The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A.

J.D.H. Spears, S.M. Holub, M.E. Harmon, and K. Lajtha

Abstract: This study investigated the effect of coarse woody debris (CWD) on mineral soils at the H.J. Andrews Experimental Forest in the central Cascade Range of Oregon, U.S.A. Nutrients in CWD leachates were compared with (*i*) forest floor (control) leachates, (*ii*) over a decay chronosequence, and (*iii*) among CWD of four species. There were few differences among CWD leachates and forest floor leachates. Soils under CWD were warmer but not wetter than control soils. Water-soluble organic carbon was higher in soils under CWD than in controls at 5–15 cm depth ($p <$ 0.02), but soil C concentrations did not differ. Gross N mineralization was faster in control soils. We found no differences in N, P, microbial biomass, Biolog plate assays, or enzyme activity in soils. Nutrient leachate differences among CWD species were small. Differences in solutions and in soils among CWD and controls were largest during the middle decay classes. This study suggests that either (*i*) CWD has no long-term effect and does not contribute large amounts of organic matter to the soil profile or (*ii*) the effect of CWD is so prolonged that no spatial affect is noticeable because all soils have been affected by CWD at some time.

Résumé : Cette étude porte sur l'effet des débris ligneux grossiers (DLG) sur le sol minéral à la forêt expérimentale H.J. Andrews située dans la partie centrale de la chaîne des Cascades en Oregon, aux États-Unis. Les nutriments présents dans les lessivats des DLG ont été comparés (*i*) à ceux présents dans des lessivats de la couverture morte (témoin), (*ii*) pour une chronoséquence de décomposition et (*iii*) pour quatre espèces. Il y avait peu de différence entre les lessivats des DLG et ceux de la couverture morte. Sous les DLG, le sol était plus chaud mais pas plus humide que le sol témoin. Le carbone organique soluble dans l'eau était plus élevé dans le sol sous les DLG à une profondeur de 5 à 15 cm (p < 0,02) mais la concentration en C du sol ne différait pas. La minéralisation brute de N était plus rapide dans le sol témoin. Nous n'avons pas observé de différences pour l'azote, le phosphore, la biomasse microbienne, les tests sur plats Biolog ou l'activité enzymatique dans les sols. Les différences dans le lessivage des nutriments entre les différentes espèces de DLG étaient faibles. Les différences dans les solutions et les sols entre les DLG et les témoins étaient les plus marquées dans les classes de décomposition intermédiaire. Cette étude porte à croire ou bien (*i*) que les DLG n'ont pas d'effet à long terme et n'apportent pas de quantités importantes de matière organique dans le profil de sol ou bien (*ii*) que leur effet est tellement à long terme qu'il n'est pas apparent dans l'espace parce que tout le sol a été affecté par les DLG à un moment ou à un autre dans le temps.

[Traduit par la Rédaction]

Introduction

Coarse woody debris (CWD) has been considered by some researchers as a stockpile of C on the forest floor that may increase mineral soil organic C through leaching inputs during ecosystem development (Harmon et al. 1986; Sollins et al. 1987). Since soils contain the largest pool of C in terrestrial ecosystems (Post et al. 1990) and fluxes of C into and out of forest soils are critical components of the global C cycle, leaching of C from CWD to mineral soil may be an important, yet often overlooked flux in the C cycle. For example, the biomass of CWD at the H.J. Andrews Experimental Forest in the Western Oregon Cascades ranges from 80 to 140 $Mg \cdot ha^{-1}$ (Harmon et al. 1986). It is reasonable to assume that a large portion of the leachate C may be contributed to the soil, making CWD an important source of C to forest mineral soils.

CWD may contribute C to the underlying soil as dissolved organic C (DOC) during decomposition. Yavitt and Fahey (1985) hypothesized that because decaying wood is only partially oxidized, soluble organic matter could be transferred to the mineral soil. Soluble C moving through the soil

Received 27 October 2002. Accepted 9 June 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 3 November 2003.

J.D.H. Spears,[1] S.M. Holub,[2] and K. Lajtha. Department of Botany and Plant Pathology, Oregon State University, Cordley Hall 2082, Corvallis, OR 97331, U.S.A.
M.E. Harmon. Department of Forest Science, Oregon State University, Corvallis, OR 97331, U.S.A.

[1]Corresponding author (e-mail: spearsj@lifetime.oregonstate.edu).
[2]Present address: U.S. Environmental Protection Agency, ORD/NRMRL/SPRD, Ecosystem and Subsurface Protection Branch, Ada, OK 74820, U.S.A.

 doi: 10.1139/X03-148

profile may contribute to the formation of soil organic matter. Indeed, Krzyszowska-Waitkus et al. (in review[3]) found that mineral soils under CWD in later decay stages contained significantly more C than control soils in a lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) ecosystem. The difference between mineral soil C under CWD and control mineral soils in their study, however, was small and limited to the surface horizons. Conversely, Busse (1994) reported a decrease in total C in soils beneath CWD in an eastern Oregon lodgepole pine forest.

Leachate from CWD may also contribute nutrients to the underlying mineral soils. Pathways of soil nutrient enrichment may include (*i*) nutrient losses from CWD by fungal sporocarps (Harmon et al. 1994), (*ii*) N fixation and associated leaching of N (Roskoski 1980; Hicks 2000), and (*iii*) leaching losses of N, P, and cations in the interstitial water of CWD and soil (Yavitt and Fahey 1985).

Nitrogen fixation in CWD in Pacific Northwest forests has been estimated at approximately 1 $kg \cdot ha^{-1} \cdot year^{-1}$ (Harmon et al. 1986) or approximately one-eighth of the total annual input of N to these old-growth Pacific Northwest ecosystems. Nitrogen may leach from CWD as dissolved organic N (DON) to the underlying soil, increasing soil N pools and influencing N cycling rates. Yavitt and Fahey (1985) found that concentrations of DON leaching from well-decayed CWD were twice as large as concentrations of DON in throughfall and were two to five times larger than concentrations of DON in soil solution. In contrast, lower amounts of mineralizable N were found in B-horizon soils beneath well-decayed CWD than in control soils in British Columbia (Kayahara et al. 1996). In eastern Oregon, Busse (1994) found lower concentrations of inorganic N under CWD. CWD leachates may also affect soil P pools. Using log chronosequences, a net efflux of P has been shown as logs decompose (Grier 1978; Lambert et al. 1980; Sollins et al. 1987).

We investigated the effect of CWD on soil biology and nutrient cycling by examining the nutrient inputs from CWD leachates and changes in soil nutrient pools, microbial biomass, and microbial community structure using a chronosequence of decayed CWD. We hypothesized that (*i*) DOC concentrations in CWD leachate would be highest in late stages of decay because there would be more C leaching as decomposition proceeds, (*ii*) mineral soils underlying well-decomposed CWD would contain more C because of prolonged inputs of DOC-rich leachates, (*iii*) there would be lower N and P in soils under CWD than in soils under the forest floor due to leaching losses of P and microbial immobilization of N in CWD, and (*iv*) changes in nutrient pools and N fluxes that occur as CWD ages will change the microbial community structure by favoring organisms that are able to degrade more recalcitrant, lignin-rich substances.

We also investigated potential differences in nutrient leaching among four species of CWD. Major constituents of wood chemistry are similar among coniferous species, but secondary compounds may differentially influence the decomposition of CWD and thus leachate quality. We therefore hypothesized that species that are less resistant to decay should release C and nutrients faster than more resistant species.

Materials and methods

To compare differences in leachates, soil solutions, and mineral soils among CWD of different age-classes, an old-growth stand in the H.J. Andrews Experimental Research Forest was chosen. The site is approximately 4 ha in size and is located approximately 550 m above sea level in the Willamette National Forest in the Western Cascade Province of the Oregon Cascade Range (44°13′53″N, 122°13′40″W). The climate is Csb-Mediterranean with warm dry summers and mild wet winters (Köppen). Precipitation averages 250 $cm \cdot year^{-1}$ and average annual temperature is 10 °C. Dominant tree species include large Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). Soils are classified as coarse loamy mixed mesic Typic Hapludands (Dixon and Noller 2002). This site has also been used as one of the sites of a long-term CWD decomposition experiment (see below) (Harmon 1992).

Experimental design

Our experimental design included naturally occurring CWD that was greater than 50 cm in diameter and identifiable as Douglas-fir. We designated CWD into decay classes using the criteria outlined in Triska and Cromack (1979). We also used four different species of class 2 CWD that were previously placed in situ during a CWD decomposition experiment at six different sites (Harmon 1992). The sites primarily differed by elevation and vegetative community composition, but all six sites were within the H.J. Andrews Experimental Forest. For a more detailed description of the sites, see Harmon (1992).

To compare leachate and soil solution among different decay classes of Douglas-fir CWD, five logs each of decay classes 3 and 4 were chosen adjacent to five experimentally placed class 2 CWD (Harmon 1992). Five control areas were designated adjacent to the CWD. To collect leachates, zero-tension lysimeters were made by cutting a 15.3-cm-diameter PVC pipe into 10.2-cm-long pieces and then cutting them lengthwise in half at a diagonal and capping the ends. Nipples and Tygon tubing were attached at the deeper end and connected to 1-L Nalgene bottles. The lysimeters were sealed against class 2, 3, and 4 logs with silicone caulking. Lysimeters were checked frequently to ensure that no water could seep into the lysimeters from the outside of the log. Zero-tension lysimeters were also placed immediately beneath the forest floor in control areas where no logs were evident (hereafter referred to as control lysimeters).

To collect soil solution, Prenart tension lysimeters were installed under class 2, 3, and 4 logs at 30 cm and only under class 4 at 50 cm. Tension lysimeters were also placed in areas with no logs at 30 and 50 cm as controls. Tension was applied at 5 kPa on the evening before collection. Leachate was collected biweekly from the fall of 1999 until the spring of 2002 when water was available and road access was not blocked by snow. The first two samples were discarded to avoid a disturbance signal from lysimeter installation. All zero-tension and tension lysimeter samples were filtered im-

[3] A. Krzyszowska-Waitkus, G.F. Vance, and C.M. Preston. Influence of coarse woody debris on soil organic matter in a rocky mountain coniferous forest. Soil Sci. Soc. Am. J. In review.

mediately after collection through a Whatman GFF filter (0.7-μm pore size) and frozen until analyzed.

To compare differences in the mineral soil beneath Douglas-fir CWD, we sampled soils under class 4 and 5 CWD where we expected to find the most pronounced effect of CWD on soils. A total of 10 class 4, 10 class 5 CWD, and 10 areas with no CWD (hereafter referred to as control soils) were chosen from within the same area as the leachate and soil solution sampling and were as close to the class 4 CWD as possible. Five of the class 4 CWD were the same CWD used in the leachate and soil solution sampling. When this was the case, soil sampling was at least 1 m from the lysimeters. Control mineral soil samples were taken after removing the forest floor where there was no evidence of CWD.

In the spring of 2000, we used a 10-cm-diameter soil auger to collect soils to a depth of 60 cm and homogenized the soils within four depths: 0–5, 5–15, 15–30, and 30–60 cm. In the fall of 2000, a second set of soil samples were collected from 0–15 cm under the same CWD and controls to test for seasonal differences in biological activity under CWD. These collections were made more than 0.5 m but not more than 1 m from the previously sampled areas.

In the fall of 2001, soils were resampled for gross N mineralization analyses. Temperature dataloggers (Stow Away Tidbit; Onset Computer Corp., Cape Cod, Mass.) were placed immediately under the class 3 CWD and immediately under the forest floor for a short period in the spring of 2000 to determine if mineral soil temperatures were affected by CWD. Temperature was recorded every 15 min for 3 weeks. Soil moisture was determined gravimetrically on 10–20 g of soil at each depth at each collection.

To compare leachate differences among different species of CWD, zero-tension lysimeters were installed under four different species of class 1 CWD at six sites within the H.J. Andrews Experimental Forest and are described in detail in Harmon (1992). At each site, there was one log of each species (*Thuja plicata*, *Pseudotsuga menziesii*, amabilis fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes), and *Tsuga heterophylla*). Equal volumes of lysimeter solutions from each tree species were composited (volume weighted) over two seasons (September 1986 and February 1987). Total Kjeldahl N (TKN) was analyzed from November 1990 until April 1992.

Chemical analysis

Leachates and soil solutions were analyzed for DOC with a Shimadzu TOC analyzer. Solutions were analyzed for dissolved inorganic N (NH_4^+, NO_3^-) and total dissolved N (TDN) with an Orion Scientific AC 100 autoanalyzer after digestion in alkaline persulfate (Cabrera and Beare 1993). DON was calculated as the difference between TDN and DIN. Dissolved inorganic P (DIP) was analyzed with an Orion Scientific AC 100 autoanalyzer by the ascorbic acid method (Lajtha et al. 1999). DIP in soil solution from 30 and 50 cm was below detection limits of 0.001 $mg \cdot L^{-1}$.

Soils were sieved through a 4-mm-mesh sieve and extracted with K_2SO_4 for microbial biomass C (Voroney et al. 1999). KCl-extractable NH_4^+-N and NO_3^--N in soils were measured on an Orion Scientific AC100 autoanalyzer. Phosphatase and β-glucosidase enzyme assays were analyzed by the method of Caldwell et al. (1999) as an index of general microbial activity. Water-soluble organic C (WSOC) was extracted using a 2:1 water–soil extraction. Slurries were filtered through a GF/F filter and analyzed on a Shimadzu TOC analyzer. Labile P was extracted with resin strips and sodium bicarbonate using the first two steps of the Hedley fractionation as described in Lajtha et al. (1999) and analyzed on an Orion AC100 autoanalyzer.

Soil microbial community differences were assessed with Biolog® SFP2 plates (Zak et al. 1994). One gram of field-moist soil was added to 10 mmol of phosphate buffer (pH = 6.8), shaken for 20 min, and allowed to settle. One hundred and fifty microlitres of the buffer solution was pipetted into each well and allowed to incubate for 5 days. If the extracted microbes degrade the substrate in each well, the well turns turbid. We scored the results as positive when the well became cloudy and negative when there was no change. We realize that Biolog® plates do not identify community type or functional groups, but rather indicate differences in microbial preferences and this may include only those microbes that reproduce during the incubation time.

For total C and N analysis, soils were powdered with a spex-mixer mill and analyzed on a Carlo Erba NA1500 CHN analyzer at the Stable Isotope Biology Laboratory at the University of Georgia.

To determine potential gross N transformation rates in soils under CWD and control soils, we used the isotope-pool-dilution technique (Hart et al. 1994) in the fall of 2001 on five soils from 0–5 cm under class 4 and 5 CWD and control soils. Soils were thoroughly mixed and incubated in the laboratory at 25 °C, and therefore, rates do not represent in situ mineralization rates but rather potential transformation rates. Microbial biomass N and C were also analyzed on subsamples of these samples (Voroney et al. 1999).

Leachates from different species of CWD were analyzed for cations by USEPA method No. 200.7 with a Bausch & Lomb model 3580 ICPAES. TKN was analyzed after Kjeldahl digestion with H_2SO_4, $CuSO_4$–KC1, and Nessler finish. Nitrate (Technicon industrial method No. 100-70W) and NH_4^+ (No. 417F) (American Public Health Association 1980) were analyzed on a Technicon Auto-Analyzer II. DOC was analyzed with a Shimadzu TOC-5000A analyzer using method No. 5310B (American Public Health Association 1989).

Statistics

Results from the chemical analyses of mineral soils were compared at each depth using analysis of variance (ANOVA) and the means were compared using Tukey's test ($\alpha = 0.05$).

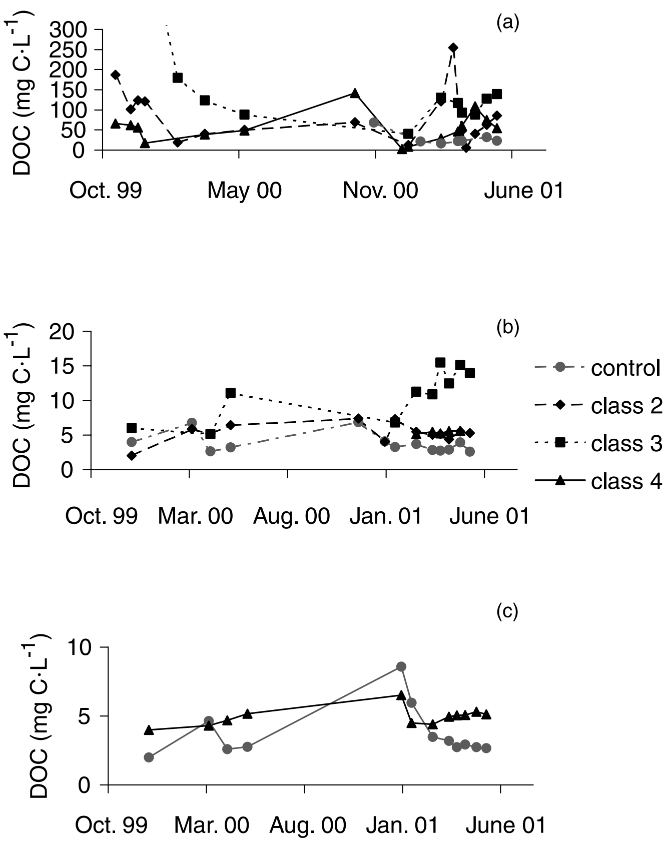
Nutrient concentrations in solution were graphed over time for visual inspection. It was not possible to use repeated measures ANOVA for all dates because lysimeters did not produce adequate samples at all dates. If no effect of date on solution concentration was seen, samples were averaged across all sample dates and the mean concentrations and standard errors were presented. DOC concentrations varied considerably over time and thus were presented in graphs.

To determine if there was a difference among species, we used ANOVA and compared the means for each season with Tukey's HSD multiple comparison test ($\alpha = 0.05$). Lysimeter solutions for the different species of CWD were composited for two seasons, and thus, it was only valid to compare among species for differences.

Statistical analyses were performed using SAS (SAS Institute Inc., Cary, N.C.). The Nonmetric Multidimensional Scaling program using the Sorenson distance measure in PC-ORD (version 4.19) (MjM Software Design, Gleneden Beach, Ore.) was used to analyze microbial communities in soils as indicated by Biolog® plates for both seasons.

We realize that this is an observational study because the CWD was not randomly selected for this study, and therefore, the scope of this study is limited to a mesic old-growth forest in the Oregon Cascades with a limited sample size. No cause and effect conclusions may be drawn from this study.

Fig. 1. Dissolved organic C (DOC) concentrations (*a*) from zero-tension lysimeters under coarse woody debris (CWD) of decay classes 2, 3, and 4 and controls under the forest floor (forest floor lysimeters were not sampled until November of 2000), (*b*) at 30 cm under CWD of decay classes 2, 3, and 4 and in control lysimeters (class 4 lysimeters did not provide samples until November of 2000), and (*c*) at 50 cm under CWD of decay class 4 and in control lysimeters. No lysimeters were installed under classes 2 and 3 at 50 cm.



Results and discussion

DOC in CWD leachates was approximately three times higher in concentration than in leachates from the forest floor. DOC in leachate from zero-tension lysimeters was often highest under class 3 CWD, although concentrations varied over time (Fig. 1). A one-time peak of 935 mg C·L^{-1} that decreased with time for leachates under class 3 CWD may have been the prolonged result of disturbance from lysimeter installation. DOC concentrations from control zero-tension lysimeters were lowest of all treatments throughout the year, averaging 20 mg C·L^{-1}. Even at 30 cm, soil solution from class 3 CWD had three times higher DOC concentrations than control soil solutions. This indicates that unless there is a large amount of microbial degradation of DOC in mineral soils under CWD, there should be a large input of C via sorption to the soils underlying class 3 logs. However, soil C concentrations did not differ among soils under decay classes 4 and 5 and control soils at any depth (Table 1).

The amount of carbon leaching from CWD as DOC was large when compared with inputs from the forest floor; we estimated the amount of C contributed by CWD to forest soils through leaching inputs. From the leachate collected in this study, we calculated the volume-weighted amount of C that could be lost via DOC leaching from class 2 through class 4 from CWD. For each age-class, we calculated the leaching flux of DOC per year and multiplied that by the number of years that the log remains in the respective age class (after Sollins et al. 1987). The total amount of C lost from CWD as DOC in leachate over 87 years was estimated to be 4.5 kg C·m^{-2}.

To compare the amount of C lost via leaching with the total amount of C stored in a log, we used a class 1 log with an average diameter of 1 m (Sollins et al. 1987). If we assume a CWD bulk density of 0.45 g·cm^{-3}, the total amount of C stored in the log is estimated to be 180 kg C·m^{-2}. If we further assume that 50% of the log C is lost by the time it reaches class 4, then the total C lost via respiration or DOC leaching over 87 years is 90 kg C·m^{-2}. Comparing this number with the estimated amount of DOC lost, we find that the amount of C lost via DOC leaching only accounts for 5% of the total C lost from the bole. CWD leachate concentrations of DOC are large when compared with forest floor leachates but are only a minor proportion of the total amount of C lost from CWD. This suggests that because most of the C leaves CWD as CO_2 via respiration, there would be little increase in total soil C under CWD compared with soil under the forest floor. Other researchers have also found small, if any, increases in total soil C under CWD (Krzyszowska-Waitkus et al., in review[3]; Kayahara et al. 1996; Busse 1994).

Class 3 CWD may have the most profound effect on soils because it had the largest concentrations of DOC in leachate and is the most active stage of decomposition (Krankina et al. 1999). Indeed, Busse (1994) found a large increase in microbial biomass C but a large decrease in total soil C in mineral soils under class 3 CWD. However, no difference in microbial biomass was detected among soils from under CWD and control soils in either season or at either depth (Table 2).

We expected that there would be more labile C compounds such as WSOC in mineral soils under the forest floor because the forest floor is richer in more labile C substrates than CWD and that the corresponding microbial enzyme activity would be higher under the forest floor. However, β-glucosidase and phosphatase activities did not differ significantly among soils under CWD or control soils (Table 2). There were no statistically significant differences in WSOC among soils at 0–5 cm either. At 5–15 cm, soils under class 4 CWD had higher WSOC than soils under class 5 CWD

Table 1. Mean percent total C and N and mean labile P from soils at four different depths under decay class 4 and 5 coarse woody debris and from control soils.

	Total C (%)			Total N (%)			Labile P (mg·g soil^{-1})		
Depth (cm)	Control	Class 4	Class 5	Control	Class 4	Class 5	Control	Class 4	Class 5
0–5	4.67 (0.37)	5.80 (1.07)	4.55 (0.59)	0.19 (0.01)	0.18 (0.02)	0.17 (0.01)	0.30 (0.03)	0.34 (0.04)	0.26 (0.05)
5–15	2.88 (0.15)	3.11 (0.31)	2.85 (0.35)	0.14 (0.01)	0.13 (0.006)	0.13 (0.01)	0.30 (0.03)	0.31 (0.03)	0.24 (0.03)
15–30	1.57 (0.19)	2.03 (0.28)	1.58 (0.12)	0.096 (0.01)	0.10 (0.008)	0.09 (0.003)	0.22 (0.03)	0.29 (0.04)	0.17 (0.03)
30–60	1.03 (0.16)	1.31 (0.17)	0.81 (0.06)	0.07 (0.01)	0.07 (0.006)	0.06 (0.004)	0.10 (0.02)	0.14 (0.04)	0.08 (0.02)

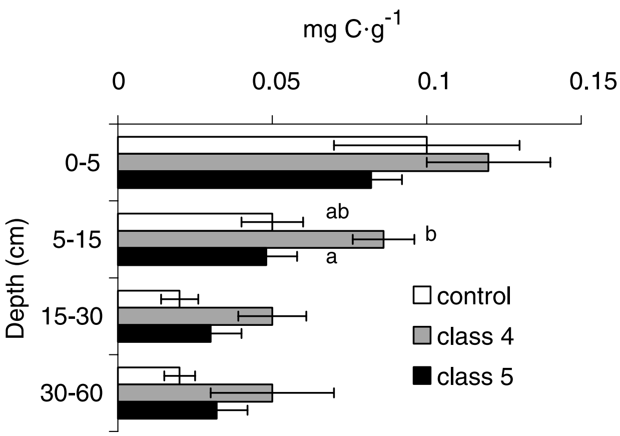
Note: Standard errors are given in parentheses. Mean labile P is the sum of resin- and bicarbonate-extracted P.

Table 2. Mean percent microbial biomass C (milligrams per gram) and enzyme activities (micromoles per gram per hour) from 0–5 and 5–15 cm soils under class 4 and 5 coarse woody debris and from control soils (n = 10).

Depth and treatment	Microbial biomass C	Microbial biomass N	Microbial biomass C/N	β-Glucosidase activity	Phosphatase activity
Spring					
0–5 cm control	0.51 (0.05)			11.9 (2.1)	43.0 (5.5)
0–5 cm class 4	0.41 (0.06)			7.3 (2.6)	36.9 (5.4)
0–5 cm class 5	0.38 (0.05)			6.6 (1.9)	31.2 (4.6)
5–15 cm control	0.36 (0.06)			17.1 (2.8)	54.0 (6.9)
5–15 cm class 4	0.29 (0.05)			15.8 (5.5)	36.2 (4.4)
5–15 cm class 5	0.25 (0.07)			19.1 (6.5)	52.5 (11.5)
Fall					
0–5 cm control	0.24 (0.02)			10.8 (7.0)	36.8 (15.1)
0–5 cm class 4	0.16 (0.03)			9.3 (6.5)	34.7 (28.3)
0–5 cm class 5	0.17 (0.02)			5.2 (4.1)	17.5 (8.5)
5–15 cm control	0.26 (0.12)			4.4 (2.1)	18.2 (5.4)
5–15 cm class 4	0.14 (0.03)			3.3 (2.1)	14.9 (11.4)
5–15 cm class 5	0.13 (0.03)			1.9 (0.9)	9.6 (3.2)
^{15}N					
0–5 cm control	0.67 (0.06)	0.19 (0.88)	6.7		
0–5 cm class 4	0.61 (0.10)	0.35 (0.12)	4.7		
0–5 cm class 5	0.55 (0.11)	0.09 (0.04)	9.3		

Note: Mean microbial biomass C and N values for soils used for gross mineralizations in the fall of 2001 (n = 5). Standard errors are given in parentheses.

Fig. 2. Mean water-soluble organic C in soil from under coarse woody debris of decay classes 4 and 5 and control soils to a depth of 60 cm. Bars represent 1 SE and letters represent statistical difference using Tukey's HSD multiple comparison test. Treatments with different letters are significantly different at α = 0.05.



(p < 0.02) (Fig. 2), which suggests that there may have been more labile C than we expected under CWD. Perhaps there is a persistent labile source of C under CWD, such as throughfall inputs or leaching from the organic layer that covers well-decayed CWD, that may provide the more labile C substrates necessary to sustain the microbial biomass at levels comparable with the forest floor.

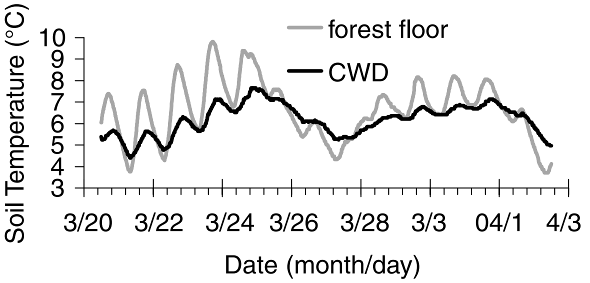
There were no noticeable differences in microbial community functioning as represented by enzyme activities or the Biolog® plates, which would also suggest that CWD and forest floor DOM inputs to the mineral soil were similar in quality and quantity. Results from the Biolog® plates indicate no clear differences in substrate specificity between soils under class 5 CWD and control soils from under the forest floor. A nonmetric multidimensional scaling ordination graph produced a two-dimensional result with a Monte Carlo test result (p = 0.02), and the proportion of variance explained by the two axes was 84%. However, there was a clear separation of the soils by season along the two axes, suggesting that much of the variance was attributable to seasonal (i.e., temperature or moisture) rather than to treatment

Table 3. Mean lysimeter concentrations (milligrams per litre) and standard errors (in parentheses) for dissolved organic N (DON), NH_4^+-N, NO_3^--N, and dissolved inorganic P (DIP).

Depth	Decay	DON	NH_4^+-N	NO_3^--N	DIP
0 cm (leachate)	Control	0.54 (0.07)	0.02 (0.01)	0.012 (0.002)	0.52 (0.07)
	Class 2	1.27 (0.29)	0.17 (0.04)	0.22 (0.13)	0.58 (0.09)
	Class 3	0.81 (0.12)	0.04 (0.01)	0.04 (0.01)	0.68 (0.18)
	Class 4	0.60 (0.06)	0.08 (0.02)	0.17 (0.06)	0.38 (0.08)
30 cm (soil solution)	Control	0.04 (0.02)	0.005 (0.003)	0.009 (0.006)	0.08 (0.06)
	Class 2	0.14 (0.09)	0.007 (0.006)	0.03 (0.02)	0.002*
	Class 3	0.21*	0.009*	0*	na
	Class 4	0.17 (0.08)	0.02 (0.01)	0.016 (0.007)	0.19 (0.18)
50 cm (soil solution)	Control	0.07 (0.03)	0.03 (0.03)	0.63 (0.42)	na
	Class 4	0.12 (0.03)	0.001 (0.001)	0 (0)	0.002

Note: Samples were averaged over two water years after visual inspection suggested no effect of date on concentrations. na, no sample available.
*n = 1; no standard error.

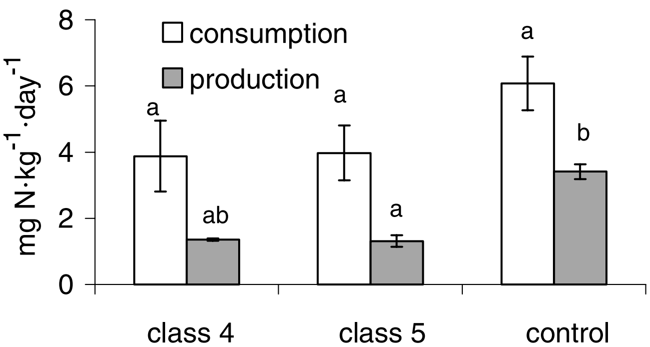
Fig. 3. Mean mineral soil temperatures from under decay class 3 coarse woody debris (CWD) and under the forest floor in the spring of 2001.



differences. In the spring, mean soil moisture from 0–5 cm was higher in soils under CWD (mean 55.3%, SE = 5.09%) than in soils under the forest floor (mean 46.2%, SE = 6.62%), although it was not significantly different. In the fall, no difference was detected between soil moisture under CWD (mean 37.3%, SE = 2.33%) and that under the forest floor (mean 39.3%, SE = 2.36%). There was less diurnal variability in soil temperatures under class 3 CWD compared with soils under the forest floor in the spring (Fig. 3). A decrease in temperature variability may prevent freeze–thaw cycles in soils under CWD, which disrupt biological activity and can lead to nutrient leaching losses while also increasing microbial activity by moderating temperature extremes. However, since there were no differences seen in microbial community indices, the differences in temperature and moisture under CWD and in control soils may not affect the microbial communities to a large extent.

Nutrient concentrations in leachates, soil solution, and mineral soils were variable and very few clear patterns were discernable from the results. DON concentrations from zero-tension leachate and in leachate from 30 and 50 cm showed no clear pattern, and variation between treatments was large (Table 3). Ammonium and NO_3^- in zero-tension leachates and in soil solutions at 30 and 50 cm were near detection limits and showed no consistent differences with regard to CWD decay classes or controls. Total soil N did not differ among soils under decay classes 4 and 5 and control soils at any depth (Table 1).

Fig. 4. Mean gross NH_4^+ production and consumption rates for soil under decay class 4 and 5 coarse woody debris and control soils. Bars represent 1 SE and letters represent statistical difference using Tukey's HSD multiple comparison test. Treatments with different letters are significantly different at α = 0.05.



Results of a preliminary net N mineralization study using the buried bag technique suggested no difference in net mineralization rates between CWD and control soils. There were also no differences between KCl-extractable NH_4^+ and NO_3^- between soils under the logs and soils without logs in the spring and summer of 1999 (J.D.H. Spears, unpublished data). Gross N mineralization rates were significantly higher in mineral soils under the forest floor than in mineral soils under CWD (p < 0.015) (Fig. 4). Gross NH_4^+ production was 2 mg·kg^{-1}·day^{-1} lower for soils under CWD, while gross NH_4^+ consumption was also 2 mg·kg^{-1}·day^{-1} lower for soils under CWD.

Total N concentrations tend to be highest in the most decayed material, while N fixation is most active when the CWD is moderately decayed, e.g., classes 2 and 3 (Hicks 2000). After averaging the concentrations in soil solutions over time, we found that class 2 had the highest rates of N efflux in CWD leachate as DON, while N concentrations in control leachate were consistently lower than in any decay class of CWD. Nitrate and NH_4^+ were very low in leachates, and thus, DON was the major form of N loss from the CWD. This agrees with Yavitt and Fahey (1985) who found DON to account for 80% of N loss from well-decayed

Table 4. Mean cation concentrations (milligrams per litre) and percent dissolved organic C (DOC) and total Kjeldahl N (TKN) from zero-tension lysimeters under class 1 species from four tree species.

	Abies amabilis	*Pseudotsuga menziesii*	*Thuja plicata*	*Tsuga heterophylla*
Sept. 1986				
Al	0.27 (0.17)	0.10 (0.00)	0.10 (0.00)	0.10 (0.03)
Fe	0.05 (0.05)	0	0	0
Ca	0.63 (0.08)a	0.55 (0.04)a	1.30 (0.29)b	0.43 (0.09)a
K	6.17 (2.09)	2.67 (0.49)	3.00 (0.52)	3.83 (0.75)
Mg	0.18 (0.03)ab	0.10 (0.00)b	0.30 (0.07)a	0.16 (0.03)ab
Mn	0.08 (0.02)a	0.03 (0.02)ab	0.0 (0.00)*b*	0.08 (0.03)a
P	1.48 (0.67)	0.4 (0.12)	0.38 (0.10)	0.87 (0.23)
S	1.60 (0.26)	1.53 (0.30)	1.77 (0.47)	1.45 (0.43)
DOC	18.04 (2.91)	18.81 (1.64)	19.74 (1.25)	19.22 (4.36)
TKN	0.30 (0.03)	0.20 (0.02)	0.26 (0.02)	0.24 (0.03)
Feb. 1987				
Al	0.09 (0.03)	0.25 (0.03)	0.15 (0.03)	0.25 (0.06)
Fe	0.02 (0.01)	0.05 (0.01)	0.050 (0.01)	0.04 (0.01)
Ca	0.73 (0.26)	1.15 (0.23)	2.24 (0.93)	0.95 (0.25)
K	0.55 (0.27)	0.38 (0.17)	0.34 (0.18)	1.02 (0.49)
Mg	0.14 (0.03)	0.19 (0.04)	0.36 (0.14)	0.26 (0.09)
Mn	0.04 (0.01)ab	0.08 (0.02)ab	0.03 (0.01)b	0.16 (0.05)a
P	1.46 (0.57)	0.73 (0.16)	0.73 (0.35)	1.47 (0.37)
S	1.27 (0.43)	0.71 (0.23)	0.90 (0.25)	0.58 (0.12)
DOC	40.72 (15.24)	32.42 (5.97)	26.08 (3.53)	33.17 (4.76)
TKN	0.53 (0.21)	0.31 (0.03)	0.42 (0.10)	0.31 (0.04)

Note: Standard errors are given in parentheses. Letters following the mean indicate that the solutions are significantly different for that element at $\alpha = 0.05$.

CWD. Even at 30 and 50 cm, DIN was only a minor component of N in soil solution.

We expected an increased rate in gross N mineralization in mineral soils beneath CWD because of the high organic N inputs. Contrary to this hypothesis, however, rates of N cycling in mineral soils were faster under forest floor than under well-decayed CWD. Although gross production of NH_4^+ was higher in control mineral soils than in mineral soils under CWD, the difference between gross NH_4^+ consumption and gross NH_4^+ production was approximately equal (Fig. 4). Thus, net mineralization rates remained similar among treatments, while gross mineralization techniques showed that N cycles more quickly under the forest floor than under CWD. The more labile C sources in forest floor leachate most likely allowed for quicker mineralization than the more recalcitrant C sources under CWD. Thus, C quality in leachates may control the rates of N cycling in these soils, as has been found by many other researchers.

Zero-tension lysimeter DIP was similar among treatments and was extremely low for solutions at all depths (Table 3), and there was no difference in labile P concentrations among decay classes and control soils (Table 1). We had hypothesized that hydrophobic DOC leaching from CWD would displace phosphates into the soil solution, flushing P from the soil exchange sites and leaching labile P from the system, because CWD leachates have a high percentage of hydrophobic compounds (Yavitt and Fahey 1985), and hydrophobic DOC compounds have a stronger affinity for soil exchange sites than P (Kaiser and Zech 1996). However, labile soil P pools were not lower in mineral soils underlying CWD than in soils underlying the forest floor, suggesting that little leaching of P occurs from soils underlying CWD.

Species differences

There were few differences in leachate chemistry collected under class 1 logs of different species. There were no significant differences in CWD leachates among species in concentrations of N, DOC, Al, Fe, K, P, NH_4^+, NO_3^-, or S (Tables 4 and 5). The few differences in leachate chemistry may be because the time period of most active leaching is in stages of decay later than those of the CWD examined in this study.

Calcium concentrations in *Thuja plicata* leachates were higher than in other species in September 1986 ($p < 0.005$). *Thuja plicata* had higher concentrations of Mg in leachate than *Pseudotsuga menziesii* ($p < 0.02$), but it was not statistically different from those in *Abies amabilis* or *Tsuga heterophylla* in September 1986. In February 1987, there were no differences in Mg concentrations between species. In September 1986, concentrations of Mn in *Thuja plicata* leachate were significantly lower than in *Abies amabilis* and *Tsuga heterophylla* but not *Pseudotsuga menziesii* ($p < 0.03$). In February 1987, concentrations of Mn in *Thuja plicata* leachate were lower than in *Tsuga heterophylla* ($p < 0.05$) but were similar to concentrations of Mn in *Pseudotsuga menziesii* and *Abies amabilis* leachates.

We had hypothesized that species less resistant to decay would release C and nutrients more rapidly. Major constitu-

Table 5. Mean NH_4^+-N and NO_3^--N concentrations (milligrams per litre) from zero-tension lysimeter solutions collected under four class 1 coarse woody debris species.

	Abies amabilis	*Pseudotsuga menziesii*	*Thuja plicata*	*Tsuga heterophylla*
NH_4^+-N				
Dec. 1990	0.26 (0.05)	0.17 (0.02)	0.46 (0.29)	0.43 (0.11)
Apr. 1991	0.97 (0.35)	1.24 (0.48)	0.70 (0.14)	1.19 (0.28)
Oct. 1991	4.94 (1.40)	2.96 (1.16)	1.79 (0.75)	4.26 (2.40)
Dec. 1991	0.62 (0.26)	0.64 (0.23)	0.99 (0.40)	0.80 (0.29)
Apr. 1992	2.01 (0.49)	3.63 (1.17)	2.80 (0.89)	2.05 (0.85)
NO_3^--N				
Dec. 1990	0.22 (0.04)	0.21 (0.04)	0.30 (0.08)	0.19 (0.04)
Apr. 1991	0.07 (0.01)	0.10 (0.01)	0.14 (0.04)	0.14 (0.07)
Oct. 1991	0.09 (0.01)	0.08 (0.01)	0.09 (0.02)	0.11 (0.02)
Dec. 1991	0.16 (0.06)	0.10 (0.01)	0.09 (0.01)	0.17 (0.04)
Apr. 1992	0.16 (0.06)	0.15 (0.04)	0.19 (0.05)	0.10 (0.02)

Note: Standard errors are given in parentheses.

ents of wood chemistry are similar among coniferous species, but secondary compounds can differentially influence the decomposition of CWD and thus influence the quality of CWD leachates. However, our results did not support this hypothesis. The most resistant tree species to decay was *Thuja plicata*, and indeed, *Thuja plicata* lost less Mn in leachates that other species. However, *Thuja plicata* lost more Mg and Ca through leaching than other species. The species least resistant to decay was *Abies amabilis* and so we expected *Abies amabilis* to shown the largest nutrient and DOC losses. For example, K is a very mobile cation and leaches quite readily from CWD during decomposition (Holub et al. 2001), and therefore, K should have been most prevalent in leachate from *Abies amabilis*. In September 1986, K was higher in concentration in *Abies amabilis* leachate than in other species in accordance with our hypothesis, but in February 1987, concentrations of K were highest in *Tsuga heterophylla* leachate, which, again, is contradictory to our hypothesis.

Although our results indicate that CWD has little effect on soils, we cannot be certain that the control soils had never been affected by coarse or fine woody debris. Our control soils showed no visual evidence of CWD to a depth of 60 cm and thus had not been influenced by CWD over the timescale of log decomposition. The possibility exists that CWD may have been present at some time during pedogenesis but had completely decomposed, leaving only a signature that would therefore be indistinguishable from soils currently underlying CWD. Additionally, our sample size may have been too small to detect differences among treatments, as soils are extremely variable spatially.

We had hypothesized that the wood imprint on soils would be spatially discrete and visible under the most highly decayed CWD; however, this study suggests that either (*i*) CWD has no long-term effect and does not contribute large amounts of organic matter to the soil profile or (*ii*) the effect of CWD is so prolonged that no spatial affect is noticeable because all soils have been affected by CWD at some time.

Acknowledgements

We would like to acknowledge the helpful and insightful comments from Dick Waring, Pat Muir, and Kermit Cromack Jr. as well as the two anonymous reviewers and the Associate Editor. Funding was provided by NSF DEB-0087081 and USDA NRICGP 97-35101-4256. We acknowledge the support provided to the H.J. Andrews Experimental Forest by the Pacific Northwest Station, USDA Forest Service, and the Willamette National Forest. Additional support to the Forest was provided by the H.J. Andrews Long Term Ecological Research program funded by the National Science Foundation, Division of Environmental Biology.

References

American Public Health Association. 1980. Standard methods for the examination of water and wastewater. 15th ed. *Edited by* L.S. Clesceri, A.E. Greenberg, and R.R. Trussell. American Public Health Association, Washington, D.C.

American Public Health Association. 1989. Standard methods for the examination of water and wastewater. 17th ed. *Edited by* L.S. Clesceri, A.E. Greenberg, and R.R. Trussell. American Public Health Association, Washington, D.C.

Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Sci. Soc. Am. J. **581**: 221–227.

Cabrera, M.L., and Beare, M.H. 1993. Alkaline persulfate oxidation for determining total nitrogen in microbial biomass extracts. Soil Sci. Soc. Am. J. **57**: 1007–1012.

Caldwell, B.A., Griffiths, R.P., and Sollins, P. 1999. Soil enzyme response to vegetation disturbance in two lowland Costa Rica soils. Soil Biol. Biochem. **31**: 1603–1608.

Dixon, J., and Noller, J.S. 2002. How low can you go? Applying GIS to soil-landscape mapping at large scales. Annual meeting abstracts. American Society for Agronomy, Indianapolis, Ind.

Grier, C.C. 1978. A *Tsuga heterophylla – Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Can. J. For. Res. **8**: 198–206.

Harmon, M.E. 1992 Long-term experiments on log decomposition at the H.J. Andrews Experimental Forest, Oregon. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-280.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133–302.

Harmon, M.E., Sexton, J., Caldwell, B.A., and Carpenter, S.E. 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. Can. J. For. Res. **24**: 1883–1893.

Hart, S.C., Nason, G.E., Myrold, D.D., and Perry, D.A. 1994. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology, **754**: 880–891.

Hicks, W.T. 2000. Modeling nitrogen fixation in dead wood. Ph.D. dissertation, Oregon State University, Corvallis, Ore.

Kaiser, K., and Zech, W. 1996. Nitrate, sulfate, and biphosphate retention in acid forest soils affected by natural dissolved organic carbon. J. Environ. Qual. **25**: 1325–1331.

Kayahara, G.J., Klinka, K., and Lavkulich, L.M. 1996. Effects of decaying wood on eluviation, podzolization, acidification, and nutrition in soils with different moisture regimes. Environ. Monit. Assess. **39**: 485–492.

Krankina, O.N., Harmon, M.E., and Griazkin, A.V. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. Can. J. For. Res. **29**: 20–32.

Lajtha, K., Driscoll, C.T., Jarrell, W.M., and Elliot, E.T. 1999. Soil phosphorus: characterization and total element analysis. *In* Standard soil methods for long-term ecological research. *Edited by* G.P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins. Oxford University Press, New York. pp. 115–142.

Lambert, R.L., Lang, G.E., and Reiners, W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology, **616**: 1460–1473.

Post, W.M., Peng, T., Emanuel, W.R., King, A.W., Dale, V.H., and DeAngelis, D.L. 1990. The global carbon cycle. Am. Sci. **78**: 310–326.

Preston, C.P., Sollins, P., and Sayer, B.G. 1990. Changes in organic components for fallen logs in old-growth Douglas-fir forests monitored by ^{13}C nuclear magnetic resonance spectroscopy. Can. J. For. Res. **20**: 1382–1391.

Roskoski, J.P. 1980. Nitrogen fixation in hardwood forests of the northeastern United States. Plant Soil, **54**: 33–44.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., and Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Can. J. For. Res. **17**: 1585–1595.

Triska, F.J., and Cromack, K., Jr. 1979. The role of wood debris in forests and streams. *In* Forests: fresh perspectives from ecosystem analysis. *Edited by* R.H. Waring. Oregon State University Press, Corvallis, Ore. pp. 171–190.

Voroney, R.P., Winter, J.P., and Beyaert, R.P. 1999. Soil microbial biomass C and N. *In* Soil sampling and methods of analysis. *Edited by* M.R. Carter. Canadian Society of Soil Science, Pinawa, Man. pp. 277–286.

Yavitt, J.B., and Fahey, T.J. 1985. Chemical composition of interstitial water in decaying lodgepole pine bole wood. Can. J. For. Res. **15**: 1149–1153.

Zak, J.C., Willig, M.R., Moorhead, D.L., and Wildman, H.G. 1994. Functional diversity of microbial communities: a quantitative approach. Soil Biol. Biochem. **26**: 1101–1108.