Litter decomposition in western red cedar and western hemlock forests on northern Vancouver Island, British Columbia

R.J. Keenan, C.E. Prescott, J.P. Kimmins, J. Pastor, and B. Dewey

Abstract: Litter decomposition and changes in N and organic chemicals were studied for 2 years in two forest types: old-growth western red cedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarge) and 85-year-old stands of western hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes) that developed after a major windstorm. We tested the hypothesis that lower rates of mass loss and different patterns of nutrient release in decomposing litter could explain lower nutrient availability in the cedar–hemlock type. Decomposition rate of a standard litter substrate, lodgepole pine needles, was almost identical in the two forest types indicating that each type had similar microenvironmental conditions for decomposers. Salal leaves had a lower lignin to N ratio and decomposed and released N more rapidly than the conifer litters. Among the conifers, cedar had poorer litter quality (higher lignin to N ratio), decomposed more slowly, and released considerably less N during the study. Cedar litter contributes to lower N availability in cedar–hemlock forests, but other factors, such as lower external N cycling and complexing of N with secondary carbon compounds during later stages of decomposition, are also likely to have a major influence on N availability.

Key words: *Thuja plicata*, *Tsuga heterophylla*, decomposition, litter quality, N cycling.

Résumé : Les auteurs ont étudié la décomposition de la litière et les changements de la composition en N et en substances organiques pendant 2 ans, dans deux types de forêt : une forêt agée de *Thuja plicata* Donn (thuya rouge de l'ouest) et de *Tsuga heterophylla* (Raf.) Sarge (prûche de l'ouest) et une station vieille de 85 ans dominée par la prûche de l'ouest et l'*Abies amabilis* (Dougl.) Forbes (sapin gracieux) qui s'est regénérée suite à un chablis majeur. Les auteurs ont vérifié l'hypothèse selon laquelle des taux de mouvement de masse plus faibles et des patrons de relâchement des nutriments différents, au cours de la décomposition des litières, pourraient expliquer la plus faible disponibilité en nutriments dans le type thuya–prûche. Le taux de décomposition d'une litière standard, les aiguilles du pin lodgepole, est presqu'identique dans les deux types de forêt, ce qui indique que chaque type présente des conditions micro-environmentales pour les décomposeurs. Les feuilles du salal ont des teneurs lignine à N plus faibles et se décomposent et relâchent l'azote plus rapidement que les feuilles de conifères. Parmi les conifères, le thuya présente les moins bonnes qualités (rapport lignine à N plus élevé), se décompose plus lentement, et a relâché beaucoup moins d'azote au cours de cette étude. La litière de thuya est en partie responsable de la plus faible disponibilité en azote dans les forêts thuya–prûche, mais d'autres facteurs tels que le cyclage plus faible de l'azote externe et la formation de complexes azotés avec des composés carbonés secondaires, au cours des derniers stades de décomposition, sont également susceptibles d'exercer une influence majeure sur la disponibilité de l'azote.

Mots clés : *Thuja plicata*, *Tsuga heterophylla*, décomposition, qualité de la litière, cyclage de l'azote.
[Traduit par la rédaction]

Introduction

Cycling of nutrients is a fundamental component of forest ecosystem functioning, and in mature forests, the majority of nutrients required for plant production are made available through the decomposition of litter and other plant remains (Waring and Schlesinger 1985). A number of factors interact to determine litter decomposition rate. Meentemeyer (1978) established the importance of climatic conditions, such as temperature and moisture, in controlling decomposition rate in different regions but also found that where climate is less limiting, substrate 'quality' for decomposers is an important determinant of the rate of mass loss. Quality is a general term incorporating availability to decomposers of energy contained in C compounds and the amount and availability of nutrients in litter material. More recent studies confirmed the importance of litter quality in determining both the rate of decomposition and nutrient dynamics in decomposing litter (e.g., Aber and Melillo 1982; Melillo et al. 1982; Flanagan and Van Cleve 1983; Berg and McClaugherty 1989; Aber et al. 1990; Harmon et al. 1990; Taylor et al. 1991), and there is considerable evidence to indicate that plants can exert a major influence on soil properties through the effect of litter quality on

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decomposition in both forests (Flanagan and Van Cleve 1983; Nadelhoffer et al. 1983; Pastor et al. 1984; Zak et al. 1986; Hobbie 1992; Stump and Binkley 1993) and grasslands (Wedin and Tilman 1990).

It is generally considered that slower litter decomposition contributes to lower rates of nutrient mineralization, but this depends on the nutrient in question (Waring and Schlesinger 1985). This can potentially set up a positive feedback cycle between lower nutrient mineralization and litter quality, because litter quality tends to be poorer on nutrient poor sites (Gosz 1981; Edmonds et al. 1990). However, Keenan et al. (1995*a*, 1995*b*) argue that this feedback is controlled by the extent to which different species can withdraw nutrients at the time of leaf senescence.

Despite the importance of litter decomposition to ecosystem functioning, there are few studies of litter decomposition in coastal conifer forests of the Pacific Northwest of the U.S.A. or British Columbia (Fogel and Cromack 1977; de Catanzaro and Kimmins 1985; Harmon et al. 1990; Edmonds 1980, 1984). This study compared foliar litter decomposition in the two dominant forest types on better drained sites on northern Vancouver Island. These two forest types exhibit substantial differences in forest floor N availability and a number of hypotheses have been put forward to explain these differences (Prescott and Weetman 1994). Our aim was to test the hypothesis that differences between species in litter quality, rates of mass loss, and nutrient dynamics during decomposition could contribute to lower N availability in old-growth forests of western red cedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarge. We compared (*i*) decomposition rates of a standard litter (lodgepole pine needles) between the two forest types; (*ii*) decomposition rates of local species, including three conifers and the dominant shrub, salal (*Gaultheria shallon* Pursh.); and (*iii*) initial concentrations and dynamics of N and organic chemicals in local species litter.

Study area

The study area is a gently undulating coastal plain generally less than 300 m in elevation near the town of Port McNeill on northern Vancouver Island (latitude 50°60′N). Description of the soils and vegetation can be found in Lewis (1982) and Keenan et al. (1993, 1995*a*, 1995*b*). The two main forest types are the following: (*i*) the cedar–hemlock type that consists of old-growth western red cedar with a broad size distribution ranging up to 260 cm in diameter at a height of 1.3 m, with a lesser component of western hemlock, and an understorey dominated by salal; (*ii*) the hemlock – amabilis fir type, which are more uniform stands of western hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes that largely originated after a catastrophic windstorm in 1906. Very little light passes through the dense canopy in the hemlock – amabilis fir type and the understorey is dominated by ferns and mosses. The two types differ significantly in forest floor nutrient availability (Prescott et al. 1993). All forest floor layers in the cedar–hemlock type had significantly lower concentrations of total N (e.g., 0.90 compared with 0.99 $mg \cdot g^{-1}$ in the F layer) and extractable N (0.08 compared with 0.1 $mg \cdot g^{-1}$ in the F layer). In a 40-day aerobic laboratory incubation, 120 $\mu g \cdot g^{-1}$ of N was mineralized in F-layer material from the hemlock – amabilis fir type compared with 2 $\mu g \cdot g^{-1}$ in material from the cedar–hemlock type. These differences have strong effects on the productivity of conifer seedlings on clear-cut sites (Weetman et al. 1989*a*, and 1989*b*).

The climate is wet with mild winters and relatively cool summers. Mean annual precipitation is approximately 1700 mm, mean annual temperature is 7.9°C, and the daily average ranges from 2.4°C in January to 13.8°C in August. Wildfire is uncommon and the major source of natural forest disturbance is windstorms. Both forest types have deep (10 cm to 1 m) mor forest floors overtopping medium-textured Humo-ferric Podzols derived from unconsolidated morainal and fluvial outwash material of sedimentary, soft volcanic, and hard volcanic origin.

Methods

Three sites were chosen for investigation. Each contained representative examples of the two forest types in close proximity on similar aspect and in similar topographic positions. A plot of 0.25 ha (50 × 50 m) was established in each type at each site.

To compare conditions for decomposers between the two types, lodgepole pine (*Pinus contorta* var. *contorta*) needles collected from the Rocky Mountains were used as a standard litter. Nylon mesh bags, 10 × 10 cm in size with a pore size of 1 mm, were used. One gram of dried pine needles was placed in each bag. Thirty-five bags were systematically located in each plot in February 1990. Five bags were brought back from each site at 6-month intervals for 3 years, and the contents of each bag were dried for 24 h at 70°C and weighed.

Fresh litterfall of four local litter types, i.e., cedar, hemlock + fir, salal in the cedar–hemlock forests, and hemlock + fir in the hemlock – amabilis fir forests, was collected on mesh laid out in each plot and dried at 70°C for 24 h and placed in mesh bags, as above. Hemlock and fir needles were not separated, as there was a similarly small component of fir in both forest types. Cedar and hemlock were mixed in the cedar–hemlock type to replicate conditions for decomposers more accurately. Salal was included in the study because it dominates the understorey of cedar–hemlock forests and some authors have argued that its litter may contribute to lower N availability through either being recalcitrant or contributing tannins or other secondary carbon compounds that complex with N during later stages of decomposition (de Montigny et al. 1993).

In February 1991, 35 bags each containing 1 g of cedar and 1 g of mixed hemlock + fir foliage from cedar–hemlock forests, and 35 bags each containing a single salal leaf of known dry weight were placed at systematically located points in each cedar–hemlock plot, and 35 bags each containing 2 g of mixed hemlock + fir foliage were placed in adjacent hemlock – amabilis fir plots. Five bags of each litter type were retrieved at about half yearly intervals for 2 years and the contents of each bag were dried and weighed as above. Litter in bags containing a mixture of cedar and hemlock + fir foliage were sorted into these two categories and reweighed.

Chemical analyses were undertaken on initial litter samples and on the combined litter from the five litter bags from each collection time for each litter type. This gave three samples for each litter type for the five collection times from 0 to 2 years. Each sample was ground in a Wiley mill, and subsamples were ashed at 450°C for 4 h. Total C and N were measured using a LECO CHN 800 analyser. Samples were analysed for carbon fractions by sequential extraction as follows: first, for nonpolar compounds (waxes, fats, and oils) by repeated filtration through Gooch crucibles with dichloromethane following sonication (Tappi 1976); next for polar compounds (sugars, starches, and tannins) by hot-water extraction (Tappi 1975) with the extract analysed for tannins by Folin-Denis reaction; and finally, in a two-stage sulfuric acid digest (Effland 1977) followed by autoclaving in 1 mol/L sulphuric acid to remove cellulose and hemicellulose. The residue after these extractions was assumed to be lignin + ash. The mass of all fractions was then expressed on an ash-free basis. All analyses were undertaken at the Natural Resources Research Institute laboratory in Duluth, Minn. from April to November 1993.

Fig. 1. Percent mass remaining in relation to time for lodgepole pine needles decomposing in old-growth western red cedar – western hemlock forests (——) and adjacent hemlock – amabilis fir forests (--) on northern Vancouver Island.

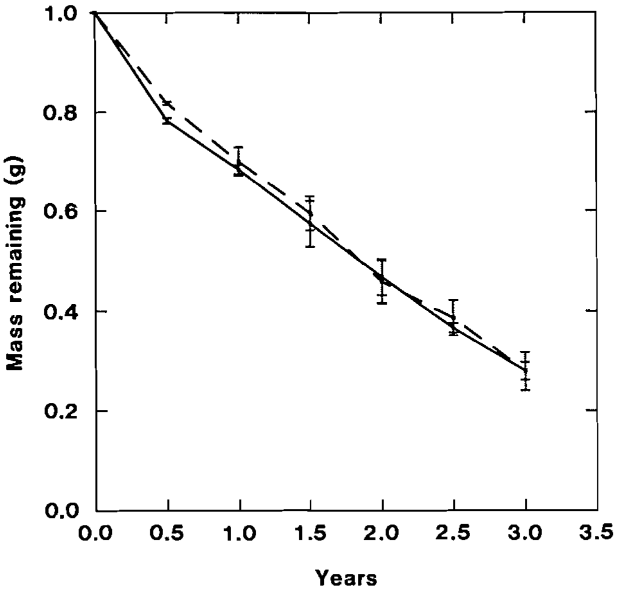
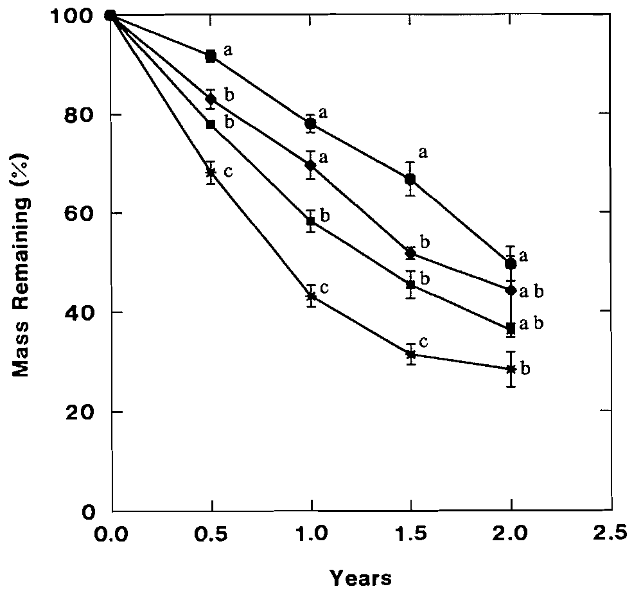


Fig. 2. Percent mass remaining in relation to time for four litter types in cedar–hemlock and hemlock – amabilis fir forests on northern Vancouver Island. Bars are 1 SE of the mean of values from three sites. Site values are the mean of five observations at each collection time. Different letters beside each point indicate significant difference ($\alpha \leq 0.05$). ●, cedar at cedar–hemlock sites; ■, hemlock + fir at cedar–hemlock sites; ♦, hemlock + fir at hemlock – amabilis fir sites; *, salal at cedar–hemlock sites.



Calculations and statistical analysis

Mean values of mass remaining from the three sites were calculated for the four litter types at each collection time. Site means were used to compare litter types. We used univariate ANOVA to compare between types at each time and Tukey's HSD test for post-hoc comparisons. To analyse differences in decomposition patterns over time, multivariate repeated measures analysis was used to partition the time and time × litter type sum of squares into linear and quadratic contrasts. Multivariate orthogonal contrasts were used to make the following comparisons across time: (*i*) all conifers and salal, (*ii*) cedar and hemlock + fir from both forest types, and (*iii*) hemlock + fir in the cedar–hemlock and the hemlock – amabilis fir forests. We compared initial chemical data using the three site means for each species in one-way ANOVAs and Tukey's HSD test for post-hoc comparisons. The α level used in all comparisons was 0.05, unless otherwise indicated. All analyses were carried out using SYSTAT (Wilkinson 1990).

Results

Mass loss

The rate of mass loss for the standard litter, lodgepole pine needles, is almost identical in the two forest types, with about 30% lost after 1 year, 45% after 2 years, and 70% after 3 years (Fig. 1).

For local species litter (Fig. 2), multivariate analysis indicated a significant ($p = 0.028$) quadratic contrast over time, due to curvature in the decay curve for salal, and a significant litter type × time interaction (Wilkes' λ, $p = 0.084$; θ, $p = 0.041$). This interaction was dominated by the main effect of litter type ($p < 0.001$) and the generally linear trends over time for the conifers. Orthogonal contrasts following the repeated measures analysis revealed that salal leaves decomposed significantly more rapidly than conifer needles (58.4% mean mass loss after 1 year and 71.7% after 2 years). Cedar litter decomposed more slowly than the hemlock + fir needles in either forest type (22.0% mass loss after 1 year and 50.5% after 2 years). Hemlock + fir needles decomposed significantly more slowly in the hemlock – amabilis fir type (30.4% mass loss after 1 year and 55.9% after 2 years) than in the cedar–hemlock type (41.7% mass loss after 1 year and 63.8% after 2 years). Differences between litter types were consistent across the three sites.

Initial litter chemistry

C concentration was fairly constant across the conifer species (about 52%) but significantly lower in salal leaves (48%; Table 1). N concentration was significantly higher in salal leaves (1.07%) than the two conifer species in the cedar–hemlock type. Mean N concentration in cedar litter (0.66%) was lower than hemlock in either forest type, but this difference was not statistically significant.

Nonpolar extractives (NPE; waxes, fats, and oils) were highest in cedar (9.42%) and lowest in salal leaves (4.52%). Water-soluble, polar compounds (WS; sugars and starches but not tannins) were significantly higher in salal leaves and in hemlock + fir litter in the hemlock – amabilis fir type than in either cedar or hemlock + fir in the cedar–hemlock type. Initial concentrations of acid-soluble compounds (AS; cellulose and hemicellulose) were similar in all species.

Lignin concentration was significantly higher in cedar litter (42%) and hemlock + fir litter (39%) from the cedar–hemlock type than hemlock + fir in the hemlock – amabilis fir type (32%). Concentration of lignin in salal leaves (22%) was significantly lower than the conifers (32–42%). Tannin concentrations were significantly higher in salal leaves (4.8%) and in hemlock + fir litter (4.5%) in the hemlock – amabilis fir type than cedar or hemlock + fir in the cedar–hemlock type (1.65 and 1.29%)

Dynamics of litter chemistry

For conifer litters, all C fractions were generally lost in proportion to mass, whereas in salal, lignin increased proportionally during decomposition (Figs. 3 and 4).

C concentrations (Fig. 3*a*) showed little change during decomposition in all litter types, while N concentrations (Fig. 5) increased in all species. The increase was highest in salal and this occurred almost entirely during the 1st year. N was mobilized in all litter types except cedar over the 2 years (Fig. 5). N was immobilized in cedar litter in the first 6 months, with only a small net release over the remaining 1.5 years.

NPE concentrations (Fig. 3*d*) remained fairly constant over the study, indicating that these compounds were lost at about the same rate as mass (Fig. 4*d*). Cedar had about twice the amount of these compounds remaining after 2 years.

Concentration and absolute amounts of water soluble compounds, including tannins, were initially higher in salal and hemlock + fir in the hemlock – amabilis fir type but declined in the first 6 months to about the level of the other two litter types. (Figs. 3 and 4). This suggests that these compounds (sugars and starches) were rapidly leached or converted to other substances by microbial decomposers. Over the next 18 months, there was only a slight decline in all litter types.

Initial lignin concentration in salal was significantly lower than in the conifer litters. After 2 years, this increased to a similar level as the conifers. Absolute mass of lignin increased in hemlock + fir in the hemlock – amabilis fir type in the first 6 months and in salal in the last 6 months of the study.

Discussion

This study aimed to test the hypothesis that differences between species in litter quality, rates of mass loss, and nutrient dynamics in decomposing litter could explain lower forest floor N availability in cedar–hemlock forests. Similar mass loss rates of the common litter type, lodgepole pine needles, in the two forest types suggested that the microenvironment for decomposers was similar in both forest types. Higher N availability in hemlock – amabilis fir forest floors did not result in faster decomposition of lodgepole pine needles, confirming the suggestion that exogenous N availability does not influence litter decay rate (Pastor et al. 1984; Prescott 1995).

Litter quality and rates of mass loss

The initial lignin concentration (Meentemeyer 1978; Upadhyay et al. 1989; Taylor et al. 1991) and the lignin to N ratio (Melillo et al. 1982; Harmon et al. 1990) have been the most successful indices of litter quality in predicting decomposition rates in comparisons between litter types on equivalent sites. There were significant differences in both these indices between the four litter types used in this study.

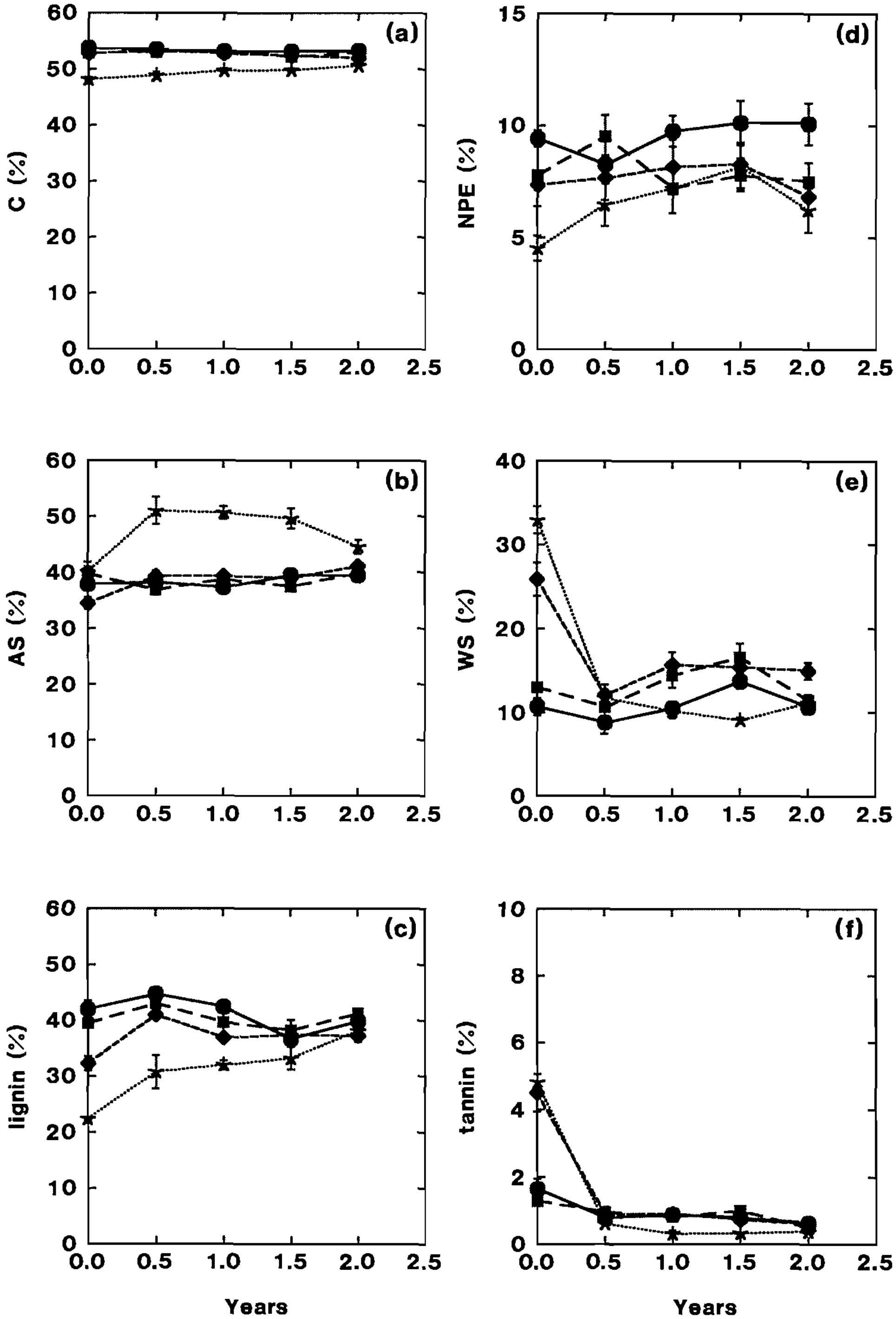
Litter from the broad-leaved shrub, salal, had a significantly lower lignin concentration, higher N concentration, and lower lignin to N ratio, and it decomposed more rapidly than the conifer litters. Significantly higher initial tannin con-

Table 1. Initial concentrations (%) of C, N, nonpolar extractives (NPE), water soluble extractives (WS), acid-soluble extractives (AS), lignin, and tannins of four litter types from two forest types (CH, cedar–hemlock; HA, hemlock – amabilis fir) on northern Vancouver Island.

Litter type	Forest	C	N	NPE	WS	AS	Lignin	Tannin	Ratio of lignin to N
Cedar	CH	53.7 (0.18)*a*	0.66 (0.055)*b*	9.42 (0.361)*a*	10.71 (1.008)*c*	37.88 (0.660)	41.98 (1.504)*a*	1.65 (0.301)*b*	64.6 (4.42)*a*
Hemlock + fir	CH	52.8 (0.29)*a*	0.81 (0.062)*b*	7.79 (1.399)*a*	13.03 (0.176)*c*	39.75 (1.266)	39.44 (0.226)*a*	1.29 (0.061)*b*	49.4 (3.57)*b*
Salal	CH	48.2 (0.36)*b*	1.07 (0.058)*a*	4.52 (0.562)*b*	32.95 (1.612)*a*	40.11 (1.803)	22.43 (0.234)*c*	4.82 (0.245)*a*	21.1 (0.965)*c*
Hemlock + fir	HA	52.8 (0.36)*a*	0.84 (0.043)*ab*	7.35 (0.224)*ab*	25.89 (1.979)*b*	34.48 (1.020)	32.28 (1.284)*b*	4.50 (0.558)*a*	38.6 (3.35)*b*

Note: Values in the same column followed by a different letter are significantly different at $\alpha \le 0.05$. Figures in parentheses are standard errors. Values are means from three sites, with 5 samples analyzed from each site.

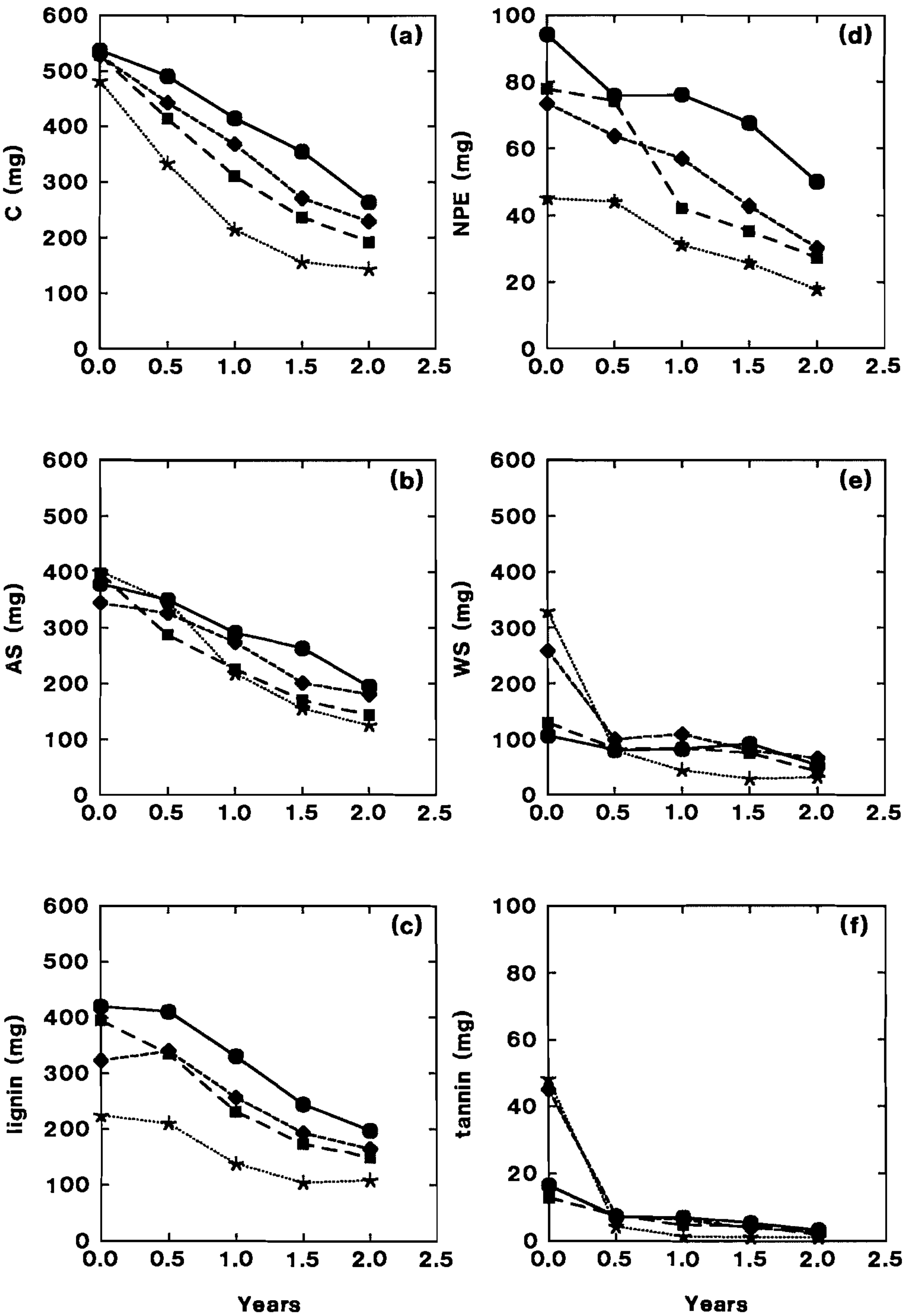
Fig. 3. *Concentration in relation to time for (a) C, (b) acid-soluble extractives (AS), (c) lignin, (d) nonpolar extractives (NPE), (e) water-soluble extractives (WS), and (f) tannins during decomposition of four litter types in western red cedar and western hemlock forests on northern Vancouver Island.* ●, western red cedar from cedar–hemlock sites; ■, hemlock and amabilis fir from cedar–hemlock sites; ♦, hemlock and amabilis fir from hemlock – amabilis fir sites; *, salal from cedar–hemlock sites. Note different y-axis scale for NPE and tannin.



centration in salal was not reflected in slower litter decomposition rate. Salal tannin concentration rapidly declined during decomposition, but the presence of tannins may influence N availability during later stages of decomposition. This possibility is discussed below.

Cedar litter had higher lignin, lower N, and a significantly higher lignin to N ratio (Table 1), and it decomposed more slowly than the other litter types. Harmon et al. (1990) reported slower decomposition of cedar litter (mean mass loss of 28.5% after 1 year) compared with hemlock (51.5% mass

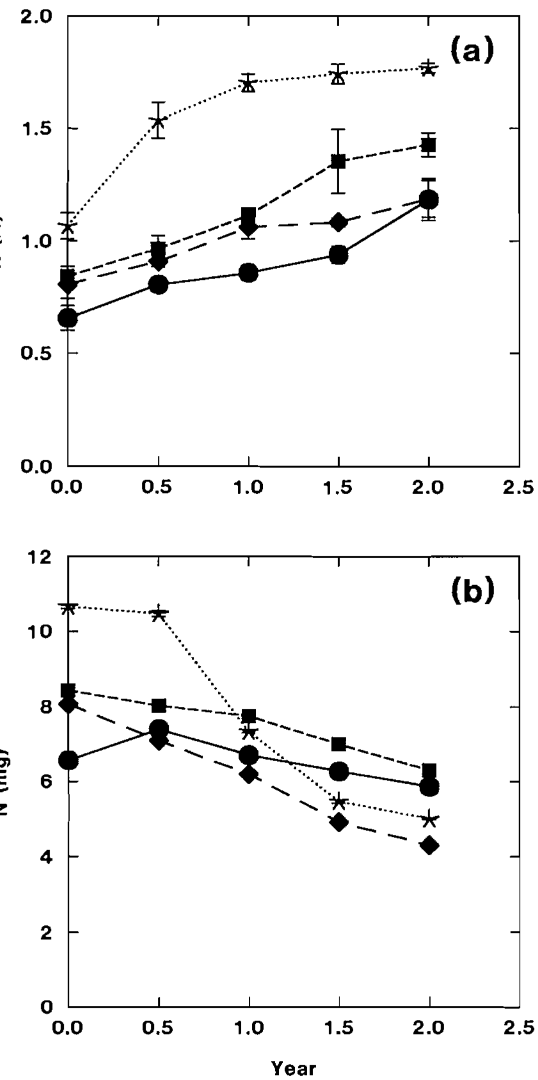
Fig. 4. Absolute mass (mg) in relation to time for (*a*) C, (*b*) acid-soluble extractives (AS), (*c*) lignin, (*d*) nonpolar extractives (NPE), (*e*) water-soluble extractives (WS), and (*f*) tannins during decomposition of four litter types in western red cedar and western hemlock forests on northern Vancouver Island. ●, western red cedar from cedar–hemlock sites; ■, hemlock and amabilis fir from cedar–hemlock sites; ◆, hemlock and amabilis fir from hemlock – amabilis sites; *, salal from cedar–hemlock sites. Note different *y*-axis scale for NPE and tannin.



loss after 1 year) in forests in the Olympic National Park in Washington State. More rapid overall decay rates in their study suggests that climatic conditions, particularly higher mean annual temperature, may be more favourable for decomposition than those in our study area.

Slower decomposition of cedar and faster decomposition of salal litter was therefore predictable in terms of previously reported indices of litter quality. Hemlock + fir needles had litter quality values intermediate to cedar and salal and decomposed at an intermediate rate. However, while hemlock + fir

Fig. 5. Concentration (*a*) and absolute mass (*b*) of N in relation to time during decomposition of four litter types in western red cedar and western hemlock forests on northern Vancouver Island. ●, western red cedar from cedar–hemlock sites; ■, hemlock and amabilis fir from cedar–hemlock sites; ♦, hemlock and amabilis fir from hemlock – amabilis fir sites; *, salal from cedar–hemlock sites.



needles from cedar–hemlock forests had significantly higher initial lignin concentration and a higher mean value for lignin to N ratios (49.4) than those from the hemlock – amabilis fir type (38.6; Table 1), those from the cedar–hemlock type decomposed more rapidly. Harmon et al. (1990) suggested that the lignin to N ratio is less useful as a predictor of decay rate for values above 30. Differences in the way other carbon compounds are mobilized and complexed during decomposition may have a greater influence on decomposition rate than lignin and nitrogen in litters with relatively high lignin and low N. For example, hemlock – amabilis fir litter had significantly higher initial tannin concentrations and was the only litter type to exhibit a net lignin gain; these factors could have produced slower decomposition of hemlock + fir needles in the hemlock – amabilis fir type.

Stand-level nutrient cycling

Salal leaves decomposed relatively rapidly, had higher nutrient concentration, and released N fairly freely during the study, indicating that in the early stages of decomposition, salal does not contribute to lower N availability in the cedar–hemlock type.

Cedar litter exhibited slower decomposition and little N release over the 2 years. Cedar dominates cedar–hemlock stands in terms of basal area, but many of these trees are old with small crowns, and cedar contributes only about 43% of foliar litterfall in the cedar–hemlock type (Keenan et al. 1995*b*). On the other hand, hemlock and amabilis fir contributed about 49% of foliar litterfall in cedar–hemlock forests. This litter decomposed at a higher rate and released proportionally more N in cedar–hemlock forests compared with hemlock – amabilis fir forests.

Therefore, while slower initial decomposition rate and nutrient dynamics in cedar litter could contribute to lower forest floor N availability in the cedar–hemlock type, the presence of cedar is unlikely to completely explain observed differences in N availability between the two forest types. Other factors that might contribute to differences in nutrient availability include the following: (*i*) lower aboveground N inputs: aboveground litterfall mass and litterfall N concentrations were lower in cedar–hemlock than in hemlock – amabilis fir forests. Thus, there was a substantially lower N input to the forest floor in aboveground litterfall and lower amounts of N cycling in the external, litterfall – decomposition – plant uptake pathway in cedar–hemlock forests (Keenan et al. 1995*b*). In a computer modelling study, Keenan et al. (1995*a*) found that differences in litter inputs and decomposition rate could potentially produce 50% higher rates of nutrient mineralization in hemlock – amabilis fir forests. (*ii*) Root litter quality and decomposition rate: while the objects of this study were foliar litter quality and decomposition rate, a considerable proportion of forest production is directed belowground. Differences in root litter quality and decomposition may be having as great, or greater, an impact on organic matter turnover and nutrient availability as foliar litter (McClaugherty et al. 1985*b*). (*iii*) N and organic-chemical transformations during later stages of decomposition: while the overall amount of N in detritus in the two types was similar (Keenan et al. 1993), the forest floor in the cedar–hemlock type contained a significantly greater mass of H layer material (91.3 Mg/ha), with a lower N concentration, than that in the hemlock – amabilis fir type (43.0 Mg/ha). Analysis of this material using ^{13}CPMAS–NMR and cupric oxide oxidation found there was a greater *o*-alkyl C content (waxes and cutins) and a lower ratio of carbohydrate to lignin monomer units, which is indicative of less effective decomposition of carbohydrates in the cedar–hemlock type. The ratio of vanillic acid to vanillin (acid to aldehyde) was higher in the hemlock – amabilis fir type, indicating more extensive decomposition of lignin. The higher tannin content in the nonwoody horizons of the cedar–hemlock type may have originated in salal (de Montigny et al. 1993).

The natural mixture of species in this study has made it difficult to separate the potential of a particular species to influence nutrient availability. In 34-year-old, planted, single-species stands of cedar, hemlock, and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) on adjacent sites with previously similar forest composition near Haney, British Columbia, Prescott and Preston (1994) found lower total, extractable, and mineralized N in forest floors under cedar and less N mineralized during laboratory incubations from cedar litter than the other two species. Cedar foliar litter also had higher concentrations of alkyl C in the acid insoluble fraction. Thus, through poorer litter quality, western red cedar appears to be having a considerable effect on forest floor processes, resulting in a reduction in N availability compared with the other two species.

In conclusion, we found no evidence to indicate any differences between microenvironmental conditions for decomposers between the two forest types or that differences in forest floor nutrient availability affected the decomposition rate of similar substrates. Poorer litter quality, slower decomposition rate, and lower initial nutrient release in western red cedar litter may contribute to lower forest floor N availability in cedar–hemlock forests. Other factors, such as lower external N cycling and the complexing of N with other organic chemicals during later stages of decomposition, are also likely to have a major influence on N availability.

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