from these data: aromaticity (area from 96 to 106 ppm as a proportion of total area), and the ratio of alkyl to *O*-alkyl C. These parameters have been proposed as indexes of decomposition of forest floor and peat materials (Baldock and Preston 1995).

The types of C in each chemical shift region have been established from previous studies (see Baldock and Preston 1994). The alkyl region (0–50 ppm) arises from extractable lipids such as surface waxes and cutin, with small contributions from the aliphatic C of amino acids and the acetate CH_3 of hemicellulose. The *O*-alkyl region (50–90 ppm) arises from carbohydrates (C-2 to C-6 of cellulose and hemicellulose), the 3-carbon side-chain and methoxyl C of guaiacyl lignin, carbons C-2 and C-3 of condensed tannins, and carbons adjacent to N in amino acids. The peak in the di-*O*-alkyl region (96–110 ppm) comes mainly from the anomeric C of carbohydrates, with some contribution from condensed tannins. In the aromatic region (110–140 ppm), C-2, C-5, and C-6 of guaiacyl lignin occur at 115–118 ppm and C-1 at 131 ppm, and several carbons of condensed tannins occur at 115–131 ppm. There is also some contribution from aromatic carbons of amino acids, proteins, and cutin. In the phenolic region (140–160 ppm), C-3 and C-4 of guaiacyl lignin occur at 153 ppm, and condensed tannins give rise to peaks at 145 and 155 ppm. The carboxyl region (160–185 ppm) includes contributions from the acetate of hemicellulose and the carboxyl groups of amino acids and cutin.

Statistical analysis

The mean values for nutrient concentrations, pH, and rates of mineralization in the three plots were compared using one-way ANOVA followed by Scheffé's multiple range test. When variances were not homogenous, log-transformed values were used. Pearson correlation coefficients were calculated to examine relationships between rates of C and N mineralization and litter

TABLE 2. Nutrient concentrations in needle litter in adjacent plantations of western red cedar, western hemlock, and Douglas-fir

Element	Cedar	Hemlock	Douglas-fir
C (%)	48.44*a*	47.21*a*	47.58*a*
N (%)	0.48*b*	0.58*ab*	0.71*a*
P (%)	0.04*a*	0.06*a*	0.05*a*
S (%)	0.05*b*	0.10*a*	0.09*a*
K (%)	0.11*a*	0.07*c*	0.09*b*
Ca (%)	1.61*a*	0.53*c*	1.18*b*
Mg (%)	0.07*a*	0.06*b*	0.07*a*
Lignin (%)	37.94	33.90	30.81
Tannin (%)	0.12	0.23	0.19
Lignin/N	79.0	58.4	43.4
C/N	100.9	81.4	67.0

NOTE: Each value is the mean of three samples. Values for the three species followed by the same letter are not significantly different ($p < 0.05$) based on one-way ANOVA and Scheffé's multiple range test. Values for lignin and tannin concentrations are the average of duplicate analyses of one sample.

quality parameters (percent N, C/N, percent lignin, lignin/N) of the three species. SPSS^x (SPSS Inc. 1988) was used for all analyses, and the accepted level of significance was $p < 0.05$.

Results

Chemistry of forest foors

Concentrations of nutrients in forest floor FH material differed among the three plots (Table 1). N concentrations were significantly higher in the forest floor of Douglas-fir (1.49%) than in western red cedar (1.10%), and western hemlock was intermediate (1.29%). Average C/N ratios in forest floor material were similar: 27 in cedar, 29 in hemlock, and 26 in Douglas-fir. P and S concentrations were also lowest in the cedar forest floor. The forest floor in the western hemlock stand had the highest K concentrations and the lowest Ca concentrations. The pH of the hemlock forest floor (4.21) was lower than those of cedar (5.07) and Douglas-fir (5.18).

N mineralization and respiration in forest floors

Concentrations of extractable N in forest floor FH material were significantly higher in the Douglas-fir plot than in the cedar plot, and hemlock was intermediate (Table 1). The amounts of N mineralized during the 28-day incubation were greater in Douglas-fir than in cedar or hemlock forest floors (Table 1). The proportion of the total amount of N in the forest floor sample that was mineralized during the incubation was 0.5% in cedar, 0.7% in hemlock, and 1.0% in Douglas-fir (Table 1).

The amounts of C mineralized in forest floor samples during the 28-day incubation were significantly less in the cedar plot than in hemlock and Douglas-fir (Table 1). However, the same proportion (1.5%) of the total amount of C in the forest floor sample was mineralized in all three plots (Table 1). The ratio of amount of N mineralized to amount of C mineralized during the incubation was 0.011 in cedar, 0.016 in hemlock, and 0.029 in the Douglas-fir forest floor. The ratio of percent of total N mineralized to percent of total C mineralized during the incubation was 0.33 in cedar, 0.47 in hemlock, and 0.71 in Douglas-fir (Table 1).

Litter quality

Concentrations of nutrients in needle litter differed among the three species (Table 2). N concentrations were highest in Douglas-fir and lowest in cedar, and C/N ratios were 67 in Douglas-fir, 81 in hemlock, and 101 in cedar. Cedar foliage had slightly smaller concentrations of S and higher concentrations of Ca and Mg than the other species. Cedar litter had the highest concentrations of lignin, Douglas-fir litter had the lowest, and lignin/N ratios were 43 in Douglas-fir, 58 in hemlock, and 79 in cedar needle litter. Tannin concentrations were lowest in cedar and highest in hemlock.

The relationships between the parameters of litter quality and the rates of N and C mineralization during incubation were explored through correlation analysis. There were strong correlations between net N mineralization and each of the litter quality parameters tested (percent N $r^2 = 0.999$, C/N $r^2 = 0.960$, percent lignin $r^2 = 0.964$, lignin/N $r^2 = 0.959$). Correlations between litter quality and C mineralization rates were not as strong ($r^2 = 0.471$–0.635), and the correlation was poor between rates of C mineralization and net N mineralization in forest floors of the three species ($r^2 = 0.433$).

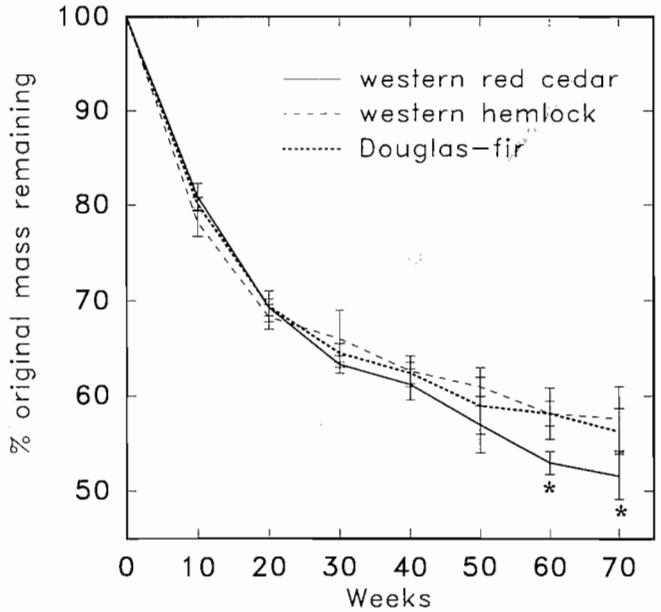

FIG. 1. Rate of decomposition in laboratory microcosms of needle litter from adjacent plantations of western red cedar, western hemlock, and Douglas-fir. The mean values of five samples of each litter type at each sampling time are shown. Asterisks indicate significant differences between the three species in the percent mass remaining at that time.

Litter decomposition

The rates of decay of needle litter of cedar, hemlock, and Douglas-fir under identical conditions in laboratory microcosms are shown in Fig. 1. At no time during the first 50 weeks was there a significant difference among the three species in the mass of litter remaining. Cedar litter decomposed significantly faster than hemlock or Douglas-fir during the final 20 weeks of the incubation.

NMR analyses

Solid-state ^{13}C NMR spectra of foliar litter and forest floors of the three species are shown in Fig. 2, and the relative areas of each chemical shift region are shown in Table 4. There were small differences between the spectra of litter and forest floors, indicative of changes in the composition of the litter as it decomposes. There was a slight decrease in *O*-alkyl C in Douglas-fir and a slight increase in alkyl C in

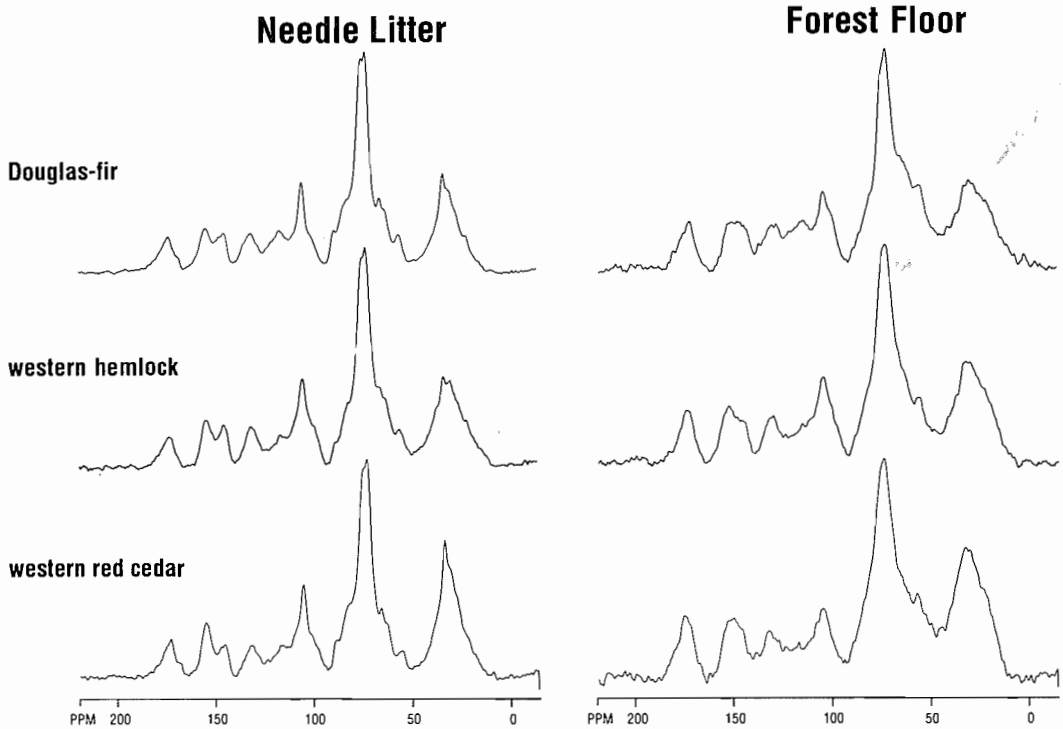

FIG. 2. ^{13}C NMR spectra of foliar litter and forest floor material from adjacent plantations of western red cedar, western hemlock, and Douglas-fir.

TABLE 3. Area of chemical shift regions in ^{13}C NMR spectra of foliar litter and forest floors from adjacent plantations of western red cedar, western hemlock, and Douglas-fir

	Chemical shift region (ppm)							
	Alkyl (0–50)	*O*-alkyl (50–96)	di-*O*-alkyl (96–110)	Aromatic (110–140)	Phenolic (140–160)	Carboxyl (160–185)	Aromaticity (110–160)	Alkyl C/ *O*-alkyl C
Foliar litter								
Cedar	26.0	40.9	11.2	8.8	8.2	4.9	17.0	0.64
Hemlock	24.8	42.5	11.5	8.9	8.5	3.8	17.4	0.58
Douglas-fir	20.6	44.3	9.0	12.6	8.7	4.8	21.3	0.47
Forest floor								
Cedar	27.4	40.5	5.6	9.0	8.4	9.1	17.4	0.68
	27.5	39.6	7.2	10.6	8.1	7.0	18.7	0.69
Hemlock	23.3	44.3	9.6	10.3	6.7	5.8	17.0	0.53
	24.2	40.1	9.7	11.1	8.9	6.0	20.0	0.60
Douglas-fir	22.9	42.2	8.7	12.8	7.8	5.6	20.6	0.54
	23.0	40.9	8.4	13.8	8.1	5.8	21.9	0.56

NOTE: Values are from one composite sample of foliar litter and two composite samples of forest floors of each species. Relative areas refer to areas under peaks within each of the chemical shift regions as a proportion of the total area under the shift.

cedar between litter and forest floor samples. The ratio of alkyl C/*O*-alkyl C increased between litter and forest floor samples in Douglas-fir and cedar, but not hemlock. Aromaticity was the same in litter and forest floor samples.

There were only minor differences in the ^{13}C NMR spectra of the three species (Fig. 2, Table 3). Cedar litter and forest floors had the greatest proportion of alkyl C and the greatest alkyl C/*O*-alkyl C ratio, and Douglas-fir had the lowest. Cedar litter and forest floors also had the least di-*O*-alkyl C and the greatest carboxyl C. Aromaticity was slightly greater in Douglas-fir litter and forest floor samples. Tannins, indicated by a peak at 145 ppm (deMontigny et al. 1993), were evident in litter of all three species, and in hemlock and Douglas-fir forest floors. Tannin content appeared to be smaller in cedar litter and forest floors than in the other species.

Discussion

The relatively low concentrations of extractable and total N and the low rates of N mineralization in the forest floor in the western red cedar plantation in this study support the hypothesis that cedar creates conditions of low N availability. The presence of cedar in the old-growth cedar–hemlock forests on northern Vancouver Island may therefore

contribute to the low availability of N in these forests (Prescott et al. 1993), and the nutrient supply problems in plantations in cutovers of these forests (Weetman et al. 1989). This supports the conclusion from the modelling study of Keenan et al. (1995), which suggested that the lower N availability in cedar–hemlock forests could be attributed, at least in part, to the presence of cedar.

The smaller rates of C mineralization in cedar forest floors support the hypothesis that slower decomposition of organic matter contributes to lower N availability in cedar forest floors. However, the same proportion of the total amount of C in the sample was respired in all three species, and a smaller amount of N was mineralized per unit C mineralized in cedar forest floors. These findings suggest that some factor in addition to slow decomposition contributes to the slow mineralization of N in cedar forest floors. Perhaps some characteristic of cedar litter causes N to remain unavailable or unextractable, even as the organic matter is broken down. Tannins are known to interfere with N mineralization (deMontigny et al. 1993; Gallardo and Merino 1992), but cedar litter had the lowest concentrations of tannins of the three species. Alternatively, a greater proportion of the N in cedar litter may be bound in the acid-insoluble (Klason lignin) fraction, where it is less likely to be mineralized than the more labile N, or is tranformed into this type of material during decomposition (Berg and Theander 1984; Berg 1988). Harris and Riha (1991) also reported a poor relationship between rates of net N mineralization and CO_2 evolution in forest floors under four different tree species and suggested that factors other than the rate of decomposition of organic matter determine N availability. Discrepancies between rates of C mineralization and net N mineralization may also result from differences in rates of re-immobilization of mineralized N by microorganisms, which may be substantial (Davidson et al. 1992; Scott 1994).

The nearly identical rates of mass loss of foliar litter of the three species in microcosms during the 70-week incubation also indicate that differences in rates of decomposition of litter of these three species are not responsible for the differences in N availability in the forest floors. The only difference was the faster mass loss from cedar litter during the final 20 weeks. This result was surprising, since other studies have reported that cedar litter decays more slowly than litter of other species. Harmon et al. (1990) reported slower decomposition of cedar litter compared with hemlock and Douglas-fir, but the comparison was confounded by the use of green hemlock needles. In a field experiment on northern Vancouver Island, cedar litter lost mass more slowly than mixed hemlock–fir litter (Prescott et al. 1995*a*). However, in another laboratory experiment (Daubenmire and Prusso 1963), cedar litter lost mass more rapidly than hemlock litter. Slower decomposition of cedar litter has been attributed to its relatively large lignin concentration and small N concentration (Harmon et al. 1990; Keenan et al. 1995; Prescott et al. 1995*a*). These characteristics were also found in the cedar litter in this study, but they did not result in slower decomposition of cedar litter in the microcosms.

Our results supported the hypothesis that rates of net N mineralization in forest floors of these species can be predicted from the quality of litter that they produce. There were highly significant correlations between rates of N mineralization during laboratory incubations and each of the parameters of foliar litter quality tested (percent N, C/N, percent lignin, lignin/N). These findings support the suggestions of Gower and Son (1992) that litter quality influences N availability and cycling under different species and that characteristics of litter, such as lignin/N, may be useful for predicting relative rates of N mineralization. None of the litter quality parameters were closely correlated with rates of C mineralization in the forest floor. This result was surprising, since many studies have reported good relationships between these litter quality parameters and rates of litter decomposition (Taylor et al. 1991). The limited data in the present study suggest that litter quality is more useful for predicting rates of net N mineralization than rates of decomposition in forest floors of different tree species.

The ^{13}C NMR spectra of the three species in this study were similar to other spectra of conifer litter and forest floors (deMontigny et al. 1993; Kogel-Knaber et al. 1988*a*, 1988*b*; Norden and Berg 1990; Preston et al. 1993; Zech et al. 1987). The small differences between spectra of litter and forest floors were surprising and indicate that there is a considerable amount of nonselective mass loss during decomposition of litter. There was little in the spectra to explain the slow N mineralization in cedar forest floors. However, the proportion of alkyl C and the ratio of alkyl C/*O*-alkyl C was greatest in litter and forest floors of cedar. This suggests that cedar litter contains relatively less carbohydrate and relatively more waxes and cutin, which could lead to slower mineralization. Studies of peat have shown that decomposition proceeds with accumulation of alkyl C and an increasing ratio of alkyl C/*O*-alkyl C (Baldock and Preston 1995) and that accumulations of alkyl C are characterisitic of situations where decomposition is hindered or incomplete. deMontigny et al. (1993) reported greater alkyl/*O*-alkyl ratios in forest floors in cedar–hemlock forests than in hemlock–fir forests on northern Vancouver Island and suggested that decomposition may be less complete in cedar–hemlock forest floors. Similar findings in forest floors under a pure cedar stand in this study suggest that these characteristics of cedar–hemlock forest floors result from the greater proportions of alkyl C in cedar litter, rather than incomplete decomposition.

The NMR spectra did not indicate that cedar litter had a greater lignin content than the other species. The greater lignin concentrations reported for cedar litter have been based on the Klason lignin fraction of proximate analysis. This fraction includes structural lipids such as cutin (Zech et al. 1987), and the greater lignin concentrations reported in cedar litter may result from greater concentrations of these materials. Lignin estimates based on proximate analysis have proven useful for predicting rates of litter decomposition (Taylor et al. 1991). Alkyl C content, rather than lignin per se, may be the component most resistant to decomposition and may therefore be a better predictor of decomposition rates.

The litter and forest floors of western red cedar, western hemlock, and Douglas-fir described in this study are from single plots of each species on one site. Therefore, we cannot with certainty attribute the differences between the three plots to effects of the tree species. However, three lines of evidence support our suggestion that these differences are related to the species composition of the overstories. First, in another (again unreplicated) trial on a cutover peat bog in Ireland, rates of net N mineralization in the forest floors were also in the order Douglas-fir > western hemlock >

western red cedar (Prescott et al. 1995*b*). Second, N concentrations and net mineralization rates in the three plots in the present study were correlated with N concentrations in the litter and could be predicted from the quality of litter in each plots. Third, the three plots were very close together and received identical treatment during development, so the major difference between them was the composition of the overstory. Our conclusion that rates of N mineralization are low in cedar forest floors and high in Douglas-fir forest floors requires further testing in replicated plantations.

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