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Patterns of log decay in old-growth Douglas-fir forests[1]

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Fallen boles (logs) of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western red cedar (*Thuja plicata* Donn) in old-growth stands of the Cascade Range of western Oregon and Washington were compared with regard to their physical structure, chemistry, and levels of microbial activity. Western hemlock and western red cedar logs disappeared faster than Douglas-fir logs, although decay rate constants based on density change alone were 0.010/year for Douglas-fir, 0.016/year for western hemlock, and 0.009/year for western red cedar. We were unable to locate hemlock or red cedar logs older than 100 years on the ground, but found Douglas-fir logs that had persisted up to nearly 200 years. Wood density decreased to about 0.15 g/cm^3 after 60–80 years on the ground, depending on species, then remained nearly constant. Moisture content of logs increased during the first 80 years on the ground, then remained roughly constant at about 250% (dry-weight basis) in summer and at 350% in winter. After logs had lain on the ground for about 80 years, amounts of N, P, and Mg per unit volume exceeded the amount present initially. Amounts of Ca, K, and Na remained fairly constant throughout the 200-year time span that was studied (100-year time span for Na). N:P ratios converged toward 20, irrespective of tree species or wood tissue type. C:N ratios dropped to about 100 in the most decayed logs; net N was mineralized during anaerobic incubation of most samples with a C:N ratio below 250. The ratio of mineralized N to total N increased with advancing decay. Asymbiotic bacteria in fallen logs fixed about 1 kg N ha^{-1} year^{-1}, a substantial amount relative to system N input from precipitation and dry deposition (2–3 kg ha^{-1} year^{-1}).

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Des troncs gisant sur le sol de douglas (*Pseudotsuga menziesii* (Mirb.) Franco), de pruche occidentale (*Tsuga heterophylla* (Raf.) Sarg.) et de cèdre occidental (*Thuya plicata* Donn) dans des forêts de première venue des monts Cascade dans l'ouest de l'Oregon et de Washington ont été comparés quant à leur structure physique, leur état chimique et aux niveaux d'activité microbienne. Les troncs de la pruche et du cèdre se sont décomposés plus rapidement que ceux du douglas, bien que les taux de décomposition fondés sur les seuls changements de densité étaient de 0,010 par année pour le douglas, de 0,016 par année pour la pruche et de 0,009 par année pour le cèdre. On a été incapable de localiser des troncs de pruche ou de cèdre au sol agés de plus de 100 ans, mais on a trouvé des troncs de douglas ayant persisté durant près de 200 ans. La densité du bois a diminué à environ 0,15 g/cm^3 après une période de 60 à 80 ans sur le sol, suivant l'essence, puis elle est demeurée quasi constante. Le contenu en humidité des troncs a augmenté durant les 80 premières années sur le sol, puis il est demeuré pratiquement constant à environ 250% d'aprés le poids sec) en été et à 350% en hiver. Après que les troncs fussent demeurés sur le sol durant environ 80 ans, la quantité de N, P et Mg par unité de volume a dépassé la quantité initialement présente. La quantité de Ca, K et Na est demeurée plutôt constante durant la période de 200 ans couverte par l'étude (100 ans dans le cas de Na). Les ratios N:P convergaient vers 20, quelles que soient l'essence ou le tissu ligneux. Le ratio C:N a diminué à environ 100 dans les troncs les plus décomposés; N net a été minéralisé pendant l'incubation anaérobique de la plupart des échantillons avec un ratio C:N au dessous de 250. Le ratio de N minéralisé à N total a augmenté à mesure que la décomposition progressait. Les bactéries asymbiotiques dans les troncs gisants ont fixé environ 1 kg ha^{-1} d'azote par année, ce qui représente une quantité substantielle par rapport à la production du cycle de N provenant des précipitations et de la décomposition sèche (2–3 kg ha^{-1} année^{-1}).

[Traduit par la revue]

Introduction

Fallen boles (logs) are an important component of the coniferous forest ecosystem. They can account for as much as half of the organic matter in old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests, excluding that in the soil (Grier and Logan 1977; Harmon *et al.* 1986). Nutrient concentrations, initially low, increase as the wood decays (Cowling and Merrill 1966; Grier 1978; Lambert *et al.* 1980; Graham and Cromack 1982), and logs in advanced states of decay can be important as germination sites and nutrient sources for the forest vegetation (Triska and Cromack 1980; Christy and Mack 1984; Sachs and Sollins 1986). Decaying logs also provide habitat for small mammals, including species that disperse mycorrhizal spores critical for stand reestablishment (Maser *et al.* 1978; Franklin *et al.* 1981). Finally, large logs can strongly influence stream-channel morphology and thus affect sediment dynamics and aquatic biological productivity (Swanson and Lienkaemper 1978).

Current management policy is radically decreasing the abundance of large logs left in the forests of the U.S. Pacific Northwest. Predicting the consequences of this policy requires more extensive information about the decay processes large logs undergo to produce nutrients available for uptake by trees. We therefore measured changes in physical structure, chemistry, and microbial activity during log decay. Our study extended previous studies by contrasting decay patterns in three species dominant in old-growth Douglas-fir stands: Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western red cedar (*Thuja plicata* Donn). Our study included more detailed measurements of microbial activity and nitrogen availability than did previous studies. Finally, we extended the time span of previous studies by including logs that had been on the ground more than 200 years.

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TABLE 1. Characteristics of study sites, number of logs sampled, and sampling dates

Location	No. of boles sampled	Date sampled	Elevation (m)	Aspect	Stand age (years)	Mean annual temp. (°C)	Mean annual precip. (mm)	Range and township
H. J. Andrews Experimental Forest, Oregon								
Lookout Creek	12[a]	June–Sept. 1980	460	SE	450–550	8.5	2300	Rge.5E, tp.15S, sec. 28
High 15	84	Feb., Aug. 1981	840	S	450–550	8	2150	Rge.5E, tp.15S, sec. 15
Squaw Creek, Oregon	17	July 1981	1160	N	750	—[b]	—	Rge.5E, tp.14S, sec. 17
Carbon River valley, Mount Rainier National Park, Washington								Rge.8E, tp.17N
River Terrace	6	Sept. 1981	610	Level	550	7.6	1760	Unsurveyed
Green Lake Trail	4	Sept. 1981	790	NE	>1000	7.3[c]	—	Unsurveyed
Ipsut Creek	10	Sept. 1981	980	NW	>1000	6.8[c]	—	Unsurveyed
Cararact Creek	4	Sept. 1981	1070	N	>1000	6.6[c]	—	Unsurveyed

[a]Three to five cross sections per log.
[b]No data.
[c]Assuming lapse rate of 2.25°C/1000 m (Greene and Klopsch 1985).

Methods and materials

Study sites

Our seven sites were on the west slope of the Cascade Range in Oregon and Washington; six of these were near the transition between the western hemlock and silver fir vegetation zones (Franklin and Dyrness 1973) (Table 1). All sites were mesic to moist, with soils (Inceptisols) derived from volcanic parent materials. The three Oregon sites supported old-growth Douglas-fir stands 450–750 years old that had become established after fire. The Washington sites, all in the Carbon River Valley at Mount Rainier National Park, were wetter and colder than the Oregon sites. The Mount Rainier river terrace supported a vigorous stand of Douglas-firs averaging 550 years of age (S. Greene and M. Hemstrom, pesonal communication). At the other Mount Rainier sites, we found Douglas-fir bark fragments, scattered live Douglas-firs, and massive western hemlocks with stilt root systems >2.5 m in diameter. Therefore, we inferred that Douglas-firs were once dominant but had died since the last fire over 1000 years ago (cf. Hemstrom and Franklin 1982).

Log decay classification system

Logs were classified according to the following five-class system developed by R. Fogel, M. Ogawa, and J. Trappe (unpublished report) and used widely in the Pacific Northwest (Triska and Cromack 1980; Graham and Cromack 1982; Sollins 1982): class I, logs freshly fallen, bark and all wood sound, current-year twigs attached; class II, sapwood decayed but present, bark and heartwood mainly sound, twigs absent; class III, logs still support own weight, sapwood decayed but some still present, bark sloughs, heartwood decayed but still structurally sound; class IV, logs do not support own weight, sapwood and bark mainly absent, heartwood not structurally sound, branch stubs can be removed; class V, heartwood mainly fragmented, forming ill-defined, elongate mounds on the forest floor sometimes invisible from surface.

Log selection

Logs were selected systematically at High 15 (our intensive study site at the H. J. Andrews Experimental Forest) and at Squaw Creek (Table 1). At High 15, two parallel lines (total length of 1195 m) were laid out about 100 m apart along a relatively level bench. The lines crossed 346 logs that were >15 cm diameter at the point of intersection. For each log, we recorded species, decay class, length (to a 15-cm minimum diameter), and diameter at each end. Only Douglas-fir, western hemlock and western red cedar logs were included, but these species accounted for >99% of the fallen logs.

Logs in decay classes I–IV were grouped by species and class. Most class V logs lacked bark and identifiable wood structure; indistinguishable as to species, they were combined into a single group. Next, 84 logs were selected systematically for intensive study so that the proportion in each species and decay-class group was the same as along the lines. At least four logs were included in each group, except for western red cedar in classes I and III because fewer than four examples were intersected.

In Squaw Creek, four lines were laid out in a diamond pattern in order to randomize log orientation with respect to the slope. Every fourth log was sampled intensively, a total of 17 out of the 66 logs that intersected one of the lines. Because most class V logs at Squaw Creek were much older than those at High 15, data for these logs were kept separate in all analyses.

At the Mount Rainier sites, logs were selected subjectively in an attempt to sample the oldest recognizable logs. The most ancient examples, completely invisible from the surface, were located by trenching. Only class V logs were sampled. As at Squaw Creek, data on these logs were kept separate for analysis.

Work at Lookout Creek, included here in order to increase sample size, preceded the sampling at the other sites. Logs were selected subjectively to include western hemlock and Douglas-fir in all five decay classes. Several cross sections were cut from each log at Lookout Creek, but each cross section was treated as a separate log in some of the analyses in order to combine the Lookout Creek data with those from the other sites.

In all, diameters showed a wide range typical of fallen logs in mid-elevation stands (Table 2). Diameters of class I to IV Douglas-fir logs ranged from 40 to more than 70 cm at the sampling point. Diameters for the other species and decay classes averaged 20–40 cm except for the single class I red cedar, which was quite large. Average length decreased with advancing decay, perhaps because other logs had fallen on them and scattered them.

Log age

How long a log had lain on the ground (referred to here as age) was determined in two ways. Some logs had scarred nearby trees when they fell; rings were counted in cores taken from the sides of such scars. Other logs had trees (nurselings) established on them whose age could be determined from ring counts. At High 15 and Lookout Creek, the age of 11 fallen logs could be determined from both scars and nurselings. The scar ages averaged 18.7 years (SE = 3.0) older than the nurseling ages, reflecting the time required before seedlings can

TABLE 2. Physical characteristics of decaying logs at sites on the west slope of the Cascade Range in Oregon and Washington

Species and decay class	Age (years)	Diameter (cm) Base	Diameter (cm) Top	Length (m)	Density (g/cm^3)	Volume (m^3)
Western hemlock						
I	4	52	15	34	0.348	3.9
	(0.4;5)	(4.2;4)	(0;4)	(3.8;5)	(0.025;8)	(1.1;4)
II	9	26	21	15	0.300	1.3
	(4.4;3)	(5.4;6)	(6.0;6)	(4.3;7)	(0.019;9)	(1.0;6)
III	25	25	16	14	0.224	0.5
	(8.5;7)	(1.5;13)	(0.7;13)	(2.1;14)	(0.011;16	(0.1;13)
IV	81	24	20	14	0.172	1.0
	(0.3;3)	(4.9;6)	(3.3;6)	(7.1;6)	(0.031;6)	(0.6;6)
Western red cedar						
I	5	102	15	43	0.318	18.0
	(—;1)	(—;1)	(—;1)	(—;1)	(—;1)	(—;1)
II	17	37	15	19	0.259	1.8
	(3.5;2)	(9.5;4)	(0.3;4)	(4.4;4)	(0.39;4)	(1.2;4)
III	30	42	24	16	0.248	2.1
	(13.0;2)	(6.4;7)	(5.8;7)	(4.2;7)	(0.030;7	(0.8;7)
IV	85	35	25	11	0.154	0.9
	(6.0;2)	(5.2;3)	(5.5;3)	(1.7;3)	(0.003;3)	(0.2;3)
Douglas-fir						
I	3	97	34	41	0.386	25.3
	(1.4;5)	(29.7;4)	(15.6;4)	(11.0;5)	(0.013;7)	(15.3;4)
II	11	73	31	38	0.343	8.9
	(4.6;6)	(15.6;4)	(7.6;4)	(7.9;7)	(0.018;16)	(4.3;4)
III	50	73	38	32	0.247	10.5
	(3.9;10)	(9.2;10)	(6.8;10)	(5.8;12)	(0.018;19)	(3.2;10)
IV	87	42	29	27	0.151	3.3
	(5.8;11)	(4.3;13)	(3.6;13)	(3.3;14)	(0.007;20)	(0.7;13)
Unidentified						
H.J. Andrews, V	122	34	34	8	0.146	1.0
	(11.7;9)	(3.1;8)	(3.1;8)	(2.4;8)	(0.11;13)	(0.4;8)
Squaw Creek, V	143	19	18	12	0.138	0.4
	(29.5;4)	(1.5;10)	(1.6;10)	(3.2;12)	(0.007;12)	(0.2;10)
Mount Rainier sites, V	192	—	—	—	0.145	—
	(6.5;4)				(0.012;24)	

NOTE: Each value is the mean with SE and sample size in parentheses.

establish. Therefore, 19 years was added to those ages that were based on nurseling ages. Some fallen logs could not be dated from scars or nurselings. Of these, some lay directly beneath or atop a log whose age was known; if both logs were in the same decay state, they were assumed to be the same age. In all, ages were established for 66 of 84 logs at High 15, 4 of 17 at Squaw Creek, and 4 of 24 at Mount Rainier.

Log sampling

Logs located along transect lines were sampled 1 m to the left or to the right of the point of intersection. A cross section, 8–10 cm thick, was cut with a chain saw. Punky logs tended to fragment readily; we secured an 8 cm wide canvas band around them before they were cut and then held a plywood board up against the cross section and tipped it onto the board. Boles at High 15 were resampled in summer, after approximately 6 months, at a point 0.5 m beyond the first cut.

Each cross section was categorized by tissue type: outer bark, inner bark, sapwood, and heartwood. The sapwood and heartwood were further classified into internal decay types wherever the wood differed in appearance. Each cross section was photographed, and its position in the tree was recorded along with the presence or absence of insect galleries, roots, and fungal rhizomorphs. Temperature was recorded for each tissue and internal decay type.

Four replicate volumetric samples were taken from each internal decay type within the sapwood and heartwood with a steel corer (2.6 or 5.1 cm in diameter) driven by an extra-large screw clamp mounted on a plywood platform. The outer and inner bark, which comprised one internal decay type each, were cut into roughly rectangular pieces with a hatchet or knife. Samples were stored in plastic bags in a cooler. Sample 1 was used for measurement of fresh weight, dimensions, and respiration; sample 2 for acetylene reduction, dry weight, and nutrient analyses; sample 3 for microarthropod extraction (results not included here); and sample 4 was a reserve.

Laboratory methods

Density of each sample was determined from dry weight and either its measured dimensions or, for punky material, from the volume of the corer. Moisture content was based on oven-drying at 70°C.

Material for total element analysis was ground to pass a 0.5-mm sieve. N was determined by Kjeldahl digestion of 0.5-g subsamples followed by ammonium analysis (Technicon method 334-74A/A).[3]

[3]Mention of trade names or commercial products does not constitute endorsement by Oregon State University.

Three *ad hoc* standards, prepared from class II, III, and V Douglas-fir heartwood from the High 15 site, were submitted to 10 researchers in the United States, Canada, and Great Britain for N analysis. Results from eight of these researchers agreed very closely with ours, but two researchers reported N values 1.5 to 2.0 times ours. We are encouraged by the close agreement and have no explanation for the discrepancies.

A second subsample (1 g) was digested in a nitric – perchloric acid mixture and analyzed for P by an automated molybdate blue colorimetric procedure and for cations by atomic absorption. Douglas-fir heartwood samples were analyzed for total C by dry combustion with a Leco Automatic Carbon Analyzer. Because total C varied by at most 7% among decay classes (see Results), we assumed that admixture of mineral soil was negligible and did not adjust nutrient concentrations for ash content.

Material for analysis of available N was kept field moist and coarsely ground. We assayed for extractable ammonium (2 M KCl, 24 h of shaking) before and after 7 days of anaerobic incubation at 40°C (Waring and Bremner 1964). Ammonium was measured with an HNU Systems electrode calibrated hourly against ammonium chloride standards and cross-checked against the autoanalyzer. About 10% of the samples were analyzed for nitrate (Cd reduction method on an autoanalyzer), but only trace amounts were ever detected. Net N mineralized was calculated, therefore, as ammonium extractable after incubation less the amount extractable before incubation.

To measure acetylene reduction (nitrogenase activity), we sealed wood cores in a glass jar with ~10% acetylene atmosphere and incubated them in the dark for 6–12 h. After incubation, a gas sample was withdrawn and analyzed for ethylene with a Hewlett–Packard model 5830A gas chromatograph fitted with a flame-ionization detector and a 2-m, 80–100 mesh Poropak R column at 70°C. N_2 (40 mL/min) served as carrier gas and acetylene as an internal standard (McNabb and Geist 1979). Endogenous ethylene production and background ethylene levels were checked routinely and subtracted from measured ethylene production values. Cores were oven-dried after incubation. Amount of acetylene reduced was then converted to amount of nitrogen fixed (per unit dry weight) by multiplying by 3.52, the ratio determined by ^{15}N labeling of logs at Lookout Creek (Silvester *et al.* 1982). Samples collected at different sites (and from High 15 on different weeks) were incubated at different temperatures. Results were adjusted to the mean winter and summer temperatures for the Andrews Experimental Forest, which were obtained from the meteorological station near the Lookout Creek site, assuming a Q_{10} relation between paired values for internal decay types that had been measured in both winter and summer. The Q_{10} values showed little pattern with species, decay class, or tissue type, so we averaged all values (mean = 1.8, SE = 0.1, n = 80).

To measure respiration, we placed wood cores in jars and incubated them overnight at the mean temperature of the logs measured in the field. The next day, jars were sealed and gas samples were removed immediately (time 1) and after 3–4 h (time 2). Each wood core was then oven-dried at 70°C. Accumulation of CO_2 between time 1 and time 2 was measured with the gas chromatograph (with thermal conductivity detector) and expressed as micrograms CO_2 per gram dry weight per hour. A temperature adjustment was made as described above for respiration based on a Q_{10} of 2.2 (SE = 0.1, n = 150).

Calculations

Data for individual internal decay types were combined in stages. First, the area of each internal decay type within each cross section was determined by projecting the photograph of the section on a grid. A mean was then calculated for each tissue type, weighting values for each internal decay type according to its area. Second, a mean was calculated for each cross section, weighting values for each tissue type according to its area. Finally, data for cross sections were summarized by species and decay class.

Biomass and nutrient content per hectare of logs at High 15 were calculated with line–intercept statistics (Pickford and Hazard 1978). The 84 logs that were sampled for nutrient content and microbial activity were considered to be a subset of the 346 logs encountered along the transect lines (De Vries 1974). It should be noted that our lines at High 15 were not randomly oriented, which could have biased our results.

Results and discussion

Age, structural features, and density

The individual fallen logs studied ranged in age from less than 1 to over 200 years old. All identifiable class V logs were Douglas-fir. Identifiable class V western hemlocks and western red cedars were not encountered. Western hemlock progressed through the decay stages faster than the other two species and reached class III and IV status about 30 years sooner, on average (Table 2).

Data on proportion of logs suspended above ground indicate the change in overall structural integrity with advancing decay (Fig. 1A). For example, nearly all western red cedar logs in class II were suspended, compared with 20% of the Douglas-firs and 45% of the western hemlocks. All class IV logs were prostrate, in keeping with the definition of that class. Incidence of insect galleries increased steadily with decay (Fig. 1B). Colonization by roots was delayed until class IV for Douglas-fir and western hemlock, whereas western red cedar logs showed a steadier increase in root colonization (Fig. 1C). Incidence of fungal rhizomorphs peaked in classes II–IV for Douglas-fir and western hemlock (Fig. 1D); rhizomorphs were absent from western red cedar logs.

Density, initially higher for Douglas-fir than for the other two species, decreased steadily up to class IV (Fig. 2A), after which it averaged 0.15 g/cm^3, irrespective of species or log age. Sapwood began to decay almost immediately irrespective of species (Fig. 2B) and reached a density of 0.10 g/cm^3 by class III, after which the sapwood sloughed off and was not sampled. Heartwood yielded patterns similar to those for entire logs.

Decay rate constants (k values), obtained by fitting a negative exponential curve to the density data, were 0.010/year (± 0.001) for Douglas-fir, 0.016/year (± 0.003) for western hemlock, and 0.009/year (± 0.001) for western red cedar. (Data from the Squaw Creek and Mount Rainier sites were excluded because graphs of N concentration versus density (see below) suggested that density change was not a good indicator of decomposition in these oldest logs). In previous studies of conifers in which rate constants were calculated from change in density alone, reported values were similar to ours (see Harmon *et al.* 1986). Several studies that took into account fragmentation, as well as change in density, yielded rate constants very near 0.03/year (Lambert *et al.* 1980; Graham 1982; Sollins 1982), although conditions varied greatly at the sites.

Even the oldest class V logs were still clearly distinguishable from mineral soil. We noted that the oldest class V logs tended to be the smallest in diameter, so perhaps the outer portion of the wood fragments and frass gradually disperse into the mineral soil. Root throw and slope movement must eventually break up the class V material, but in the absence of those processes, class V logs may persist far longer than 200 years. Equally mysterious is how class V logs become entrenched into the mineral soil. At the Ipsut Creek site (Mount Rainier), for example, we discovered one log buried beneath an old class V log that was itself well entrenched into the mineral soil. Gradual entrenchment was common everywhere we looked in the Pacific Northwest, even on what appeared to be level stable benches without obvious volcanic ash deposits.

Moisture content, respiration, and N fixation

Moisture content increased with advancing decay until class

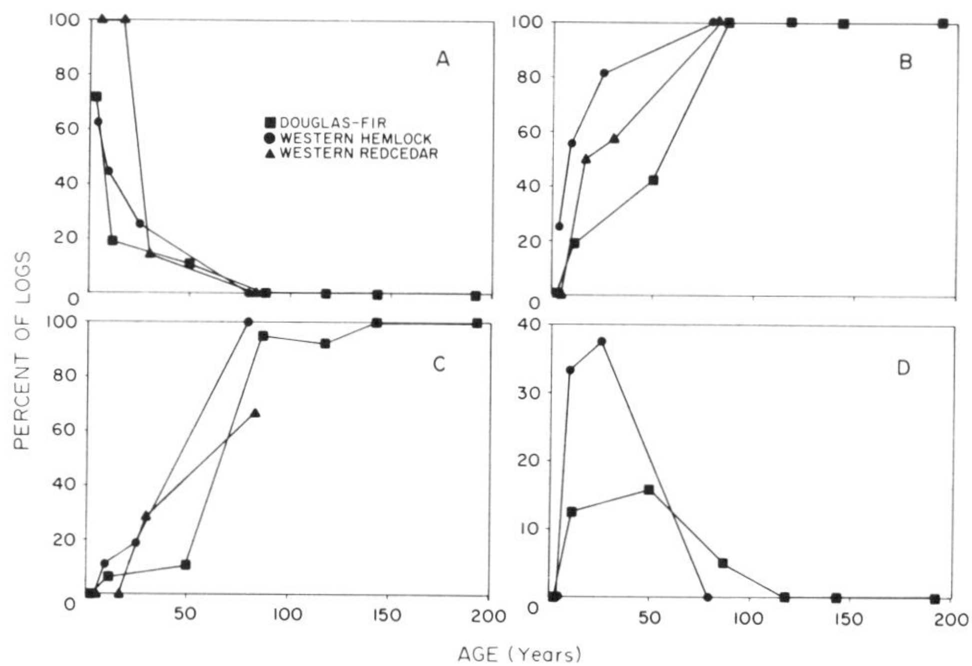

FIG. 1. Percentage of logs with various structural configurations and features: (A) suspension above the ground; (B) presence of insect galleries; (C) invasion by roots; and (D) colonization by fungal rhizomorphs. Means for decay classes I–IV are shown by points arranged from left to right along the line for each species. Means for class V logs from High 15 and for logs from Squaw Creek and Mount Rainier are the last three points on the line for Douglas-fir.

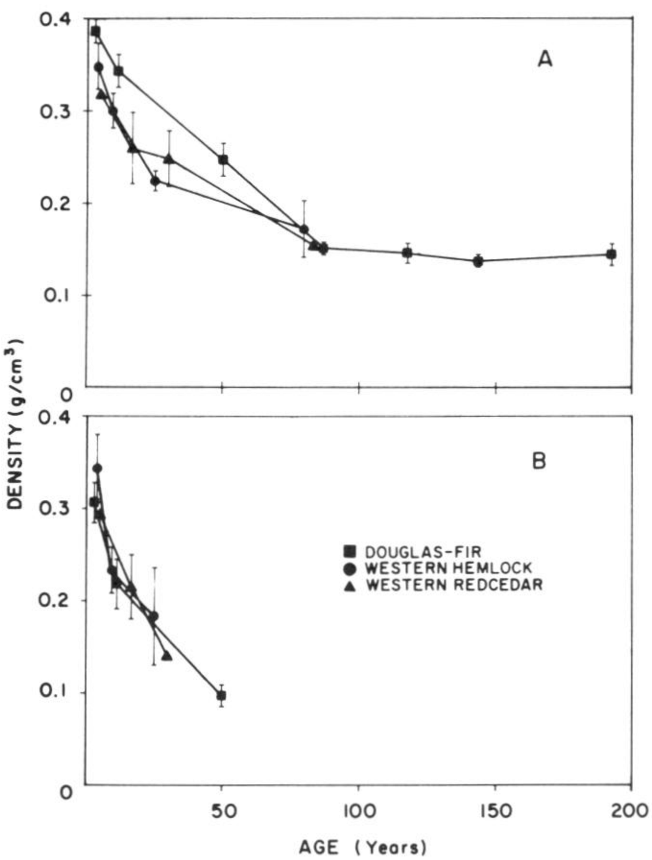

FIG. 2. Change in density during decay for (A) entire log and (B) sapwood. Decay classes are arranged from left to right along the line for each species (see Fig. 1).

IV, and then remained fairly constant at about 250% in summer and at 350% in winter (Table 3). There were no clear differences among the three species; western red cedar tended to be drier than the other two species, but few differences were significant. Sapwood was consistently wetter than heartwood, except for class III logs whose heartwood and sapwood were equally moist in the summer (~160%). Sapwood from class II and III western red cedar logs dried markedly during the summer, averaging 75 and 20% moisture, respectively, perhaps because western red cedar has so much thinner sapwood than western hemlock or Douglas-fir.

Respiration rates were high even in class I logs, which had been on the ground an average of only 3–5 years, and in logs with moisture content in excess of 300% (Table 3). Various authors have claimed that excessive moisture content inhibits fungal growth (e.g. Kaarik 1974). Our respiration data, however, showed little pattern with moisture content, species, or decay class (Table 3). Respiration may have failed to correlate with moisture content because moisture content is not the biologically appropriate variable. Because pore volume increases markedly with advancing decay, percent saturation of the pore space might be a more biologically meaningful variable, although not readily measurable. The respiration values may have been overestimates; extrapolating them to an entire year yielded k values (grams C respired per gram C per year) averaging about 1.5 times those calculated from density change. Perhaps removing and handling the cores increased aeration and stimulated respiration. In addition, adjusting rates to mean air temperature rather than mean log temperature would have increased summer rates more than it would have decreased winter rates. The respiration rates should, however, provide valid comparison among species within the same decay class.

TABLE 3. Moisture content, respiration rate, and acetylene reduction rate of decaying logs at sites on the west slope of the Cascade Range in Oregon and Washington

Species and decay class	Moisture content (%)		Respiration ($\mu g\ CO_2\ g^{-1}\ h^{-1}$)		Acetylene reduction ($nmol\ g^{-1}\ h^{-1}$)	
	Winter	Summer	Winter	Summer	Winter	Summer
Western hemlock						
I	90	101	2.4	14.5	0.136	0.142
	(11)	(11)	(0.7)	(5.0)	(0.034)	(0.041)
II	111	94	12.3	22.9	0.037	0.122
	(20)	(28)	(3.5)	(8.4)	(0.014)	(0.053)
III	166	162	13.4	24.4	0.060	0.178
	(29)	(32)	(3.0)	(6.1)	(0.021)	(0.057)
IV	335	220	6.0	9.3	0.106	0.098
	(43)	(53)	(1.9)	(1.7)	(0.036)	(0.053)
Western red cedar						
I	99	98	2.5	12.3	0.164	0.158
	—	—	—	—	—	—
II	70	36	4.8	3.8	0.088	0.124
	(12)	(12)	(1.5)	(3.2)	(0.064)	(0.122)
III	166	108	9.0	26.1	0.069	0.150
	(55)	(38)	(2.1)	(8.1)	(0.022)	(0.069)
IV	347	275	10.9	63.6	0.122	0.351
	(8)	(41)	(2.8)	(29.1)	(0.025)	(0.151)
Douglas-fir						
I	65	54	4.5	8.8	0.061	0.029
	(6)	(7)	(1.0)	(2.0)	(0.022)	(0.012)
II	95	96	5.3	24.7	0.071	0.168
	(12)	(10)	(2.1)	(6.6)	(0.035)	(0.057)
III	156	156	7.1	15.2	0.059	0.081
	(34)	(22)	(1.7)	(4.4)	(0.019)	(0.020)
IV	356	277	4.6	12.5	0.133	0.177
	(28)	(18)	(0.6)	(2.3)	(0.017)	(0.043)
Unidentified						
H.J. Andrews, V	360	241	9.4	12.7	0.110	0.253
	(44)	(45)	(2.3)	(2.7)	(0.015)	(0.174)
Squaw Creek, V	ND	255	4.8	19.6	ND	0.278
	ND	(30)	(0.9)	(5.9)	ND	(0.137)
Mount Rainier sites, V	ND	266	13.4	17.2	ND	0.030
	ND	(22)	(3.5)	(1.8)	ND	(0.013)

NOTE: Each value is the mean with the SE in parentheses. Respiration and acetylene reduction rates are expressed on a dry weight basis. ND, no data (sites were sampled only in summer).

Acetylene-reduction rates averaged 0.03–0.35 nmol $g^{-1}\ h^{-1}$ (Table 3), which were within the range of 0–0.7 nmol $g^{-1}\ h^{-1}$ measured previously at the Lookout Creek site (Silvester *et al.* 1982). N fixers were more active in summer than in winter; apparently, any differences in moisture content were offset by increased temperature in the summer. There was no clear effect of species or decay class on N fixation. As with respiration, the temperature correction probably inflated the rates.

Nutrient and carbon contents

Weighted mean nutrient concentrations for entire logs are shown in Table 4. During early decay stages, western hemlock was richer than Douglas-fir in P, K, Mn, and Mg but about equal to Douglas-fir in N, Ca, and Na. The extremely old logs from the Squaw Creek and Mount Rainier sites yielded the highest concentrations of N, P, and, especially, Na, but patterns for other elements were variable. Mn, not measured in previous studies of log decay, was present in large amounts in logs of all three species studied. Mn is also abundant in Douglas-fir foliage

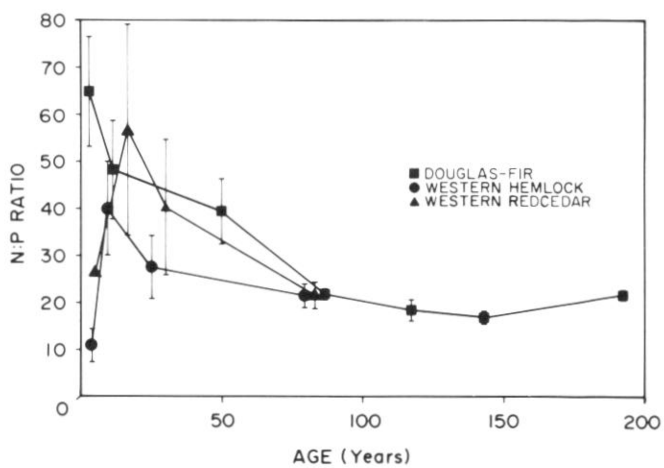

FIG. 3. Change in N:P ratio during decay of heartwood (means ± SE). Decay classes are arranged from left to right along the line for each species.

TABLE 4. Nutrient concentrations in decaying logs at sites on the west slope of the Cascade Range in Oregon and Washington

Species and decay class	% N	% Ca	Nutrients (μg/g dry wt.) P	K	Mg	Mn	Na	Ex. N	Min. N
Western hemlock									
I	0.08	0.14	92.8	760	146.0	250.3	18.0	<0.04	<0.04
	(0.01)	(0.03)	(17.0)	(181)	(11.2)	(19.2)	(5.0)	(<0.01)	(<0.01)
II	0.11	0.13	59.0	203	86.2	115.5	22.2	0.46	0.77
	(0.02)	(0.03)	(18.4)	(68)	(13.5)	(51.3)	(3.6)	(0.46)	(0.77)
III	0.12	0.17	87.7	355	201.5	291.9	41.7	4.21	3.02
	(0.01)	(0.02)	(12.7)	(70)	(22.0)	(37.4)	(5.2)	(1.86)	(1.73)
IV	0.25	0.21	135.2	208	213.3	62.2	44.5	5.26	9.44
	(0.07)	(0.06	(46.8)	(49)	(27.1)	(21.2)	(5.3)	(2.29)	(5.76)
Western red cedar									
I	0.11	0.16	48.0	279	93.0	31.0	31.0	<0.04	<0.04
	—	—	—	—	—	—	—	—	—
II	0.14	0.17	51.3	313	147.3	24.5	24.5	0.63	1.68
	(0.02)	(0.04)	(14.1)	(71)	(58.6)	(7.7)	(4.9)	(0.63)	(1.03)
III	0.17	0.16	78.4	178	134.1	50.3	31.4	6.61	13.70
	(0.04)	(0.02)	(28.9)	(27)	(21.0)	(22.9)	(4.3)	(3.45)	(10.01)
IV	0.21	0.31	107.3	283	231.7	80.3	42.0	24.67	14.33
	(0.04)	(0.08)	(35.1)	(48)	(64.8)	(24.0)	(6.9)	(8.37)	(2.60)
Douglas-fir									
I	0.09	0.14	40.3	155	70.5	55.0	24.5	<0.04	<0.04
	(0.01)	(0.02)	(1.8)	(12)	(9.7)	(7.2)	(2.5)	(<0.01)	(<0.01)
II	0.10	0.12	39.3	148	82.3	61.5	29.5	1.68	0.32
	(0.01)	(0.02)	(4.6)	(21)	(18.7)	(19.6)	(6.4)	(0.76)	(0.32)
III	0.10	0.11	41.3	141	123.3	158.2	38.7	3.44	3.18
	(0.01)	(0.02)	(7.8)	(28)	(27.4)	(59.5)	(4.3)	(1.28)	(0.94)
IV	0.24	0.17	110.8	171	252.2	52.2	49.7	17.30	24.03
	(0.02)	(0.02)	(10.3)	(15)	(28.4)	(17.0)	(5.0)	(4.59)	(11.99)
Unidentified									
H.J. Andrews, V	0.32	0.42	212.2	337	483.2	87.3	56.2	25.31	41.93
	(0.04)	(0.15)	(31.3)	(67)	(140.2)	(31.2)	(7.6)	(7.22)	(9.55)
Squaw Creek, V	0.47	0.30	311.4	332	1101.5	64.3	257.2	4.78	97.6
	(0.07)	(0.05)	(53.7)	(53)	(611.7)	(18.3)	(30.1)	(0.88)	(13.9)
Mt. Rainier sites, V	0.55	0.19	279.3	262	384.2	17.0	266.0	13.37	154.0
	(0.05)	(0.03)	(30.8)	(51)	(31.0)	(4.3)	(21.8)	(3.47)	(13.9)

NOTE: Each value is the mean with the SE in parentheses. Ex. N, exchangeable N; Min. N, mineralizable N.

and in twigs and cones from various conifers (Gessel and Turner 1976; Edmonds 1987), but we are unaware of a metabolic role for Mn that would explain its presence in such high concentrations. C concentration, measured only for Douglas-fir heartwood from High 15, changed little with decay state, rising from 49% in class I to 56% in class IV. C concentration in class V logs was only a little lower (50%), a surprising finding, because we had expected to find evidence of admixture of mineral soil.

The N:P ratio showed very different trends for Douglas-fir and western hemlock (Fig. 3). The ratio for class I Douglas-fir was 65, dropping to ~20 with advancing decay. Class I western hemlock began at only 11, because of its very high P content but also converged towards 20 by class III. Western red cedar behaved more like western hemlock than like Douglas-fir. Variability decreased markedly with advancing decay for all three species. Convergence towards an N:P ratio of 20 is common during log decay (cf. Lambert *et al.* 1980; Foster and Lang 1982; Fahey 1983).

Nutrient concentrations in sapwood and heartwood followed trends for entire logs. Bark behaved differently; concentrations of all elements measured except Na and K were initially much higher in bark than in heartwood. Concentrations stayed fairly constant in bark through time, however, so that by classes IV and V, Douglas-fir bark and heartwood had similar nutrient concentration. With yet more time (i.e., at the Squaw Creek and Mount Rainier sites), N and P concentrations in heartwood rose above those in bark. This switch was not noted in previous studies (e.g., Lambert *et al.* 1980; Foster and Lang 1982), perhaps because Douglas-fir tissues remain identifiable far longer than those of other species studied to date.

To see how nutrient content per unit volume changed with decay, we multiplied nutrient concentrations by bulk density, then divided by the amount in class I in order to normalize to 100% (Fig. 4). This calculation accounted for decrease in density, although not for fragmentation. Amounts of N, Mg, Na, and Mn stayed roughly constant initially, whereas amounts of P, K, and Ca decreased. After class III, the elements N, P, and Mg accumulated, whereas Na, Ca, and K all remained fairly constant despite mass loss. Na was conserved relative to K, perhaps because it is a macronutrient for the numerous arthropods that inhabit decaying logs (e.g., Schowalter and Crossley 1983), a pattern noted also by Lambert *et al.* (1980) and Foster and Lang (1982). Fahey (1983) reported generally similar patterns for decaying *Pinus contorta* logs, except that Mg did not accumulate. Results from other studies were generally inconsistent with ours (e.g., Grier 1978; Lambert *et*

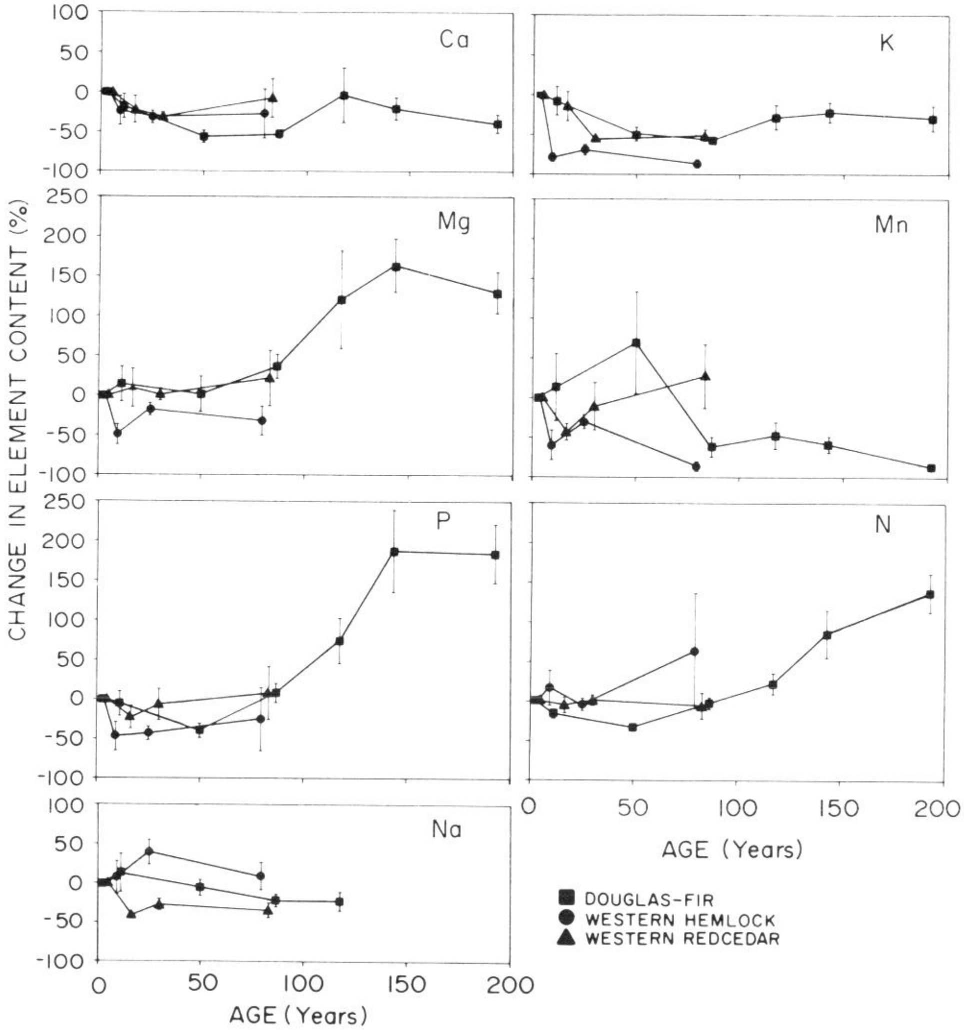

FIG. 4. Change in nutrient amount remaining during decay; the *Y*-axis shows the percent of original amount remaining relative to amount in decay class I.

al. 1980; Foster and Lang 1982; Graham and Cromack 1982; Yavitt and Fahey 1982; Edmonds 1987). Apparently, species-specific differences in wood chemistry plus edaphic factors interact to control element dynamics in ways that we have yet to understand.

Change in N content through time can be viewed indirectly by plotting density versus N. Curves for all species (and for most tissue types) sloped linearly downward (Fig. 5) but then leveled off abruptly after class IV, indicating that N is imported into logs by various processes such as hyphal translocation, N fixation, insect colonization, and throughfall interception, while density remains constant (Melillo *et al.* 1984). Because fragmentation does not alter the density of the remaining material, density is not a good measure of percent of original material remaining. Were the percent remaining plotted, the trajectory might continue downward to the right.

The amount of inorganic N in decaying logs is a rough measure of the N available for uptake by plants. KCl-extractable ammonium increased at first with advancing decay, then leveled or perhaps decreased (Fig. 6). Values were high, especially given that total N concentrations were generally $<0.3\%$. Interestingly, inorganic N was below our detection limit in all samples that contained fungal rhizomorphs, suggesting that the fungi effectively scavenge all the available N. Net anaerobically mineralized N (N_m), a crude index of potentially available N,

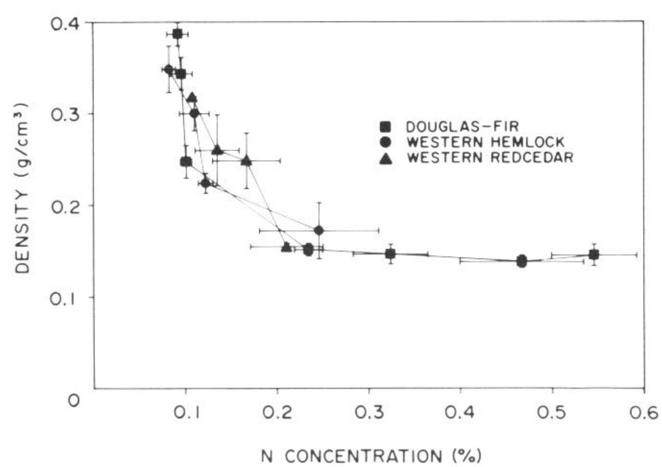

FIG. 5. Relationship between density and N concentration during decay.

increased with advancing decay irrespective of species (Fig. 7A), although Squaw Creek values were low. N_m increased markedly as the C:N ratio dropped below 250 (Fig. 7B). Various studies have shown a strong inverse correlation between this critical C:N ratio and the decomposition rate constant (*k* value) (Berg and Staff 1981; Edmonds 1987). One

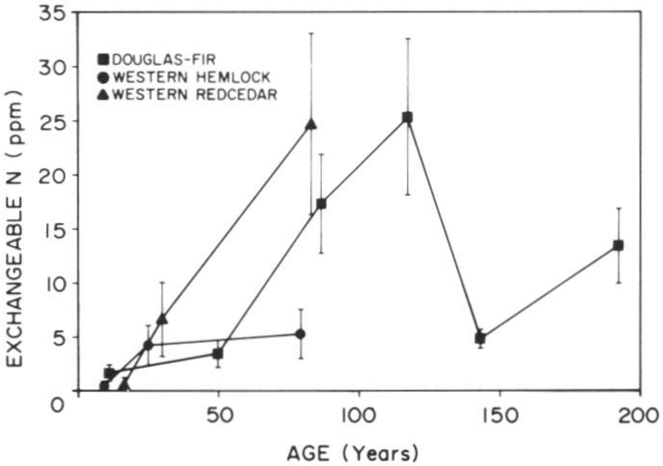

FIG. 6. Change in extractable N during decay.

explanation for the strong correlation is that microbial C assimilation efficiency decreases with decreasing *k* value (Bosatta and Agren 1985), which then requires that more C be metabolized per unit N assimilated. A simpler explanation is that the more N-poor substrates contain much carbonaceous material that is relatively inert, thus inflating C values without affecting N dynamics.

The ratio of anaerobically mineralized N to total N (N_m:N_t) increased with advancing decay, especially for heartwood (Fig. 7C). Possibly, accessibility to microflora increased as the material became increasingly fragmented. Alternatively, because N_m correlates strongly with microbial biomass (Myrold 1987), the pattern may indicate that microbial biomass increases with advancing decay.

Biomass, nutrient content, N fixation, and N availability per hectare

Total biomass at High 15 was 143 Mg/ha, at the high end of values reported for the west slope of the Cascade Range (80–140 Mg/ha in Harmon *et al.* 1986, Table 11). Our values for nutrient stores in old-growth Douglas-fir (Table 5) are more accurate than those we have reported previously (Harmon *et al.* 1986) because the present values for High 15 are based entirely on measurements made on site. Our earlier conclusion, however, that logs account for a relatively small proportion of total nutrient stores in an old-growth stand, remains unchanged.

Net N_m, on an areal basis, was mainly in class IV and V Douglas-fir logs and class III red cedars (Table 5), which together accounted for 82% of the total (0.8 kg/ha). We measured N_m in the litter layer for comparison at all of our study sites except Lookout Creek and Green Lake Trail. N_m was 785 ppm (SE = 52, n = 5) at Squaw Creek and 456 ppm (SE = 30, n = 15) across the three Mount Rainier sites that we sampled. Litter from High 15 yielded a much lower value in summer (mean = 188 ppm, SE = 41, n =5) than in fall after the onset of the rainy season (mean = 671 ppm, SE = 75, n = 5). On average, then, litter provided much more N_m per unit dry weight than did decaying logs.

If, for example, we assume litter biomass of 50 Mg/ha as typical of old-growth Douglas-fir stands (Grier and Logan 1977), N_m in litter at High 15 would be 25 kg/ha in summer and 90 kg/ha in the wet season, but it would be only 0.8 kg/ha in logs. N_m in mineral soil at a similar site about 1 km from High 15 averaged 160 kg/ha (Sollins *et al.* 1984 and unpublished data). Thus, at High 15 both litter and logs provide much less N_m than mineral soil. Soils on these portions of the Andrews

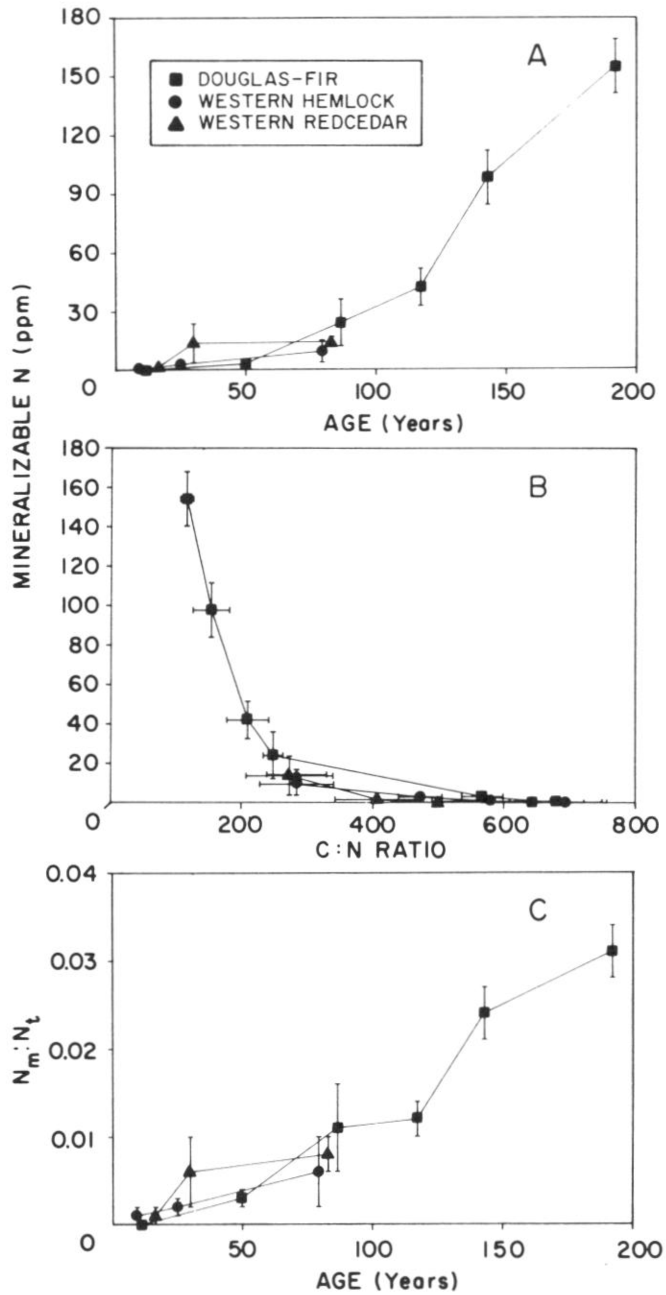

FIG. 7. Change in net anaerobically mineralized N (N_m) during decay: (A) on a dry-weight basis, (B) in relation to C:N ratio (Douglas-fir only), and (C) as proportion of total N (N_t).

Experimental Forest are mainly Andic Haplumbrepts with a moderate amount of soil organic matter and a somewhat poorly developed litter layer. The relative importance of logs, litter, and mineral soil as N sources will be different elsewhere.

Our data permit a more accurate calculation of annual N fixation per hectare than has been possible previously (Table 5). Because rates depend on temperature, we extrapolated from both winter and summer values (see Methods). Class II, III, and IV Douglas-firs accounted for the bulk (60%) of the winter total; in summer, class V Douglas-fir and class III western red cedar also contributed substantially. The overall total was about 1 kg ha^{-1} year^{-1}, very close to what Silvester *et al.* (1982) calculated from a more limited sampling.

N fixation of 1 kg ha^{-1} year^{-1} is small relative to the uptake requirement of about 40 kg ha^{-1} year^{-1} for an old-growth Douglas-fir stand (Sollins *et al.* 1980). Relative to known inputs

TABLE 5. Nutrient stores and N fixation rate per hectare of decaying logs at High 15, H. J. Andrews Experimental Forest, Oregon

Species and decay class	Biomass (Mg/ha)	No. of boles measured	Nutrients (kg/ha) N	P	K	Ca	Mg	Mn	Na	Ex. N	Min. N	N fixation (kg ha^{-1}year^{-1}) Winter	Summer
Western hemlock													
I	2.7	6	2.4	0.27	2.14	4.4	0.40	0.70	0.04	<0.01	<0.01	0.022	0.023
	(1.2)		(1.1)	(0.13)	(1.07)	(2.3)	(0.18)	(0.31)	(0.02)	(<0.01)	(<0.01)		
II	7.6	37	8.9	0.52	2.64	8.7	0.56	0.54	0.16	<0.01	<0.01	0.022	0.73
	(3.6)		(4.1)	(0.30)	(1.97)	(3.4)	(0.25)	(0.18)	(0.08)	(<0.01)	(<0.01)		
III	7.9	63	9.7	0.83	3.50	12.9	1.61	2.50	0.34	0.03	0.02	0.034	0.100
	(1.6)		(1.9)	(0.28)	(1.24)	(2.9)	(0.38)	(0.65)	(0.09)	(0.02)	(<0.01)		
IV	2.0	21	5.1	0.27	0.40	4.1	0.42	0.10	0.08	<0.01	0.02	0.015	0.014
	(0.7)		(2.1)	(0.12)	(0.15)	(1.7)	(0.14)	(0.04)	(0.03)	(<0.01)	(<0.01)		
Western red cedar													
I	1.4	1	1.4	0.07	0.40	2.4	0.13	0.05	0.04	<0.01	<0.01		
II	2.8	10	3.0	0.14	0.71	3.6	0.23	0.04	0.06	<0.01	<0.01	0.014	0.019
	(1.6)		(1.5)	(0.08)	(0.34)	(1.6)	(0.08)	(0.02)	(0.03)	(<0.01)	(<0.01)		
III	11.9	39	16.0	0.67	1.81	16.8	1.42	0.49	0.33	0.06	0.16	0.073	0.158
	(3.2)		(4.3)	(0.26)	(0.44)	(4.1)	(0.38)	(0.28)	(0.08)	(0.04)	(0.12)		
IV	0.6	5	1.2	0.05	0.16	1.7	0.12	0.04	0.02	0.01	<0.01	0.005	0.016
	(0.3)		(0.5)	(0.02)	(0.08)	(0.8)	(0.06)	(0.02)	(0.01)	(<0.01)	(<0.01)		
Douglas-fir													
I	11.1	8	14.3	0.43	1.61	17.2	0.63	0.60	0.30	<0.01	<0.01	0.065	0.031
	(6.6)		(8.9)	(0.25)	(0.96)	(10.9)	(0.37)	(0.37)	(0.18)	(<0.01)	(<0.01)		
II	26.2	14	27.1	0.94	3.41	35.6	1.82	1.22	0.81	<0.01	0.01	0.110	0.259
	(12.7)		(14.0)	(0.42)	(1.64)	(18.5)	(0.81)	(0.48)	(0.45)	(<0.01)	(0.01)		
III	22.7	38	25.4	0.91	2.66	28.6	2.52	3.33	0.81	0.11	0.10	0.141	0.193
	(6.1)		(7.0)	(0.29)	(0.72)	(10.6)	(0.78)	(1.96)	(0.22)	(0.06)	(0.05)		
IV	25.0	75	51.7	2.46	4.43	37.1	5.61	1.15	1.27	0.45	0.44	0.198	0.263
	(5.5)		(8.4)	(0.38)	(1.09)	(6.6)	(1.14)	(0.41)	(0.37)	(0.18)	(0.18)		
V	4.4	29	14.9	0.86	1.38	14.3	1.73	0.33	0.25	0.15	0.16	0.045	0.103
	(1.2)		(4.0)	(0.23)	(0.41)	(4.7)	(0.48)	(0.12)	(0.08)	(0.06)	(0.05)		
All species	143	346	199	9.1	30.7	218	18.0	12.5	4.93	0.79	0.83	0.87	1.22
	(25)		(30)	(1.1)	(4.9)	(38)	(2.1)	(2.5)	(0.84)	(0.19)	(0.20)	(0.01)	(0.03)

NOTE: Each value is the mean with the SE in parentheses. Ex. N, exchangeable N; Min. N, mineralizable N.

to the system, however, it may be significant. Wet and dry fall together add 2–3 kg N ha^{-1} year^{-1} at the Andrews Experimental Forest (Sollins *et al.* 1980); fixation in the litter layer adds at most 1 kg ha^{-1} year^{-1}, probably much less (Heath 1985). In old-growth stands, cyanophycophilous lichens fix N at rates approaching 10 kg ha^{-1} year^{-1} (Sollins *et al.* 1980), but these lichens are absent during the first 100–150 years of stand development. Where red alder (*Alnus rubra* Bong. Carr.) and *Ceanothus* spp. occur, N input often exceeds 30 kg ha^{-1} year^{-1}, but red alder does not reach the elevation of High 15 and *Ceanothus* occupies mainly the south-facing exposures. Thus, at sites such as High 15, N fixation in logs could represent a significant long-term source of N for the system.

Accurate prediction of long-term trends in forest productivity depends on understanding how components of the forest ecosystem function together. The large fallen log is an ecosystem component that could be eliminated by short-rotation forestry and by intensive utilization of forest biomass. We are beginning to understand the importance of logs in stand establishment, but work remains before we can predict long-term stand growth in the absence of large fallen logs.

Acknowledgments

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