Soil microbial biomass and microbial and mineralizable N in a clear-cut chronosequence on northern Vancouver Island, British Columbia

Scott X. Chang, Caroline M. Preston, and Gordon F. Weetman

Abstract: We studied the dynamics of microbial biomass and nitrogen in old-growth forests and in 3- and 10-year-old plantations established after clear-cutting and slash burning of old-growth western red cedar (*Thuja plicata* Donn ex D. Don) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands on northern Vancouver Island. Ten-year-old plantations, after initially growing well, were experiencing declining growth rates. Three forest floor layers: F (fermentation), woody F (Fw), and H (humus) were sampled four times in May, July, August, and October of 1992. Moisture content was significantly greater in the old-growth forests than in the plantations for F on July 16 ($p < 0.05$) and Fw ($p < 0.10$), but was not significantly different for H. Microbial biomass C and N were relatively constant throughout the sampling period, resulting in nonsignificant date effects. Microbial C content was in the order: old-growth forests > 10-year-old plantations > 3-year-old plantations. Microbial N content was significantly greater in the old-growth forest than in the young plantations for both F ($p < 0.001$) and H ($p < 0.05$) but was not different between the plantations. Therefore, the hypothesis that the microbial biomass acted as a net sink in the 10-year-old plantations by immobilizing N into the microbial N pool is rejected. Microbial C/N ratios were greater ($p < 0.05$) in the 10-year-old plantations than in the old-growth forests and in the 3-year-old plantations in H and on July 16 in F, indicating that microbial competition for N was probably a factor in the growth declining in the 10-year-old plantations. Extractable C and N and mineralizable N were generally higher in the old-growth forests than in the 3-year-old plantations and higher in the 3-year-old than in the 10-year-old plantations. As a result of better nutritional conditions, tree and understory foliage in the 3-year-old plantations had higher N concentrations and lower C/N ratios than in the 10-year-old plantations. Trees in the 10-year-old plantations displayed chlorotic symptoms and slow growth which were not observed in the 3-year-old plantations.

Résumé : Cette étude porte sur les dynamiques de la biomasse microbienne et de l'azote dans des vieilles forêts et des plantations âgées de 3 et 10 ans établies après une coupe à blanc et le brûlage des déchets de coupe dans de vieux peuplements de thuya géant (*Thuja plicata* Donn ex D. Don) et de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) dans le nord de l'île de Vancouver. Après une bonne croissance initiale, les plantations âgées de 10 ans connaissaient une baisse de leur taux de croissance. Trois couches de la couverture morte : l'horizon F (fermentation), l'horizon F ligneux (Fw) et l'horizon H (humus) furent échantillonnées quatre fois en mai, juillet, août et octobre 1992. Le contenu en humidité dans les horizons F ($p < 0,05$) et Fw ($p < 0,10$) le 16 juillet était significativement plus élevé dans les vieilles forêts qu'en plantations, mais n'était pas significativement différent dans l'horizon H. Le contenu en C et N de la biomasse microbienne était relativement constant pendant toute la période d'échantillonnage de telle sorte que les effets liés aux dates d'échantillonnage étaient non significatifs. Le contenu en C microbien apparaissait dans l'ordre suivant : vieilles forêts > plantations âgées de 10 ans > plantations âgées de 3 ans. Le contenu en N microbien dans les horizons F ($p < 0,001$) et H ($p < 0,05$) était significativement

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plus élevé dans les vieilles forêts que dans les jeunes plantations. Par conséquent, l'hypothèse voulant que la biomasse microbienne agisse comme un réservoir net dans les plantations âgées de 10 ans en immobilisant N dans le pool de N microbien est rejetée. Le ratio C/N microbien était plus élevé ($p < 0,05$) dans l'horizon H et, le 16 juillet, dans l'horizon F dans les plantations âgées de 10 ans comparativement aux vieilles forêts et aux plantations âgées de 3 ans, indiquant que la compétition microbienne pour N était probablement un facteur dans la baisse de croissance des plantations âgées de 10 ans. Le C et le N extractibles ainsi que le N minéralisable étaient généralement plus élevés dans les vieilles forêts que dans les plantations âgées de 3 ans et plus élevés dans les plantations âgées de 3 ans que dans celles qui étaient âgées de 10 ans. À cause des meilleures conditions nutritionnelles, les arbres et le feuillage en sous-étage dans les plantations âgées de 3 ans avaient une concentration de N plus élevée et un ratio C/N plus faible que dans les plantations âgées de 10 ans. Dans les plantations âgées de 10 ans, les arbres présentaient des symptômes chlorotiques et avaient une croissance lente qui n'ont pas été observés dans les plantations âgées de 3 ans.

[Traduit par la Rédaction]

Introduction

Plants and microorganisms depend on each other for N (Woods et al. 1982). Microbial biomass, considered a labile fraction of the soil organic matter, is known to be the sink and source of plant available N in soil (Jenkinson and Ladd 1981; McGill and Myers 1987). Nitrogen can be immobilized by the microbial biomass present in soil and thus microbial biomass can be considered as a sink. The N content of microbial biomass constitutes a significant amount of the mineralizable N that is a potentially available source to plants (Marumoto et al. 1982). It is the net balance between immobilization and mineralization that determines the availability of N for plant uptake. Microbial activities are easily changed by management practices such as clear-cutting (Vitousek 1981; Smethurst and Nambiar 1990*a*), litter management (Weber et al. 1985; Smethurst and Nambiar 1990*b*), forest fire (White 1986; Weber 1987; Bell and Binkley 1989), and season and successional stages (White et al. 1988; Vitousek et al. 1989), thereby affecting plant growth in the field.

By altering the amount and type of organic matter, as well as soil temperature, moisture and pH, forest harvesting can cause long-lasting impacts on microbial activity (Harvey et al. 1980) and nutrient availability (Entry et al. 1986). In areas where reforestation failures have been encountered after clear-cutting of old-growth forests, particular attention has been paid to the role of the soil microbial population and activities in the fertility decline. Niemela and Sundman (1977) and Sundman et al. (1978) studied the changes in soil bacterial population in areas 0, 4, 7 and 13 years after clear-cutting in coniferous forests in northern Finland where reforestation has frequently failed. They found that clear-cutting causes increases in bacterial biomass and changes in population structure. Entry et al. (1986) studied microbial biomass changes in a northern Rocky Mountain forest soil subjected to clear-cutting, residue removal, and burning treatments and found that, in the clear-cut and residue-burned treatment, microbial biomass was lower than in the other treatments for the most of the studied period. However, little study has been done to evaluate the effect of clear-cutting and slash burning on microbial biomass dynamics and its relationship to N cycling and tree nutrition.

Growth stagnation of planted or naturally regenerated Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western red cedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) on cutovers of old-growth western red cedar and western hemlock (CH) forests was observed in 10-year-old stands in the wetter Coastal Western Hemlock biogeoclimatic zone (CWHb) of British Columbia, in association with the invasion of an ericaceous evergreen shrub, salal (*Gaultheria shallon* Pursh.) (Weetman et al. 1989*a*, 1989*b*). Messier (1993) found that conifer seedlings planted on CH sites 8 years after clear-cutting and burning were growing slower than seedlings planted on 2-year-old CH sites with and without competing vegetation, although removal of competing vegetation helped seedling growth on the same site. Therefore, competing vegetation is not the sole factor in declining growth in the old CH cutover sites. Using solid-state ^{13}C NMR, deMontigny et al. (1993) found evidence for tannin in F humus in the CH old-growth and suggested that increasing inputs of salal tannin in CH cutovers might contribute to less effective litter decomposition; however, no direct evidence was provided. The present work was conducted to see if microbial biomass and microbial mediated processes such as N mineralization–immobilization are contributing to the declining nutrient (particularly N) availability in those CH cutover sites 8–10 years after clear-cutting and planting.

The objectives of this study were (1) to quantify the changes of microbial biomass C and N and mineralizable N in the forest floors of a CH clear-cut chronosequence (uncut old-growth forests, 3- and 10-year-old plantations) and (2) to test the hypothesis that microbial biomass acted as a net sink in the 10-year-old plantations by immobilizing more nitrogen into the microbial N pool than in the 3-year-old plantations.

Materials and methods

Study area and stand selection

The study area was in Tree Farm License (TFL) 25 operated by Western Forest Products Ltd. near Port McNeill (50°60′N, 127°35′W) in the wetter CWH zone (Pojar et al. 1987) on northern Vancouver Island, British Columbia. The study

was conducted in the CH ecosystem. In the old-growth CH stands, cedar reaches diameters at breast height of more than 200 cm, ages of greater than 1000 years, and heights of 40–45 m (Keenan et al. 1993). The understory in these stands is dominated by salal, more than 1 m tall but not very dense because of the limited amount of light available under the canopy.

This area is characterized by a gently undulating topography that rarely exceeds 300 m in elevation (Lewis 1982). The humus layer is thick (>45 cm) with large amounts of decaying wood overlying a moderately well to somewhat imperfectly drained Ferro-Humic Podzol. The area receives an annual precipitation of 1700 mm, most of which is received in the winter. The number of hours of sunshine ranges from 6.4 h/d in July to 1.5 h/d in December, reflecting the frequent occurrence of fog in the summer and frontal clouds in the winter (Keenan et al. 1993). Mean daily temperatures vary from 3.0°C in January–February to 13.7°C in July–August.

Three old-growth CH forests were selected that had similar stand structure and slope position. Three 3-year-old and three 10-year-old plantations of western red cedar on cutovers of CH forests were also selected. These had similar stand structure (based on cedar stumps) and slope position to the three old-growth forests. The nine sites selected are within 5 km of each other. The cutovers had been slash burned after logging and then planted with western red cedar. The slash burning used had little effect on the humus layer. In the 3-year-old plantations, salal was dominant but it was short (about 30 cm) and not very dense. In the 10-year-old plantations, salal was much denser and taller (50–80 cm). For convenience, the different aged stands are refered to as treatments.

Field sampling

Forest floors were sampled on May 23, July 16, August 26, and October 18, 1992. One composite sample each of fermentation (F), woody F (Fw), and humus (H) materials was taken from the forest floor in each selected stand. Each composite sample was a mixture of the same material collected at six or seven randomly selected points in each site. The F layer in the old-growth forests consisted of fine twigs and leaf litter and was about 5 cm thick. The F layer in the 3- and 10-year-old plantations was 1–2 cm thick and was the residue from burning. The Fw layer was partially decomposed, but the woody structure held when rubbed between the fingers. The H layer was more than 80% amorphous, with a greasy texture and a dark colour (deMontigny 1992). The H layer, sometimes thicker than 1 m, is the main component of the forest rooting zone.

Samples were kept in a cooler on ice for 3 days while being transported to the laboratory where they were stored at 4°C before use. All samples were analyzed within 1 week of sampling.

On the same four dates, current-year foliage of western red cedar was collected from the upper branches of at least 15 trees in each plantations. In the old-growth stands, western red cedar foliage was obtained by shooting off branches of the upper crown with a shotgun. Current-year salal foliage was collected in the plantations and the old-growth forests.

Laboratory analyses

Moisture content was measured on fresh unsieved samples by the gravimetric method at 105°C for 24 h. The rest of the sample was sieved through an 8-mm screen and visible roots were removed.

Microbial biomass C and N were measured by the chloroform fumigation–extraction method (Brookes et al. 1985; Vance et al. 1987; Wu et al. 1990). Appropriate weight portions (3-g dry weight basis for F and Fw, and 5-g dry weight basis for H) of sieved F, Fw, and H samples were fumigated with ethanol-free chloroform for 24 h at room temperature (20°C). After removal of the chloroform, fumigated samples were extracted with 0.5 M K_2SO_4 on an end-over-end shaker (150 rpm) for 0.5 h, followed by vacuum filtration through Whatman No. 42 filters. Another set of unfumigated samples used as controls were extracted in the same way at the time fumigation commenced. The filtrate was analyzed for total dissolved organic C by the wet oxidation diffusion method of Snyder and Trofymow (1984) and total N by Kjeldahl digestion and distillation (Bremner 1965). The total extractable C and N measured from the control samples are presented in the results and discussion sections as extractable organic C and N. Microbial biomass C (B_C) and N (B_N) were calculated by equations $B_C = F_C/K_C$, and $B_N = F_N/K_N$, respectively, where F_C and F_N were the differences in total dissolved organic C and total N, respectively, in fumigated and unfumigated samples, and K_C is 0.379 (Vance et al. 1987), and K_N is 0.54 (Brookes et al. 1985). Microbial C/N ratio was calculated as B_C/B_N.

Mineralizable N and pH were determined on air-dried and sieved (2-mm screen) samples of F, Fw, and H from the August 26 collection. The pH was measured in 1:2 (v/v) 0.01 M $CaCl_2$ solutions. Mineralizable N was measured after a 14-d anaerobic incubation at 30°C (Waring and Bremner 1964), followed by Kjeldahl digestion and steam distillation of pre- and post-incubation samples (Keeney and Nelson 1982).

Foliar samples were dried at 65°C overnight and ground to 20 mesh in a Wiley mill. Total N concentrations were determined by Kjeldahl analysis with steam distillation (Bremner 1965). Total C concentrations were determined using a LECO CR-12 C analyzer (Model 781-600, LECO Corporation 1981).

Statistical analyses

Homogeneity of variances and normality of distributions of data sets were checked before any further statistical analysis. Data that were not homogeneous (extractable C of unfumigated Fw samples, microbial biomass C/N ratios of Fw samples and total N content in salal) were log-10 transformed prior to analysis. Analyses of variance were performed on all experimental variables using the general linear models (GLM) procedure of the SAS package (SAS Institute Inc. 1985). Group means of independent variables were compared between treatments (age of stands) at each sampling date by using Scheffé's test when there was a significant treatment × date interaction for each type of material sampled. When treatment × date was non-significant, Scheffé's test was used to examine treatment means across the dates for each type of material sampled.

Table 1. Mean square and level of significance for water content, extractable C and N, and microbial C and N.

Measurement	Source of variation	Forest floor layer[a]		
		F	Fw	H
Water content	Treatment (T)	54 598***	11 918†	655
	Date (D)	43 252***	27 442**	8 679†
	T × D	8 625**	827	621
	Error	1 979	3 959	3 382
Microbial C	T	90 315 715***	884 712	9 894 344***
	D	1 310 444	1 244 007†	61 789
	T × D	1 962 430	255 611	1 071 386
	Error	1 437 381	462 660	1 043 986
Microbial N	T	535 819***	4 459	67 376*
	D	11 582	35 294**	18 866
	T × D	8 151	14 691	9 786
	Error	10 380	7 455	12 044
Microbial C/N ratio	T	18.94**	0.043	64.36***
	D	26.83***	0.089*	9.52
	T × D	16.31***	0.082*	1.94
	Error	2.45	0.024	5.00
Extractable organic C	T	2 927 978***	0.23***	278 707***
	D	252 575**	0.36**	46 710*
	T × D	6 669	0.07*	34 538†
	Error	49 994	0.02	14 113
Extractable organic N	T	5 818***	137.5	543.1†
	D	5 134***	461.1	3 117.9***
	T × D	233	394.0	285.6
	Error	223	400.0	202.3

[a]The difference between means is significant at †, $p < 0.10$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Degrees of freedom: treatment, 2; date, 3; and treatment × date, 6. F, fermentation layer; Fw, woody F; H, humus.

Table 2. pH and mineralizable N (μg/g) of forest floor layers in old-growth forests and 3- and 10-year-old plantations for samples collected on August 26 ($n = 3$).

Measurement	Treatment	Forest floor layer		
		F	Fw	H
pH	Old-growth	4.16*a**	3.31*a*	3.16*a*
	3 years old	3.75*a*	3.04*b*	2.85*b*
	10 years old	3.76*a*	3.20*a*	3.11*a*
Mineralizable N	Old-growth	394.1*a*	40.33*a*	148.32*a*
	3 years old	159.2*b*	25.59*a*	78.08*b*
	10 years old	140.5*b*	31.38*a*	90.24*b*

Note: Abbreviations are described in Table 1.

*Values followed by the same letter are not significantly different ($p = 0.05$ level) between treatment means for the same measurement and forest floor.

Results

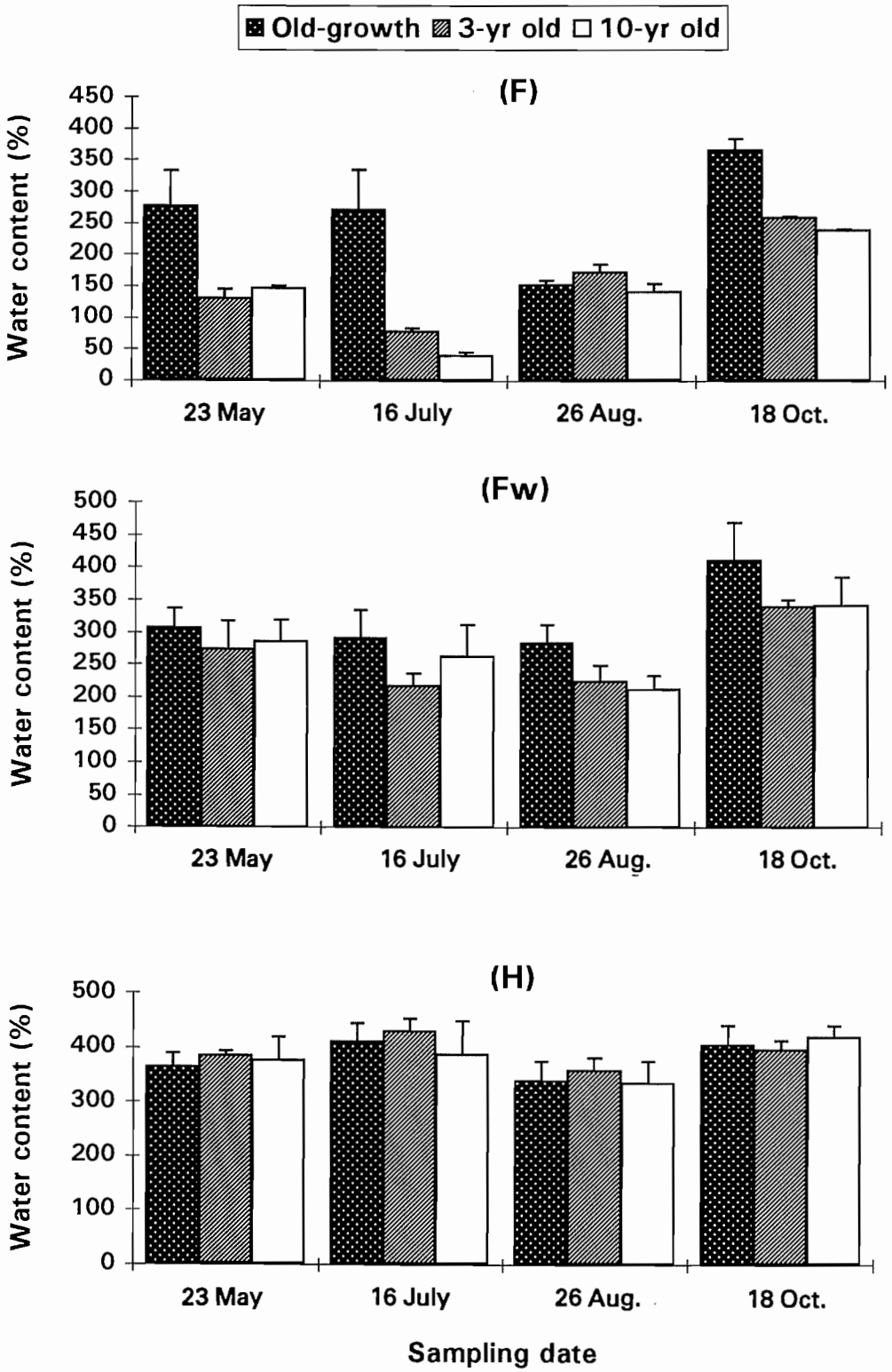
Water content and pH

Significant treatment × date interaction for water content in F resulted from the change in water content from higher (on May 23, July 16, and October 18) to lower (on August 26) in the old-growth forests than in the plantations. Water content in the F layer was significantly greater ($p < 0.05$) in the old-growth forests than in the 3- and 10-year-old plantations on July 16 (Fig. 1). Treatment × date interactions were not significant for water content in Fw and H. Water content in Fw, which is also in the uppermost horizon of the forest floor, was slightly greater in the old-growth forests than in the plantations ($p < 0.10$; Table 1). There were no differences in water content of H among the treatments. Measurements showed that F and Fw had higher water holding capacities in the old-growth forest than in the young plantations (data not shown). The effect of sampling date on water content was significant for F ($p < 0.001$), Fw ($p < 0.01$), and H ($p < 0.10$) (Table 1). The trend for pH was old-growth forests > 10-year-old plantations > 3-year-old plantations (Table 2). There were no differences in pH of F among the treatments. The Fw and H layers had significantly greater pH values in the old-growth forests and the 10-year-old plantations than in the 3-year-old plantations ($p < 0.05$).

Microbial biomass C and N

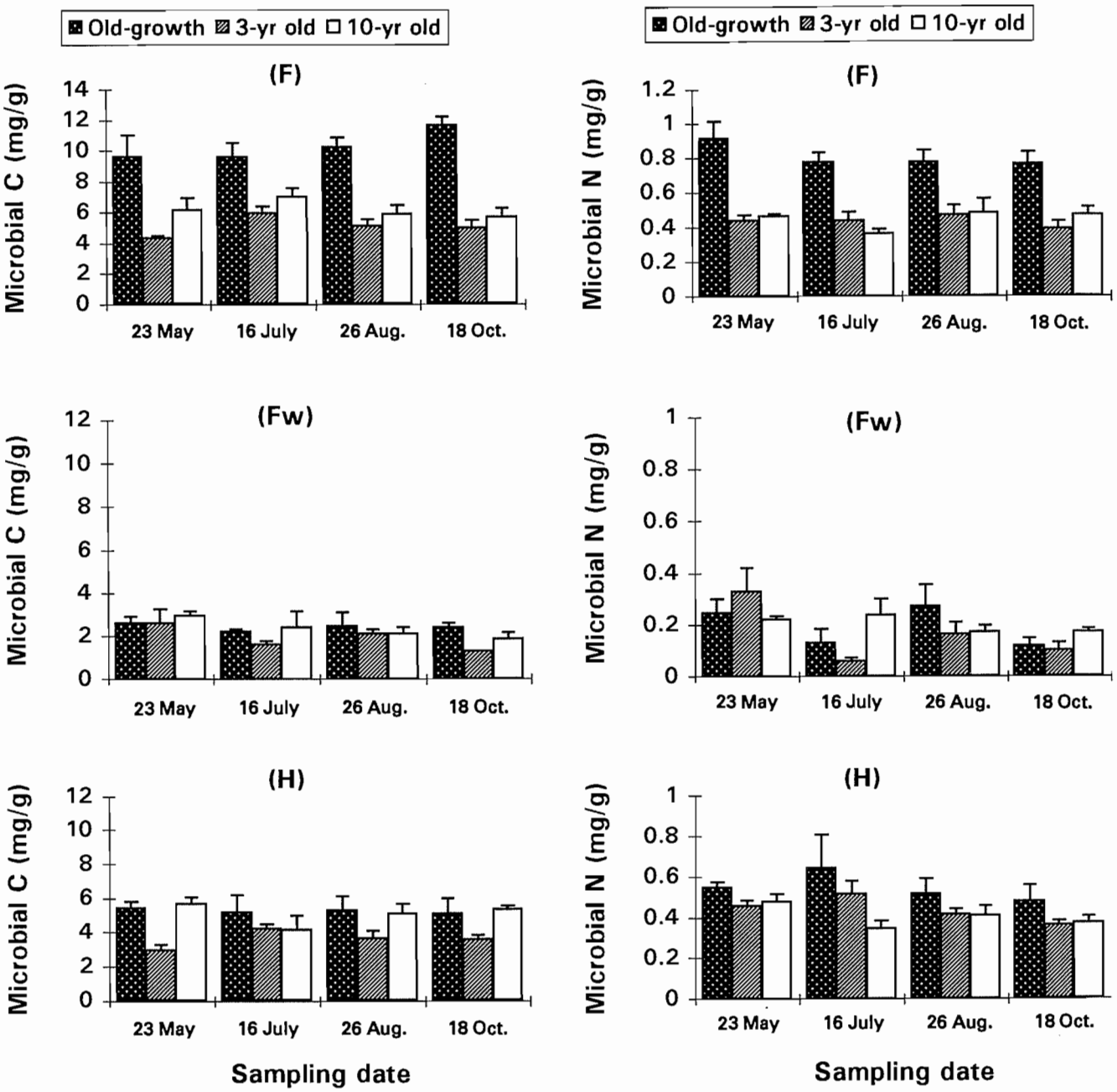
Microbial biomass C in F ($p < 0.001$), Fw (nonsignificant), and H ($p < 0.001$) was in the following order: old-

Fig. 1. Water content (%) in forest floor layers in the old-growth forests and 3- and 10-year-old plantations. Abbreviations are given in Table 1.



growth forests > 10-year-old plantations > 3-year-old plantations (Fig. 2, Table 1). However, the multiple comparison test showed that the significant treatment effect in F lies in the differences between the old-growth forests and the two young plantations ($p < 0.05$); there was no significant difference between the two plantations. For H, microbial biomass was significantly higher in the old-growth forests and in the 10-year-old plantations than in the 3-year-old plantations. The greatest amount of microbial C was in F (11.7 mg/g) and the least amount was in Fw

Fig. 2. Microbial C and N in forest floor layers in the old-growth forests and 3- and 10-year-old plantations. Abbreviations are given in Table 1.

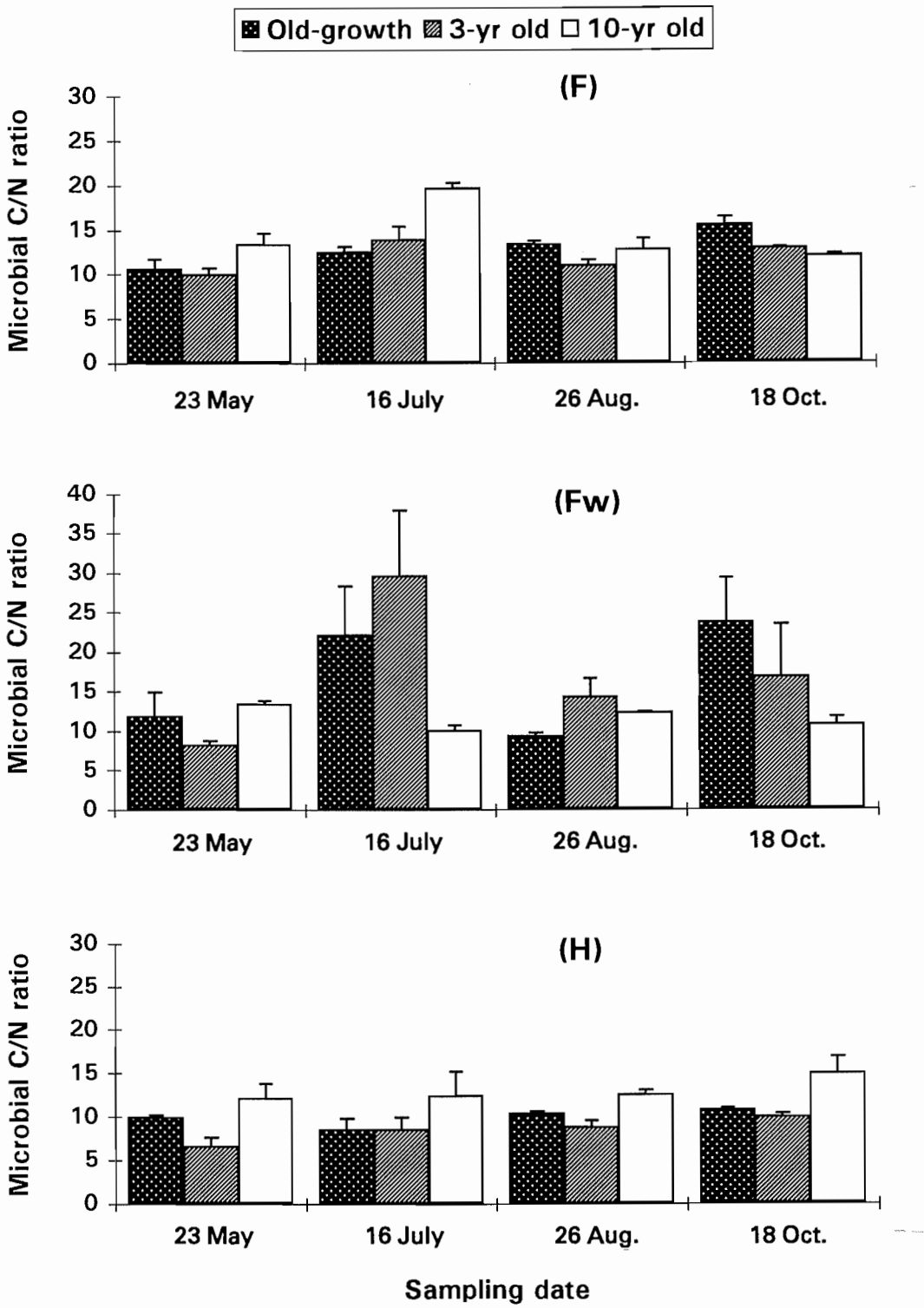


(1.3 mg/g). Microbial C in F was 225 and 55% greater than that in Fw and H, respectively. The amount of microbial biomass C in the three types of humus materials was fairly constant throughout the sampling period, resulting in non-significant sampling date effects and treatment × date interactions (Table 1).

Microbial N was significantly different among stand types for F ($p < 0.001$) and H ($p < 0.05$) (Table 1). Microbial N in Fw was not different among stand types. Similar to the seasonal changes in microbial biomass, microbial N was not affected by sampling dates (except in Fw) and no treatment × date interactions were found (Table 1). Multiple comparison tests showed that microbial biomass N was not significantly different between the 3- and 10-yr-old plantations in F (434.04 vs. 443.37 μg/g), Fw (162.86 vs. 199.92 μg/g), and H (437.80 vs. 401.23 μg/g) but was significantly greater in the old-growth forests than in the 3- and 10-year-old plantations in F and significantly greater in the old-growth forests than in the 10-year-old plantations in H ($p < 0.05$).

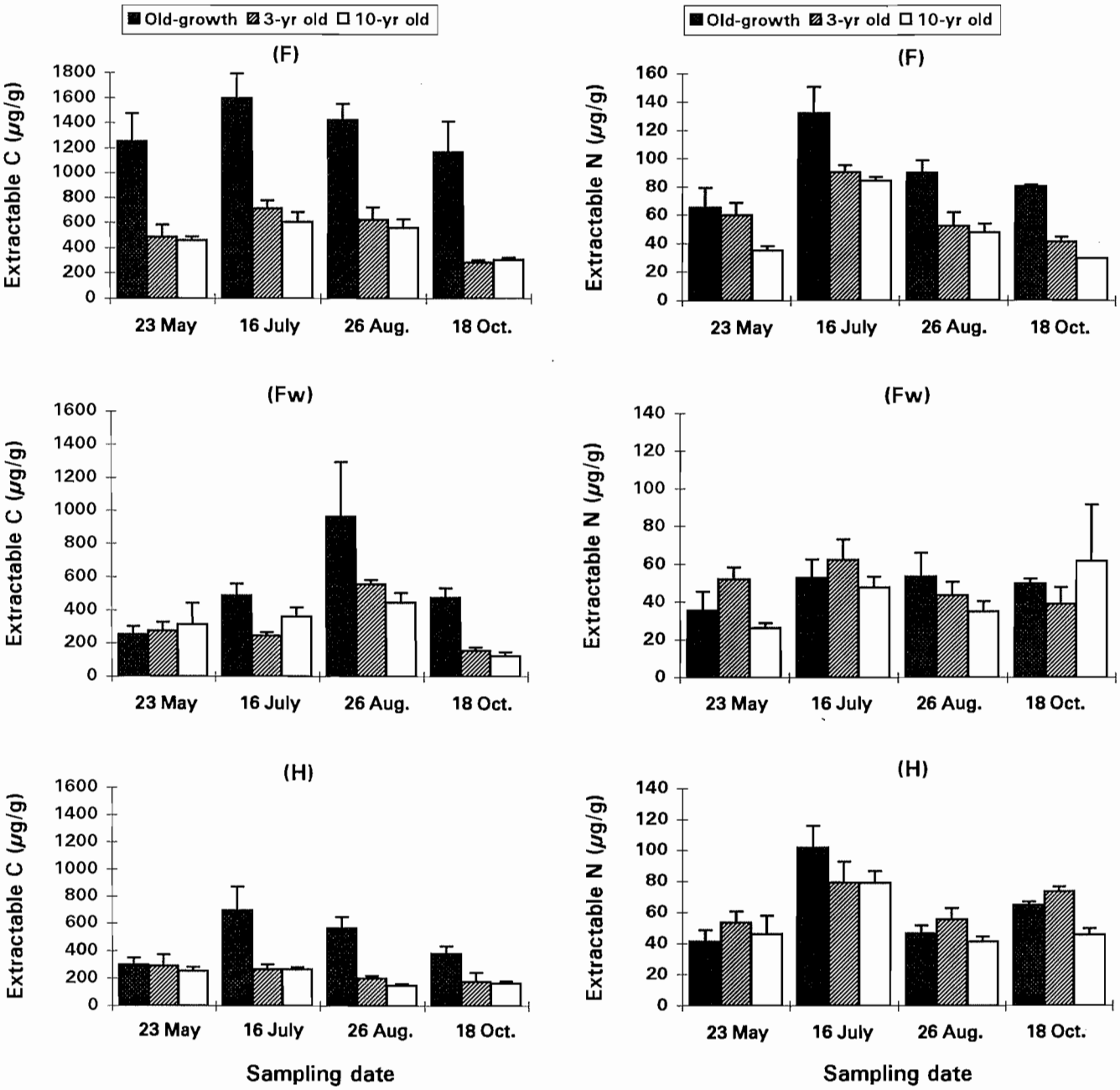
Microbial biomass C and N were both greatest in F and least in Fw. Their ratios were significantly affected by stand type in F and H and by sampling date in F and Fw (Table 1). There was no treatment effect on microbial C/N

Fig. 3. Microbial C/N ratio in forest floor layers in the old-growth forests and 3- and 10-year-old plantations. Abbreviations are given in Table 1.



ratio of Fw. The coefficients of variation for microbial C/N ratio were 12, 47, and 22% for F, Fw, and H, respectively, indicating that the data set for Fw had greater deviation from the mean, which led to the lack of significance of treatment effects. The rise in microbial C/N ratio in the old-growth forest relative to the 10-year-old plantations from the July 16 to October 18 sampling in F and from May 23 and August 26 to July 16 and October 18 sampling in Fw resulted in significant treatment × date interactions in these two materials (Fig. 3). Multiple comparison revealed that microbial C/N ratio in F was greater in the 10-year-old plantations than in the 3-year-old plantations

Fig. 4. Extractable C and N (0.5 M K_2SO_4) in forest floor layers in the old-growth forests and 3- and 10-year-old plantations. Abbreviations are given in Table 1.



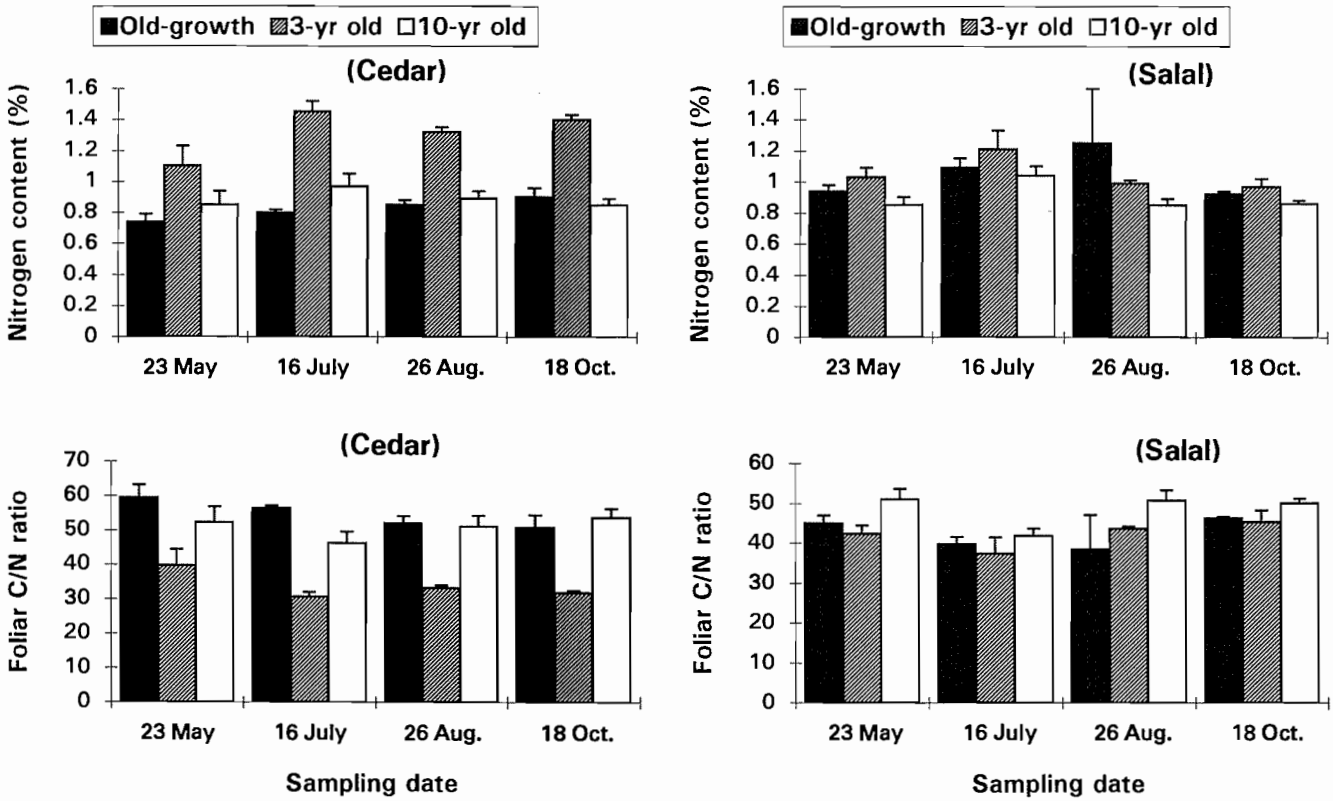
and the old-growth forests only on the July 16 sampling ($p < 0.05$); in H, microbial C/N ratio in the 10-year-old plantations was greater than those in the 3-year-old plantations and the old-growth forests ($p < 0.05$).

Extractable organic C and N

The amount of organic C extracted by 0.5 M K_2SO_4 from the unfumigated samples across the sampling dates was 159 and 107% greater ($p < 0.05$) in the old-growth forests than in the 3-year-old plantations in F and H, respectively (Fig. 4, Table 1), since there was no treatment × date interactions. Although the overall treatment effect was significant for Fw, there was no difference among the stand types at any particular sampling date because of the significant interaction. Extractable C was generally higher in the 3-year-old than in the 10-year-old plantations, for F and H (both nonsignificant). On average, F contained the greatest amounts of extractable C, and H contained the least. There was a significant sampling date effect on extractable C in all three humus layers (Table 1). The greatest extractable organic C was from the July samples in F and H and in the August samples in Fw.

No treatment × date interactions were found for extractable organic N in all of the materials studied. Extractable organic N in the F material was 51% greater in the old-growth forests than in the 3-year-old plantations ($p < 0.05$) and

Fig. 5. Foliar N concentrations and C/N ratios of western red cedar and salal in old-growth cedar–hemlock forests and 3- and 10-year-old cedar plantations.



24% greater in the later than in the 10-year-old plantations (nonsignificant). There was no treatment effect or sampling date effect on extractable N in Fw material (Fig. 4, Table 1). The statistically nonsignificant results for Fw were caused by the large variability within the data set. The coefficients of variation for extractable N were 22, 43, and 23% for F, Fw and H, respectively. In H, extractable N in the 3-year-old plantations was 3 and 23% greater than that in the old-growth forests and the 10-year-old plantations, respectively, although those differences were not statistically significant. The greatest amounts of extractable N were in the July samples, except for Fw in the 10-year-old plantations. Substantially less N was extracted from Fw than from F and H materials (Fig. 4).

Mineralizable N

The amount of N mineralized during the 14-d anaerobic incubation was greater in the old-growth forests than in the 3- and 10-year-old plantations in F and H ($p < 0.05$; Table 2). Differences between the 3- and 10-year-old plantations were not significant. F contained the highest amount of mineralizable N, followed by H and Fw.

Foliar N

Foliar nitrogen concentrations and C/N ratios were fairly constant among treatments and sampling dates resulting in nonsignificant treatment × date interactions for cedar and salal. Nitrogen concentrations in cedar foliage were consistently higher ($p < 0.05$) in the 3-year-old plantations than in the old-growth forests and the 10-year-old plantations (Fig. 5) on all four dates. Nitrogen concentrations in salal foliage were significantly higher in the 3-year-old plantations than in the 10-year-old plantations ($p < 0.05$) but were nonsignificantly higher in the former than in the old-growth forest and nonsignificantly higher in the old-growth forest than in the 10-year-old plantations. Foliar C/N ratios of cedar and salal were significantly lower in the 3-year-old than in the 10-year-old plantations and old-growth forests.

Discussion

Humus type is one of the most important factors affecting the amounts, forms, and mineralization–immobilization processes of N in forest soils (Richards et al. 1985). Woody debris is an obvious component of old-growth CH forests in coastal British Columbia (Keenan et al. 1993). Humus materials derived from coarse woody debris (large stems) and those from fine debris (small twigs and leaf litter) have different chemical and physical properties. Therefore, we differentiated forest floor layers fermentation (F) and humus (H) into F, woody F (Fw), H and woody H (Hw) types (Prescott et al. 1993). Because Hw type of humus was frequently missed during field sampling because of its discontinuous distribution in the subhorizons in the soil profile, results on Hw are not reported here.

The higher soil moisture content in F and Fw in the old-growth forest than in the plantations (Fig. 1) reflected the changes in physical properties of F and Fw after slash burning. The water-holding capacity and subsequently the

water content of F and Fw were reduced by changes in the structure of the forest floor after burning. Differences in near surface microclimatic conditions induced by changes in vegetation cover may also have affected moisture contents in F and Fw. The moisture content of H was not significantly different between treatments because this layer was less affected by slash burning. The low water content in F in the summer relative to that in early fall was related to the amount of rainfall received in the period shortly before sampling (weather data not shown).

Forest fires normally cause increases in soil pH because of the release of basic cations (Viro 1974; Pietikainen and Fritze 1993). In this study, however, the pH of F in the 3- and 10-year-old plantations that had been slash burned was less than that in the old-growth forests (nonsignificant; Table 2). In Fw and H, pH was lower in the 3-year-old than in the 10-year-old plantations and the old-growth forests ($p < 0.05$). Decreasing pH in the 3-year-old plantations may have been caused by increased release of acidic organic matter from microbial decomposition and exudation after logging and slash burning. Niemela and Sundman (1977) reported a short-term increase of organisms producing acid from sucrose after clear-cutting a spruce forest. The abundant regrowth of salal on the clear-cut sites may also contribute to the decrease of pH through increased root exudates. However, the exact reason for the decrease of pH 3 years after logging and burning cannot be determined from the available data. Higher pH in the 10-year-old than in the 3-year-old plantations reflected a slow recovery process in balancing pH to the level in the old-growth forests. The change of pH was 0.41, 0.27, and 0.31 units for F, Fw, and H, respectively, from old-growth forests to 3-year-old plantations and 0.40, 0.11, and 0.05 units for F, Fw, and H, respectively, from old-growth forests to 10-year-old plantations. In general, the change of pH in each type of humus materials was probably too narrow to cause significant changes in microbial community by treatments.

Clear-cutting alone does not reduce microbial biomass in forest soils, in fact, microbial biomass was higher in a clear-cut and residue-left treatment than in an uncut treatment in a northern Rocky Mountain forest soil (Entry et al. 1986), because of increased decomposible organic C input into the system and other beneficial effects from disposed slash. Lundgren (1982) showed that bacterial biomass increased initially after clear-cutting a Scots pine (*Pinus sylvestris* L.) forest, but decreased compared with a reference stand during the third year after clear-cutting and onwards. Sundman et al. (1978) also showed increases in bacterial counts after clear-cutting a spruce forest. However, if clear-cutting is followed by slash burning, microbial biomass would be drastically decreased (Entry et al. 1986; Pietikainen and Fritze 1993). Results from this study showed that microbial biomass was lower in the 3- and 10-year-old plantations that were clear-cut and slash burned than in the uncut and unburned old-growth forests. Higher microbial C in the 10-year-old than in the 3-year-old plantations indicated that microbial population was gradually recovering from clear-cutting and slash burning between years 3 and 10, which is in good agreement with Fritze et al. (1993).

The changes in microbial biomass may be affected by other biotic and abiotic factors. One of them is the availability of soluble carbon compounds (Wheatley et al. 1990). Greater microbial C in the old-growth forests was associated with higher extractable C (Fig. 4). A simple regression analysis showed a relationship between microbial biomass and extractable C for the old-growth forests and young plantations: microbial C (mg/g) = 2522 + 4.34(extractable-C (mg/g)), $r = 0.64$ ($p = 0.0001$). The amount of extractable C was reduced by clear-cutting and slash-burning. Pietikainen and Fritze (1993) reported that fire treatment increased the amount of extractable C and N in humus layers, but these decreased to control levels within 3 years. Their study sampled a maximum of 800 days after the fire treatment, which makes it difficult to do a complete comparison with the findings of this paper. Correlation analysis showed that microbial biomass had a weak relationship with soil moisture content ($r = -0.16$, $p = 0.0963$). This indicates that soil moisture content offers little help in explaining the dynamics of microbial biomass over the sampling period, perhaps because soil moisture content was never at a level limiting microbial biomass growth.

Microbial N showed the same patterns of changes as microbial C in the old-growth forests and 3- and 10-year-old plantations. Measured on the August 26 sampling, the percentage of total soil N found in microbial biomass was greater in the old-growth forests (8.21%) than in the 3- (4.93%) and 10-year-old (4.95%) plantations for F ($p < 0.05$). The percentage of the total N found in microbial biomass was 11.84, 6.50, and 6.32% in Fw, and 5.02, 4.58 and 4.76% in H for the old-growth forests and the 3- and 10-year-old plantations, respectively. The differences among stand types were not significant for Fw and H. This result indicated that a greater percentage of the total N was potentially available in the old-growth forests.

The seasonal variations in microbial biomass C and N were small, which resulted in nonsignificant sampling date effects for F and H. This resembles results obtained in hardwood forests by Holmes and Zak (1994). The similar microbial N pool sizes in the 3- and 10-year-old plantations led us to reject the hypothesis that the microbial biomass acted as a net sink in the 10-year-old plantations by immobilizing more N into the microbial N pool. Holmes and Zak (1994) suggested that, in maintaining a relatively constant pool, it is the turnover rate of microbial biomass that controls N availability. Therefore, further studies are needed to test if microbial biomass and N in the 10-year-old plantations have a slower turnover rate and, thus, reduced N availability than in the 3-year-old plantations.

In our study, the microbial C/N ratios in most samples were between 6.5 and 16. A few comparatively high C/N ratio values were found, i.e., Fw in the old-growth forest in the July (22.1) and October (23.6) sampling and Fw in the 3-year-old plantations in the July sampling (29.5). These values were higher than typical microbial C/N ratios found in coniferous forest soils (7–13; Fenn et al. 1993). Both Collins et al. (1992) and Dalal and Mayer (1987) reported microbial C/N ratios (about 20) close to those of bulk soils and proposed that the ratios represented that of "stabilized" microbial biomass. Microbial C/N ratios may be affected by the K_C and K_N values used in calculating

the microbial C and N, but we think comparisons between treatments within the same experiment are valid.

A change in microbial population structure is a readily available explaination for the shift in microbial C/N ratios (Wheatley et al. 1990). Anderson and Domsch (1980) and Ross (1988) reported that fungi generally have higher C/N ratios than bacteria in culture incubations. However, there has been little discussion on the implications of microbial C/N ratio changes, whether or not accompanied by population structural changes, on N availability in soils.

Microbial C/N ratios may provide an indication of the availability of microbial N for mineralization. Whether microbial biomass acts as a net source or sink of available N depends, in part, on the C/N ratio of the microbial substrates, the rate of microbial biomass growth, and the microbial demand for N (Fenn et al. 1993; Edmonds 1987). High microbial C/N ratios may be associated with the low N availability in forest floors (Edmonds and Chapell 1994). In general, low C/N ratios in microbial biomass are associated with net N mineralization, and high C/N ratios with net immobilization of N in the microbial biomass (Paul and Clark 1989; Edmonds 1987). The microbial C/N ratios in F ($p < 0.05$ on one of the sampling dates) and H ($p < 0.05$) were greatest in the 10-year-old plantations and least in the 3-year-old plantations. This suggests that microbial biomass became N stressed from year 3 to year 10 after clear-cutting and slash burning and that it is more likely to result in a net mineralization in the 3-year-old plantations while a net immobilization in the 10-year-old plantations during decomposition of organic materials. This has practical implications for N availability in those ecosystems, because the difference between microbial release of N and immobilization of N into microbial biomass largely determines the amount of N available for plant uptake (Binkley and Hart 1989; Paul and Clark 1989). Since microbial biomass had the trend to increase from the 3- to the 10-year-old plantations for the three material types studied, increases in available C and N in the soil in the 10-year-old plantations may result in further increases in microbial biomass and assimilation of the available N into microbial biomass. Therefore, even if the microbial community maintains its current C/N ratio level, microbes would be more severely competing with trees for N in the 10- than in the 3-year-old plantations to meet their maintenance requirements and growth potential.

The N-stressed situation in the 10-year-old plantations was also indicated by the extractable N and foliar N analysis results. Extractable N may serve as an indication of available N in soils. The nonsignificantly higher amount of extractable N in the 3-year-old than in the 10-yearr-old plantations (Fig. 4) indicated that the N supply tended to be better in the 3-year-old plantations, which was consistent with the results of foliar N analysis. Better N supply on the younger cutover sites has also been demonstrated by Messier (1993).

Mineralizable N is the amount of N potentially available for plant uptake upon mineralization (Powers 1980). This parameter, measured only on the August 26 sampling, is not very helpful in explaining differences between the two young plantations, because similar amounts of mineralizable N were obtained from the 3- and 10-year-old plantations for the three humus types sampled. Although there were reports that N mineralized during the 14-d anaerobic incubation at 30°C could be related to field growth performance (Shumway 1978; Powers 1980), others found that anaerobic incubations are similar to soil fumigation methods where microbial N is measured when N is released through decomposing dead microbial cells (Adams and Attiwill 1982; Myrold 1987). Therefore, the anaerobic incubation results were not surprising since microbial N was not different in the two plantations. In this study, the amount of N mineralized from the anaerobic incubation never exceeded 50% of the microbial N. The significantly greater amount of mineralizable N in the old-growth forests than in the plantations illustrated again that clear-cutting and slash burning had greatly changed the properties of the forest floor. The overall nutrient supply problems on CH cutovers has been suggested to be partially related to poor organic matter quality (Prescott et al. 1993; Prescott and Preston 1994).

Differences in microbial activities and soil nutrient dynamics were ultimately displayed in the growth performance of trees in the field. Old-growth forests consist of mature trees, which may require less N per capita for efficient photosynthesis and maintaining their growth because of more developed internal cycling mechanisms (van den Driessche 1984). Also, as trees grow older, the proportion of nutrients in the foliage tends to become less while that in the bole and bark becomes more (Wright and Will 1958). As a result of better nutritional conditions, western red cedar in the 3-year-old stands had a higher N content and lower C/N ratio in current-year foliar samples. Those in the 10-year-old stands had foliar N content and C/N ratios in the ranges of the old-growth trees and showed chlorosis symptoms and poor growth in the field.

It has been found that mycorrhizal fungi, which form ericoid mycorrhizae with salal roots, can use some simple organic N sources, such as amino acids, peptides, and proteins (G. Xiao, personal communication); therefore, salal may be more efficient in utilizing limited available N supply in the soil. However, in the 10-year-old stands, salal foliage also had lower foliar N contents and higher C/N ratios, further indicating severe nutrient deficiencies in those stands.

Conclusions

Clear-cutting and slash burning has substantially reduced microbial biomass and activities and altered environmental conditions. Water content, extractable C and N, microbial C and N, and mineralizable N were all reduced by harvesting and burning, which made the forest floor of the old-growth forests distinctively different from those of the young plantations. Greater extractable N and mineralizable N in the old-growth forests than in the young plantations suggested that the old-growth forests may be in a much better nutritional condition than the young plantations. Between the 3- and 10-year-old plantations, slower growth in the 10-year-old plantations was associated with the lower amount of available N in the forest floor, greater competition for available N from the microbial community, and more vigorous growth of competing understory salal

vegetation. Microbial activities appeared to play an important role in regulating N cycling and availability in the underground ecosystem. However, not enough evidence was obtained to conclude that microbial biomass was a net sink for available N in the older plantations. Further studies are needed to clarify if it is the reduced fluxes of nitrogen in the forest floor in the old plantations that is contributing to the N-stressed situation by using in situ mineralization methods; particularly useful would be methods that quantify gross N mineralizations (Hart et al. 1994).

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