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# NITROGEN TRANSFORMATIONS IN FALLEN TREE BOLES AND MINERAL SOIL OF AN OLD-GROWTH FOREST

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*Abstract.* I measured net N transformation rates of well-decayed boles and adjacent mineral soil under field conditions in an old-growth Douglas-fir/western hemlock/western red cedar stand in the central Oregon Cascades. Additionally, laboratory assays and incubations were used to elucidate the controls on net N transformations in these materials. Net N mineralization under field conditions was similar for well-decayed boles and mineral soils (0.83 and 0.61 g $N \cdot m^{-2}$ material$\cdot yr^{-1}$, respectively). Laboratory rates of net N mineralization per mass of total N were similar or higher in well-decayed boles compared to mineral soil. These results are surprising, given that the C:N ratio of well-decayed boles was much greater than that of mineral soil (117 vs. 26, respectively), and given the vastly different physical structure of these materials. Higher field and laboratory rates of net N mineralization relative to total N in boles compared to mineral soil suggest either that organically bound N contained in boles is in a more readily mineralizable form or that C compounds in well-decayed bole material are less readily metabolized by microbial heterotrophs (i.e., C availability is lower) than in mineral soil, resulting in a higher ratio of net-to-gross N mineralization because of reduced N demand by a C-limited microflora. A lower microbial respiration rate and smaller microbial biomass C relative to the total C pool in well-decayed boles than in mineral soil support the latter hypothesis. Furthermore, bole material exhibited a higher specific respiration rate (respired C per unit microbial biomass C), suggesting either a lower C-use efficiency of bole microflora or a lower C availability in boles compared to mineral soil. Both well-decayed bole and mineral soil materials showed low annual rates of net nitrification under field conditions. Using an estimate of the mass of class 4 and 5 boles in similar forest stands in the Pacific Northwest, I estimate that well-decayed boles contribute about 0.16–0.25 g $N \cdot m^{-2} \cdot yr^{-1}$ of plant-available N. This N flux is lower than other internal N fluxes within this forest, as well as lower than the rate of N input from the atmosphere. Total plant uptake in a nearby old-growth Douglas-fir forest has been estimated at about 4.0 g $N \cdot m^{-2} \cdot yr^{-1}$, suggesting that well-decayed boles may contribute about 4–6% of plant N uptake. Results from this study indicate that the C:N ratio is a poor predictor of net N release from contrasting forest detrital pools.

*Key words: carbon availability; coarse woody debris; coniferous forest; microbial biomass; microbial respiration; nitrification; nitrogen availability; nitrogen cycle; nitrogen mineralization; Oregon; tree boles.*

## INTRODUCTION

Coarse woody debris (CWD), in the form of standing dead trees, fallen boles, large branches, and roots, is abundant in many forest ecosystems, and plays several important ecological roles within forests (Harmon et al. 1986). These roles include the reduction of soil erosion, reservoirs for nutrient and water storage, seed beds for plant establishment, and habitat for fungi, bacteria, arthropods, and a variety of vertebrates. Coarse woody debris also has been suggested to play a key role in carbon (C) flow and nutrient cycles of many forests, but few studies have explored these ecosystem functions of CWD (Harmon et al. 1994).

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The low nutrient concentrations, decomposition rates, and mass of annual inputs of CWD compared to fine litterfall and root turnover have been used as arguments for discounting the significance of CWD in nutrient cycles during short-term periods in stand development (Arthur and Fahey 1990, Harmon and Chen 1991, Harmon et al. 1994). However, some investigators have suggested that, following catastrophic disturbances resulting from blowdown or fire, large amounts of nutrients from the massive new inputs of CWD may become available to the recovering forest, and that the timing of nutrient release may closely match nutrient demand (Harmon and Chen 1991). Furthermore, many undisturbed, old-growth forests have large accumulations of old and well-decayed CWD (McFee and Stone 1966, Harvey et al. 1981, Little and Ohmann 1988, Means et al. 1992, Keenan et al. 1993), and the nutrient dynamics of these materials may be

TABLE 1. Selected characteristics (0–0.15 m depth) of well-decayed boles (class 4 and 5) and adjacent mineral soil from an old-growth coniferous forest in Oregon.

| Substrate | Bulk density† ($Mg/m^3$) | Total C (g/kg) | Total N (g/kg) | Water content | |
|---|---|---|---|---|---|
| | | | | October 1990 (kg $H_2O$/kg dry mass) | June 1991 (kg $H_2O$/kg dry mass) |
| Bole | 0.112 | 546 | 4.66 | 2.50 | 2.94 |
| | (0.003) | (10) | (0.39) | (0.14) | (0.20) |
| Soil | 0.357 | 86.6 | 3.29 | 0.579 | 0.581 |
| | (0.011) | (8.0) | (0.03) | (0.058) | (0.035) |

*Notes:* The table reports means (one standard error in parentheses). All bole values were significantly different from corresponding soil values ($P < 0.05$; Wilcoxon signed-rank tests); $n = 8$ except for bulk density, where $n = 32$.

† Oven-dry mass of the <4-mm fraction per unit volume.

very different from nutrient dynamics of relatively young CWD (Harmon et al. 1994).

Our current knowledge of nutrient mineralization and immobilization processes in CWD of forests primarily comes from chronosequences of fallen tree bole (hereafter referred to as simply ''bole'') decomposition. For nitrogen (N), the nutrient often limiting productivity (Vitousek and Howarth 1991), these studies have shown contrasting patterns of net N dynamics during bole decomposition. Some bole chronosequence studies have shown net N immobilization fairly consistently throughout the decay process (Grier 1978, Foster and Lang 1982); however, other studies have shown little net N dynamics in boles during the early stages of decay (first 30 to 100 yr), followed by a period of net N release (Lambert et al. 1980, Means et al. 1992) or net N immobilization (Sollins et al. 1987). These indirect measurements of net N flux from boles may be misleading, because errors in estimates of N stores over long periods of time can obscure short-term N dynamics. For example, chronosequence studies frequently fail to consider fragmentation and fungal sporocarp production, both of which may transfer substantial quantities of relatively N-rich organic matter to the forest floor (Harmon et al. 1994).

In many old-growth forests of the U.S. Pacific Northwest (PNW), boles may occupy >20% of the area of the forest floor (Harmon et al. 1986). Well-decayed boles, typically >75 yr old (Sollins et al. 1987, Means et al. 1992), may occupy >5% of the forest floor area. Tree fine roots proliferate within these well-decayed boles (Vogt et al. 1995), suggesting that these boles may be important sites of water or nutrient acquisition. Plant water uptake from well-decayed boles may be significant during the summer dry period in this region, because these boles contain substantial quantities of available water relative to the rest of the soil during this period (Hope and Li 1997). However, in these N-limited forest soils (Velazquez-Martinez et al. 1992), high fine-root density also might indicate that well-decayed boles are an important source of plant-available N.

I conducted in-field incubations to determine the net rates of N mineralization and nitrification in well-decayed boles and compared these rates to adjacent surface mineral soils in an old-growth forest of the PNW. Laboratory estimates of available C and N also were conducted to elucidate the potential factors controlling net N transformations in boles and mineral soil under field conditions. Finally, my results are interpreted in the context of the importance of well-decayed CWD in N cycles of PNW forest ecosystems.

## MATERIALS AND METHODS

### *Study site*

The study was conducted at an elevation between 900 and 950 m within Reference Stand 3, an old-growth forest stand (oldest age class 550 yr) located within the H. J. Andrews Experimental Forest in the central Oregon Cascade mountains (44°14′ N, 122°11′ W). The mixed-age stand has a uniform westerly slope of about 25%, and is dominated in the overstory by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), with scattered western red cedar (*Thuja plicata* Donn ex D. Donn). The climate in this region is characterized by mild, wet winters and warm, dry summers. The stand received 1935 mm of precipitation during the one-year study period (19 October 1990 to 19 October 1991). Mean daily air-temperature during this period was 7.0°C, and mean daily soil temperature (at 0.10-m mineral soil depth) was 6.5°C. Mean daily air and soil temperatures during the ''winter'' incubation period (19 October 1990 to 4 June 1991) were 2.8 and 3.8°C, respectively; mean daily air and soil temperatures during the summer incubation period (4 June to 19 October 1991) were 13.6 and 10.8°C, respectively (see *Field Methods*).

The soil is an unclassified loamy-skeletal, mixed, frigid, Typic Dystrochrept. The stand has a moderately thick (averaging ~10 cm), mor-type forest floor (i.e., O horizon) and a moderately acidic surface (0–15 cm) mineral soil ($pH_{saturated\ paste} = 5.4$). Selected properties of well-decayed boles and mineral soil are shown in Table 1.

### *Field methods*

Eight plots (≈9 $m^2$) were chosen randomly from a group of 20 spread over about a 4-ha area, where a

well-decayed bole (class 4 or 5; Triska and Cromack 1980, Sollins 1982) was present alongside mineral soil. Decay-class 4 and 5 boles are those where the bark is detached or absent, branch stubs (if present) pull out easily, and little if any wood structural integrity remains leading to an elliptical cross-section. The well-decayed boles were present as ill-defined, elongate mounds (>0.50 m in width and 5 m in length) extending from the forest floor into the mineral soil, but all were recognizable from the ground surface (Sollins et al. 1987). This selection process resulted in two plots with class 4 boles and six plots with class 5 boles, which approximates roughly the relative areal abundance of each bole decay-class in this stand (M. E. Harmon, *unpublished data*). All identified boles within the selected plots were Douglas-fir, but three of the six selected class 5 boles could not be identified. The precise sampling location within a plot on each of two sampling dates (19 October 1990 and 4 June 1991) was determined randomly. On each sampling date, the forest floor was carefully peeled back to expose the outer surface of a well-decayed bole or the mineral soil. Two adjacent, intact bole cores and two adjacent, intact soil cores (0–0.15 m) were then removed using thin-walled polyvinyl chloride (PVC) pipe (0.05 m inner diameter × 0.20 m long) that had been sharpened at one end. Only brown-rot wood (Harmon et al. 1986) was found in the boles at this sampling depth. Bole and mineral soil sampling locations were always within 0.5 m of each other within a given plot. For each material (bole or soil), one of the paired cores (the initial core) was placed in a polyethylene bag, kept cool (~4°C), and returned to the laboratory for analysis (within 72 h of sampling). These bole and soil samples were used for laboratory incubations and determinations of initial inorganic N pool sizes, gravimetric water content, and microbial biomass (see *Laboratory incubations and analyses*). The other two cores (one bole and one soil) were used to assess net N mineralization and net nitrification rates under field conditions, using the resin-core method (Di Stefano and Gholz 1986, Binkley and Hart 1989, Hart and Firestone 1989).

Resin cores consisted of intact bole or soil cores capped at both ends by ion exchange resin (IER) bags. The purpose of the top resin bag was to capture incoming ions originating from above the bole or soil core (i.e., forest floor), while allowing water to enter freely. The bottom resin bag collected ions leached from the confined bole or soil core. The IER bags were constructed by placing 30 mL (7.8 g oven-dry equivalent) of cation + anion exchange resin beads (JT Baker [Phillipsburg, New Jersey] #M-614 16-50 mesh mixed-bed IER that had been pre-extracted with 2 mol/L KCl; Hart and Binkley 1984) in nylon stockings that contained a 0.05-m diameter latex rubber tubing ring, and then were tied shut. The resulting bag fit tightly within the PVC pipe. However, to insure against solution losses through boundary flow along the inner PVC wall, silicon glue was used to seal the outside ring to the PVC tube. The resin cores were then returned to their original holes within the plot. After making sure that a solid contact was made between the bottom resin bag and the underlying bole or soil material, the overlying forest floor horizon was carefully replaced over the resin core. Bole and soil cores sampled in October 1990 were incubated until the June 1991 sampling (hereafter called the ''winter incubation''). Cores sampled in June 1991 were incubated until 19 October 1991 (hereafter called the ''summer incubation''). This experimental design resulted in eight replicates per material type (bole or soil) and incubation period (winter and summer).

After the incubation period, resin cores were removed and kept cool until they were returned to the laboratory and processed (within 72 h). Ion exchange resin bags were removed from the resin cores, air dried, and resin beads extracted with 100 mL of 2 mol/L KCl. Quantities of $NH_4^+$ and $NO_3^-$ adsorbed on the IER were adjusted for incomplete recoveries from a single KCl extraction (Hart and Binkley 1984) using extraction efficiencies determined from a separate experiment (80 and 74% extraction efficiencies for $NH_4^+$ and $NO_3^-$, respectively; data not shown). Net N mineralization was calculated by adding the amount of inorganic N accumulated on the IER bags below the bole or soil core to the net change in soil inorganic N pool size measured before and after incubation. Similarly, net nitrification was calculated by adding the quantity of $NO_3^-$ accumulated on the bottom IER bag to the net change in the bole or soil core $NO_3^-$ pool size. Net N transformation rates were converted to a $g/m^2$ basis using the mean bulk density of each initial-incubated bole or soil core pair.

### *Laboratory incubations and analyses*

Bole and soil samples from initial and incubated cores were sieved field-moist through a 4-mm mesh screen. Water contents were not altered from their field values prior to laboratory incubation, because all bole and soil samples had water contents near field capacity (≈−33 kPa water potential) at the time of sampling, and water contents varied little among plots (Table 1). From each initial bole and soil sample on both sampling dates, two subsamples (≈10 or 15 g field-moist mass for bole and soil samples, respectively) were weighed into 20-mL scintillation vials. One was incubated for 30 d at 22 ± 1°C (aerobic incubation subsample); the other subsample was fumigated with ethanol-free chloroform vapor for 24 h and then incubated for 10 d at 22 ± 1°C after removing the chloroform vapor with repeated evacuations (chloroform fumigation-incubation subsample). Two additional subsamples (≈10 or 15 g field-moist mass for bole and soil samples, respectively) were placed in 120-mL specimen containers. To one of these specimen containers, 50 mL of deionized water were added, making sure all the soil

material was completely wetted (waterlogged or ''anaerobic'' incubation). These subsamples were then incubated at 40 ± 1°C for 7 d. After 7 d, the subsamples were extracted with 50 mL of 4 mol/L KCl. The other subsample in the specimen container was immediately extracted with 100 mL of 2 mol/L KCl and served as the initial inorganic N pool size estimate for field and laboratory incubations. Anaerobically mineralizable N was calculated by subtracting the initial $NH_4^+$ pool size from the post-incubation $NH_4^+$ pool size (Binkley and Hart 1989).

Vials containing bole and soil subsamples used for aerobic and chloroform-fumigation incubations were placed within 975-mL Mason jars and sealed with airtight lids fitted with a butyl rubber septum. About 30 mL of deionized water were placed in a 120-mL specimen container within each Mason jar to maintain bole and soil wetness (Hart et al. 1994).

Carbon dioxide concentrations were determined initially and after 10-d periods in the headspace of Mason jars containing the aerobic incubation (incubated for a total of 30 d) and chloroform-fumigation incubation (incubated for 10 d) subsamples by sampling the headspace gas with a 1-mL syringe. The headspace of each Mason jar was mixed repeatedly using a 60-mL syringe prior to taking gas samples. Headspace gas samples were introduced into a Carle AGC Series 100 isothermal gas chromatograph fitted with a thermal conductivity detector (EG&G Chandler Engineering, Broken Arrow, Oklahoma, USA). For the 30-d aerobic incubation subsamples, Mason jars were flushed with ambient air following each $CO_2$ measurement so that the $CO_2$ concentration in the headspace never exceeded 3% by volume (Hart et al. 1994). Cumulative $CO_2$ evolution (microbial respiration) during the 30-d aerobic incubation (October 1990 samples only) was calculated from the summation of increases in headspace $CO_2$ concentrations during each 10-d incubation period.

After both incubations, aerobic and chloroform-fumigation incubation subsamples were extracted with 75 mL of 2 mol/L KCl. Net N mineralization rates were calculated for each subsample by subtracting initial inorganic N pool sizes from inorganic N pool sizes determined after 30 d of aerobic incubation. Net nitrification rates were calculated by subtracting initial $NO_3^-$ pool sizes from postincubation $NO_3^-$ pool sizes (Binkley and Hart 1989).

Microbial biomass C was calculated by dividing the $CO_2$-C evolved from the chloroform-fumigation incubation subsample ($C_F$) by 0.41 (Voroney and Paul, 1984). Microbial biomass N was calculated by dividing the net accumulation of $NH_4^+$-N during the fumigation-incubation ($N_F$) by a value $k_N$, determined using the equation (Paul and Clark 1989):

$$k_N = 0.8 \times (C_F/N_F)^{-0.43}.$$

All KCl-bole, KCl-soil, and KCl-resin suspensions were shaken for 1 h on a mechanical shaker and then filtered through Whatman No. 40 filter paper. The filter papers were preleached with 50 mL of 2 mol/L KCl to remove any $NH_4^+$ and $NO_3^-$ initially present. Ammonium (salicylate/nitroprusside; Keeney and Nelson 1982) and $NO_3^-$ (diazotization following cadmium reduction; Keeney and Nelson 1982) were determined using an Alpkem RFA 300 Rapid Flow Analyzer (Clackamas, Oregon, USA). Bole and soil total C concentrations were determined on the initial samples taken in October 1990 using a LECO 12 C analyzer (LECO Corp., St. Joseph, Missouri, USA). Bole and soil total N concentrations were determined on the same samples by micro-Kjeldahl digestion (Bremner and Mulvaney 1982) followed by $NH_4^+$ analysis. Gravimetric water content (kg $H_2O$/kg dry bole or soil mass) of each sieved sample was determined from a separate subsample of similar mass by oven-drying the subsamples at 105°C for 48 h. All element concentration values are expressed on an oven-dry mass basis.

### *Statistical analyses*

Because some of the variables exhibited nonnormality, I used the Wilcoxon signed-rank test (a nonparametric equivalent of the paired *t* test) to determine significant differences in soil properties and processes for a given sampling date or incubation period between bole and mineral soil samples. All statistical analyses were performed using SigmaStat V. 2 software (Jandel Scientific, San Rafael, California, USA) at the $P = 0.05$ significance level.

## Results

Well-decayed boles had higher total C and N concentrations than adjacent surface mineral soil (Table 1). Even for this relatively C-rich mineral soil, well-decayed boles had a C concentration over six times that of the mineral soil (Table 1). Nitrogen concentrations were also higher in boles than in mineral soil, although these differences were much smaller than was the case for total C. The resulting C:N ratios of the materials were 117 and 26 for bole and mineral soil, respectively. Because of the higher C (i.e., organic matter content) of well-decayed boles compared to mineral soil, boles had a much lower bulk density and a corresponding higher gravimetric water content at the onset of both field incubation periods (Table 1). On a mass basis, well-decayed boles contained 4 to 5 times as much water as mineral soil.

Expressed on a per unit area of material basis (or volume to a depth of 0.15 m), net rates of N mineralization over either incubation period (winter or summer) or over the entire year (sum of the two periods) were similar for well-decayed boles and mineral soil (Fig. 1). For both materials, net N mineralization rates were much higher over the summer compared to the winter (Fig. 1). Net nitrification rates in both materials were low, but annual net nitrification rates were sig-

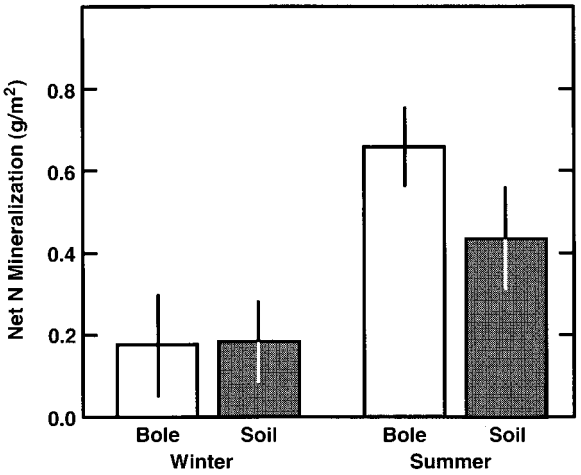


FIG. 1. Mean in-field net N mineralization rates (g N/m² of material) in the upper 0.15 m of well-decayed boles and adjacent mineral soil from an old-growth coniferous forest in Oregon. Net N mineralization rates were determined over two incubation periods (winter = 19 October 1990 to 4 June 1991, and summer = 4 June 1991 to 19 October 1991) using the resin-core method. Annual rate estimates (not shown) are equal to the sum of the two incubation periods. Vertical lines denote ±1 SE of the mean ($n$ = 8). There were no statistically significant differences between net N mineralization rates of boles and mineral soil for either incubation period or for the annual total ($P$ = 0.05 significance level; Wilcoxon signed-rank test).

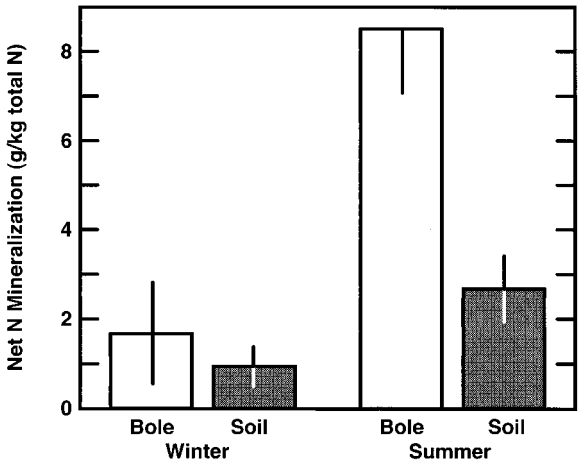


FIG. 2. Mean in-field net N mineralization rates (g/kg total N) in the upper 0.15 m of well-decayed boles and adjacent mineral soil from an old-growth coniferous forest in Oregon. Vertical lines denote ± 1 SE of the mean ($n$ = 8). Net N mineralization rates of boles and mineral soil were statistically similar for the winter incubation period, but bole material had significantly higher net N mineralization rates for the summer incubation period and for the annual total (data not shown).

nificantly higher in mineral soils than in boles (19 and 6 mg $N \cdot m^{-2} \cdot yr^{-1}$, respectively; data not shown).

However, a different pattern emerges from these results when rates are expressed as per mass of total N to assess the quality of the total N as a substrate for net mineralization (see Powers 1990). On a per-unit total N basis, net N mineralization rates were significantly higher in well-decayed boles compared to mineral soil during the summer incubation period (Fig. 2) and over the entire 1-y period (data not shown); winter rates were still similar (Fig. 2). Over the 1-y period, 1.0% of the total N in the well-decayed bole was mineralized on a net basis, compared to only ~0.4% of the mineral soil total N.

Laboratory estimates of available C (i.e., microbial biomass C, microbial respiration, specific respiration rate) and N (i.e., microbial biomass N, anaerobically mineralizable N, aerobic net N transformations) were significantly higher for well-decayed boles compared to adjacent mineral soil when values were expressed

TABLE 2. Mean (and standard error) values of laboratory estimates of C and N availability in well-decayed boles and adjacent mineral soil material sampled on two different dates from an old-growth coniferous forest in Oregon.

| Material | Sampling date | Microbial biomass C (mg C/kg) | Microbial respiration† (mg C/kg) | Specific respiration rate‡ (mg $CO_2$-C·mg MB-$C^{-1} \cdot d^{-1}$) | Microbial biomass N (mg N/kg) | AMN§ (mg N/kg) | Net N mineralization† (mg N/kg) | Net nitrification† (mg N/kg) |
|---|---|---|---|---|---|---|---|---|
| Bole | Oct. 1990 | 3124[b] | 3791[b] | 0.0409[b] | 379[a] | 113[b] | 7.8[b] | 6.5[b] |
| | | (320) | (428) | (0.0027) | (53) | (17) | (0.6) | (0.2) |
| Soil | | 1856[a] | 1231[a] | 0.0231[a] | 249[a] | 65[a] | 3.3[a] | 2.2[a] |
| | | (311) | (181) | (0.0021) | (49) | (16) | (0.4) | (0.1) |
| Bole | June 1991 | 3537[b] | n.d.‖ | n.d. | 395[b] | 102[b] | 3.0[a] | 0.2[a] |
| | | (817) | | | (73) | (13) | (1.2) | (0.2) |
| Soil | | 1633[a] | n.d. | n.d. | 213[a] | 41[a] | 3.3[a] | 0.6[a] |
| | | (776) | | | (89) | (7) | (3.2) | (0.7) |

*Notes:* Values are expressed per unit mass of oven-dry material. For a given sampling date, mean values followed by different superscript letters are significantly different ($P < 0.05$, Wilcoxon signed-ranks test; $n$ = 8).

† Amount produced over a 30-d aerobic laboratory incubation.

‡ Calculated by dividing the microbial respiration rate by the microbial biomass C (MB-C).

§ AMN = anaerobically mineralizable N.

‖ Not determined.

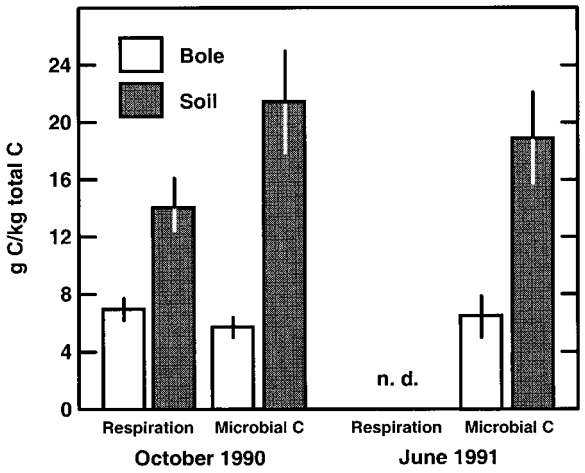


FIG. 3. Mean values of microbial respiration and microbial biomass (g C/kg total C) in the upper 0.15 m of well-decayed boles and adjacent mineral soil from an old-growth coniferous forest in Oregon. Vertical lines denote ± 1 SE ($n$ = 8). Microbial biomass C values were determined for two sampling periods (October 1990 and June 1991), which corresponded to the beginning of the winter and summer field incubations, respectively. Cumulative microbial respiration over a 30-d aerobic laboratory incubation was determined only for samples collected in October 1990. Microbial respiration and microbial biomass C values for mineral soil were significantly higher than bole values. n.d. = not determined.

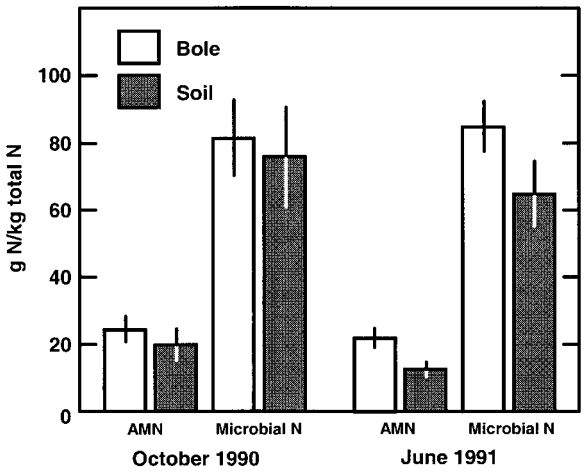


FIG. 4. Mean values of anaerobically mineralizable N (AMN) and microbial biomass N (g N/kg total N) in the upper 0.15 m of well-decayed boles and adjacent mineral soil from an old-growth coniferous forest in Oregon. Vertical lines denote ± 1 SE ($n$ = 8). Boles and mineral soil had statistically similar AMN values in October 1990, but boles had significantly higher AMN values in June 1991. Microbial biomass N values were statistically similar for bole and mineral soil materials on both sampling dates.

on a mass basis (Table 2). Exceptions to this pattern occurred for net N transformation rates during aerobic laboratory incubation in samples collected in June 1991, where there was no significant difference in rates between well-decayed boles and mineral soils (Table 2). Additionally, microbial biomass N was statistically similar in well-decayed boles and mineral soil materials collected in October 1990 (Table 2).

I expressed and analyzed results from laboratory incubations of bole and soil materials on a per unit mass of total C or N basis to explore potential differences in the relative abundances of labile C and N pools in these two materials. In contrast to values expressed on a per kg total mass basis, microbial respiration rates and microbial biomass C per unit mass of total C were significantly higher for mineral soil than for well-decayed bole material in samples collected at the beginning of the winter (October 1990) and summer (June 1991) incubation periods (Fig. 3). Microbial biomass C was only ~0.6% of total C for well-decayed boles, but was ~2.0% for mineral soil.

In contrast to available C indices, anaerobically mineralizable N (AMN) and microbial biomass N per unit mass of total N were statistically similar for well-decayed bole and mineral soil materials (Fig 4). One exception was AMN for material sampled in June 1991, where boles had significantly higher AMN than mineral soil. For each material, microbial biomass C and N as well as AMN values determined in samples collected in October 1990 were similar to June 1991 values (Fig. 3 and 4).

Aerobic laboratory incubations showed significantly higher net rates of N mineralization and nitrification per unit mass of total N in well-decayed bole compared to soil materials for samples collected in October 1990, but these rates were similar for materials collected in June 1991 (Fig. 5). Laboratory-based estimates of net

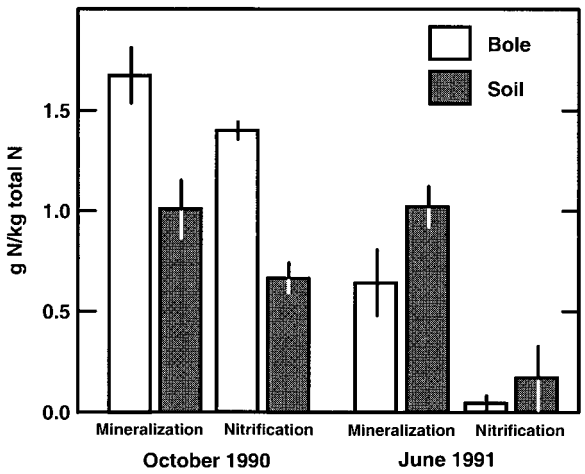


FIG. 5. Mean net N mineralization and net nitrification (g N/kg total N) over a 30-d laboratory incubation of the upper 0.15 m of well-decayed boles and adjacent mineral soil from an old-growth coniferous forest in Oregon. Vertical lines denote ± 1 SE ($n$ = 8). Bole materials had significantly higher net N mineralization and nitrification rates for samples collected in October 1990, but bole and mineral soil rates were statistically similar for material collected in June 1991.

N mineralization rates were higher in bole material collected in October compared to June; however, net N mineralization rates were similar for mineral soil materials collected on both dates (Fig. 5). Net nitrification during aerobic laboratory incubation was a large percentage of net N mineralization in both materials for samples collected in October 1990 (>65%), but comprised a much smaller proportion (<17%) of net N mineralization for materials sampled in June 1991 (Fig. 5).

## Discussion

This is the first study that has directly measured net N transformations in well-decayed boles under field conditions. On a per unit area of material basis, net N mineralization was similar for well-decayed boles and mineral soils despite their contrasting chemical and physical characteristics. Furthermore, this result suggests that boles in the advanced stages of decay act as net sources of plant-available N, as has been suggested indirectly by some bole chronosequence studies conducted in the PNW (e.g., Means et al. 1992), but not others (e.g., Grier 1978, Sollins et al. 1987). Contrasting results from bole chronosequence studies may be due simply to the inherent problems associated with using an indirect method for assessing bole net N dynamics (Harmon et al. 1994), and emphasize the need for a more direct approach, such as that used in this study.

Rates of net N mineralization in well-decayed boles were equal to or higher than rates for mineral soil incubated in the laboratory and field. These results are surprising given that the C:N ratio of well-decayed boles is much greater than that of mineral soil, and suggest that the C:N ratio is a poor predictor of net N release from contrasting forest detrital pools.

Higher rates of net N mineralization relative to total N in boles compared to mineral soil may occur because 1) on average, the organically bound N contained in boles is in a more readily mineralizable form, or 2) the C compounds in well-decayed bole material are less readily metabolized by microbial heterotrophs (i.e., C availability is lower) than those in mineral soil, resulting in a higher ratio of net-to-gross N mineralization because of reduced N demand by a C-limited microflora (Hart et al. 1994). The generally similar amounts of AMN and microbial biomass N per unit mass of total N in boles and mineral soil suggest that both materials contain comparable proportions of labile and recalcitrant forms of organic N, and fail to support the first hypothesis. In support of the second hypothesis is the lower rate of microbial respiration and smaller microbial biomass C relative to the total C pool in boles than in mineral soil. Additionally, bole material exhibited a higher specific respiration rate (respired C per unit microbial biomass C, Table 2; Pirt 1975), suggesting either a lower C-use efficiency by bole microflora or a lower C availability in boles compared to mineral soil (Hart et al. 1994, Zak et al. 1994). It is likely that well-decayed boles have a higher ratio of fungal to bacterial biomass than mineral soil (as suggested by the higher C:N ratio of the microbial biomass, Table 2; Paul and Clark 1989), and pure culture studies suggest that fungi tend to have higher C-use efficiencies than bacteria (Holland and Coleman 1987). Hence, the higher specific respiration rate in bole material also is likely indicative of low C availability.

Relatively low C availability in well-decayed conifer boles also was suggested by Preston et al. (1990) using $^{13}C$ nuclear magnetic spectroscopy (NMR). They found that carbohydrate C in Douglas-fir and western hemlock boles decreased from their initial values of ~60% of the total bole C to only 10% of total bole C during the latter stages of decay. In contrast, the C chemistry of western red cedar boles generally showed little change with increasing stages of decay. Future studies using $^{13}C$ NMR spectroscopy combined with $^{15}N$ isotope dilution techniques (Hart et al. 1994) are needed to determine unequivocally which mechanism accounts for the relatively high rates of net N mineralization relative to total N in well-decayed boles.

In this study, bole and soil samples incubated in the field were isolated from new organic matter inputs (root turnover and litterfall) for relatively long periods of time (~7 and 5 mo for winter and summer incubations, respectively), which may have increased the ratio of net-to-gross N mineralization as the available C supply to microorganisms declined during the incubation (Hart et al. 1994). However, as discussed above, because boles had lower C availability than mineral soil at the onset of both incubation periods, these periods of material isolation likely would have increased the ratio of net-to-gross N mineralization relatively more for mineral soil than for boles. If this analysis is correct, then shorter periods of soil incubation would only have increased the observed rates of bole net N mineralization relative to that of mineral soil.

Field rates of net N mineralization were similar in magnitude to laboratory rates for samples collected in October 1990, but net N mineralization rates differed between the two methods for samples collected in June 1991. Both boles and mineral soil had higher net N mineralization rates in the field during summer than winter, probably due in part to the higher soil temperatures during summer. However, the in-field rate of net N mineralization in bole material increased more dramatically than in mineral soil between the winter and summer incubation periods. In contrast, the laboratory rate of net N mineralization in bole material collected in October 1990 was higher than that measured in samples collected in June 1991, while mineral soil showed no difference. Anaerobically mineralizable N and microbial C and N pools were generally similar for a given material on both sampling dates, suggesting that changes in C and N availabilities alone can not explain these observed differences between field and labora-

tory estimates of net N mineralization. Hence, I hypothesize that the high in-field rate of net N mineralization in bole material incubated during the summer is due to the maintenance of relatively high water contents in this material during this dry season (only a total of 160 mm of precipitation fell during this period, and ~80% of this amount fell during the week preceding the end of the incubation period). The high water holding capacity of bole material (Hope and Li 1997) apparently sustained microbial activity during these warmer months, while warm summer temperatures increased mineral soil net N mineralization to a lesser degree because of substantial loss of moisture and a concomitant reduction in microbial activity during most of this period.

Both well-decayed bole and mineral soil materials showed low annual rates of net nitrification under field conditions. However, previous research using mineral soil from this same forest stand (Hart et al. 1994) and well-decayed bole material from a western hemlock/Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forest on the Oregon coast (S. C. Hart and J. M. Stark, *unpublished data*) has demonstrated that net nitrification rates may not be indicative of gross rates of the nitrification process, because of the capacity of the soil microflora in these materials to assimilate $NO_3^-$.

In contrast to field-incubated materials, net nitrification was a large fraction of net N mineralization for both well-decayed bole and mineral soil material collected in October 1990 and incubated in the laboratory. However, laboratory incubation of samples collected in June 1991 behaved more like samples incubated under field conditions and exhibited little net nitrification. Under laboratory conditions, net nitrification correlated well with net N mineralization ($r = 0.81$, $P < 0.001$ for October 1990 samples and $r = 0.96$, $P < 0.001$ for June 1991 samples), suggesting that $NH_4^+$ availability to nitrifiers was a major factor controlling net nitrification in both substrates (Hart et al. 1994). Low rates of net nitrification in field-incubated materials may be due to the continuous removal of $NH_4^+$ by leaching within the resin cores, preventing the accumulation of ammonium in the material to a level that would promote increases in $NO_3^-$ pools either by increasing gross nitrification, decreasing $NO_3^-$ immobilization, or both. In support of this hypothesis is the result that on average two-thirds of the net N mineralization estimates for both materials were due to $NH_4^+$ accumulated on the bottom IER bag (leached $NH_4^+$; data not shown).

Well-decayed boles in this forest (which is typical of other old-growth Douglas-fir/western hemlock forests in the PNW) cover only a small fraction of the stand area (~5%; M. E. Harmon, *personal communication*). Using two published estimates of the mass of class 4 and 5 boles in similar forest stands within the H. J. Andrews Experimental Forest (Sollins et al. 1987, Means et al, 1992) and assuming that my measured field rates of net N mineralization in the upper 0.15 m of bole is representative of the entire bole mass, I estimate that well-decayed boles contribute ~0.16–0.25 g $N \cdot m^{-2} \cdot y^{-1}$ of plant-available N. Total plant uptake in a nearby old-growth Douglas-fir forest has been estimated at about 4.0 g $N \cdot m^{-2} \cdot yr^{-1}$ (Sollins et al. 1980), suggesting that boles could contribute only ~4–6% of plant N uptake. This N flux is lower than annual net rates of inorganic-N flux from the forest floor to the mineral soil in this stand (0.3 g $N \cdot m^{-2} \cdot yr^{-1}$; S. C. Hart, *unpublished data*), total atmospheric N inputs (0.3–0.4 g $N \cdot m^{-2} \cdot yr^{-1}$; Sollins et al. 1980), and net N mineralization from ground-layer mosses (0.4 g $N \cdot m^{-2} \cdot yr^{-1}$; Binkley and Graham 1981) and from soil humus (0.8 g $N \cdot m^{-2} \cdot yr^{-1}$; Sollins et al. 1980) in similar old-growth stands at the H. J. Andrews Experimental Forest. Although these comparisons suggest that net N release from well-decayed boles is a relatively small ecosystem N-flux, the construct that well-decayed boles are net sources, not net N sinks, of plant-available N should be explicitly included in forest N-cycling models (Comins and McMurtrie 1993).

Bole chronosequence studies conducted in forests of the PNW have generally found similar N contents in boles of decay classes 1 through 3 (Sollins et al. 1987, Means et al. 1992; but see Grier 1978), suggesting that little net N immobilization or mineralization occurs in CWD during the early stages of decay (mean age of <40 yr). The apparent lack of net N dynamics in CWD contrasts with the very dynamic changes in N content that typically occur in fine litter within these ecosystems (Harmon and Chen 1991). However, the failure of these chronosequence studies to account for the process of fragmentation (i.e., decrease in bole volume without a change in density) results in an underestimate of bole decomposition rates, and hence may lead to an underestimate of the net rate of N release from boles (Harmon and Chen 1991). Recent time-series decomposition studies also have shown that boles can be net sources of N during each of the first 7 yr of decomposition, with fungal sporocarp production being the major pathway of N export (Harmon et al. 1994). All of these results suggest that my estimate of net N mineralization in CWD during the latter stages of decay is likely not offset by net N immobilization during the early stages of CWD decomposition in these forests.

This investigation of the role of well-decayed boles in the forest N cycle was conducted in only one forest stand; hence I can not generalize these results to other forests of the PNW. It is imperative that researchers develop a clear understanding of the role of CWD in the sustainability of forests (Graham et al. 1994). Short-rotation forestry and intensive utilization of forest biomass could reduce or eliminate the large, fallen bole ecosystem component (Sollins et al. 1987). Furthermore, recent ecosystem-based approaches to forest management (Christensen et al. 1996) need to utilize scientifically based guidelines for leaving economically valuable wood products in the field. Studies that in-

tegrate process-oriented research with manipulative experiments (i.e., presence and absence of CWD) are needed to identify clearly the role of CWD in forest nutrient cycles and in other ecosystem functions (e.g., as sources of plant water uptake) before defensible guidelines for CWD can be established.


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