Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, U.S.A.

JOSEPH E. MEANS[1]

Pacific Northwest Research Station, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, OR 97331, U.S.A.

PAUL C. MACMILLAN

Biology Department, Hanover College, Hanover, IN 47243, U.S.A.

AND

KERMIT CROMACK, JR.

Forest Science Department, Oregon State University, Corvallis, OR 97331, U.S.A.

Received September 27, 1991

Accepted April 3, 1992

MEANS, J.E., MACMILLAN, P.C., and CROMACK, K., JR. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, U.S.A. Can. J. For. Res. **22**: 1536–1546.

Logs, forest floor, and mineral soil were sampled and measured, and snags were measured, in a 450-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand on the H.J. Andrews Experimental Forest, Oregon. Logs, some still identifiable after 300 years on the forest floor, contained large amounts of organic matter (222 Mg/ha), C (100 Mg/ha), water (559 – 10 700 L/log), N (183 kg/ha), and Ca (141 kg/ha), and smaller amounts of P (5.5 kg/ha), K (22 kg/ha), Mg (14 kg/ha), and Na (3.7 kg/ha). Logs and snags covered about 17% of the forest floor and had an all-sided area index of 0.69 m^2/m^2. Through mineralization, C, N, and K were lost through time; Ca and Mg increased; and P and Na increased then decreased, showing no net change. Also through mineralization, cellulose and hot acid detergent soluble fraction decreased more rapidly than lignin. Lignin was apparently not lost until the later stages of decay, when N was also lost in significant amounts. This parallels the shift from initial dominance by white rots that degraded cellulose and lignin to later dominance by brown rots that preferentially degraded cellulose. Lignin and cellulose were eventually lost at more similar rates in later decay stages. This may have been due in part to a close association between the remaining cellulose and lignin in later decay stages. Lignin was a better predictor of the onset of N release than was the C:N ratio.

MEANS, J.E., MACMILLAN, P.C., et CROMACK, K., JR. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, U.S.A. Can. J. For. Res. **22** : 1536–1546.

Les billes, la litière et le sol minéral furent échantillonnées et mesurés, de même que les chicots furent mesurés, dans un peuplement de Douglas taxifolié (*Pseudotsuga menziesii* (Mirb.) Franco) âgé de 450 ans dans la forêt expérimentale H.J. Andrews, en Orégon. Les billes, dont quelques unes pouvaient encore être identifiées après 300 ans sur le parterre forestier, contenaient beaucoup de matière organique (222 Mg/ha), de C (100 Mg/ha), d'eau (559 – 10 700 L par bille), de N (183 kg/ha) et de Ca (141 kg/ha) ainsi que des quantités plus faibles de P (5,5 kg/ha), de K (22 kg/ha), de Mg (14 kg/ha) et de Na (3.7 kg/ha). Les billes et les chicots couvraient environ 17% du parterre forestier et avaient un indice de surface, incluant tous les côtés, de 0,69 m^2/m^2. Suite à la minéralisation, C, N et K sont perdus avec le temps, Ca et Mg augmentent, et P et Na augmentent puis diminuent sans qu'il n'y ait de changement net. Toujours à cause de la minéralisation, la cellulose et la fraction soluble dans un détergent acide chaud diminuent plus rapidement que la lignine. La lignine est apparemment détruite seulement vers la fin du processus de décomposition lorsque des quantités importantes de N sont perdues. Ceci survient parallèlement à la dominance initiale des champignons de carie blanche qui dégradent la cellulose et la lignine qui est plus tard remplacée par la dominance des champignons de carie brune qui dégradent de préférence la cellulose. La lignine et la cellulose disparaissent éventuellement à une vitesse à peu près identique vers la fin du processus de décomposition. Ceci peut en partie être dû à une association plus étroite entre la cellulose et la lignine restantes vers la fin du processus de décomposition. La lignine prédit mieux le début de la libération de N que le ratio C:N.

[Traduit par la rédaction]

Introduction

Logs and snags are important structures in forests of the Pacific Northwest (Franklin and Waring 1980). They provide habitats for birds, small mammals, cold-blooded vertebrates and invertebrates (Maser and Trappe 1984; Bartels *et al.* 1985; Neitro *et al.* 1985), and plants, including trees (Christy and Mack 1984; McKee *et al.* 1982; Harmon and Franklin 1989). Logs store nutrients and water (Sollins *et al.* 1987) and, as they decay, provide materials for humus formation (McFee and Stone 1966). Nutrient cycling, through mineralization of coarse woody debris, is an important forest ecosystem function in the Pacific Northwest (Franklin and Waring 1980; Grier 1978). Logs are also important components of nutrient cycles in eastern hardwood (Lang and Forman 1978; MacMillan 1988) and coniferous forests (Lambert *et al.* 1980). Nitrogen fixation occurs in logs in eastern deciduous forests (Cornaby and Waide 1973), Rocky Mountain coniferous forests (Larsen *et al.* 1978), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of the Pacific Northwest (Silvester *et al.* 1982; Sollins *et al.* 1987). In some Pacific Northwest forests deadwood also stores large amounts of carbon (Spies 1988; Harmon *et al.* 1986) and so is an important component of the global carbon cycle (Harmon *et al.* 1990).

This paper describes the physical and chemical characteristics of Douglas-fir logs that have been on the ground from 1 to 313 years. We estimate the organic matter of snags, forest floor, and mineral soil. We provide information not found in previous studies: measurements of lignin and cellulose in

[1]Author to whom all correspondence should be addressed.

Printed in Canada / Imprimé au Canada

1285

logs, information on all major detrital pools, and chemistry of logs up to three centuries old. We examine evidence for the control of mineralization rate and N loss by lignin.

Study site

This study was conducted in a 450-year-old (based on ring counts of stumps) Douglas-fir dominated stand, about 5 ha in size, on the H.J. Andrews Experimental Forest, Oregon, United States. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Pacific silver fir (*Abies amabilis* Douglas Forbes) share dominance of the understory at the 1040 m elevation site (see Means *et al.* 1985, for further site description). Most of our data came from the 2.325-ha western portion of the stand just before it was clear-cut in August 1976 for another study. After cutting, additional data were collected from the adjacent uncut eastern portion of the stand.

Methods

Decay classes

We assigned each log to one of five decay classes, using visual criteria (Triska and Cromack 1980; Sollins 1982) that we hypothesized would be correlated with changes in physical and chemical properties (Means *et al.* 1985). These criteria were generally applicable to all logs in our stand (all the trees were conifers), although they were originally designed for Douglas-fir. Snags were assigned a decay class of 1 through 4, using most of the criteria used for logs.

Measuring and dating snags and logs

In June 1976, the western part of the stand was mapped using a 25 × 25 m grid system with string every 5 m to increase mapping accuracy. Each snag over 5 cm DBH was mapped, and the species (when identifiable) and DBH were recorded. We estimated the height of each snag to the nearest meter for those less than 10 m tall, and to the nearest 5 m for those taller. Each log of classes 1 through 4 was mapped, and its decay class and species were recorded. Decay class 5 logs whose residence times could be determined (see below) were also mapped and identified to species.

Ages were determined for all scars caused by logs falling against live trees in the western part of the stand. All scars were apparently caused by falling logs, since in all cases logs were found next to the scar. The residence time of logs on the forest floor was determined by either (*i*) dating a scar caused by the log striking a nearby tree or (*ii*) determining the age of western hemlocks growing on the log and adding 25 years to the greatest hemlock age to account for the time between log fall and hemlock establishment. Only hemlock ages greater than 110 years were used, to minimize the effect of variation in hemlock establishment time. Residence time does not include the time a stem decays while standing, which can be quite variable (Cline *et al.* 1980). To reduce the variation in decomposition time from this source, we gave each log a decay-class age equal to the mean residence time for its decay class. Thus, two estimates of decomposition time were available for each log: residence time and decay-class age.

In four 25 × 25 m intensive study plots all logs were measured, including class 5 logs located by trenching the forest floor. Three plots in the western part of the stand were selected to span the observed range of woody debris loadings. A fourth plot was randomly placed in the eastern portion of the stand. End diameters (horizontal and vertical when different), length, and decay classes were recorded for all logs. Diameters and lengths were recorded for portions of logs in these plots.

Soil sampling

Two 1-m^2 forest floor samples were collected in each of the three intensive plots in the western portion of the stand. After chemical analyses, the values for samples within each intensive plot were pooled, then means and standard errors were calculated for the stand.

In April 1978, 19 months after clear-cutting, we sampled the mineral soil for bulk density and chemical analyses in four systematically spaced pits in the western part. The pits were placed in areas where the forest floor was apparently not physically disturbed. Samples for bulk density were extracted from each horizon by driving a 7.62 × 7.62 cm cylinder into the soil, avoiding large coarse rock fragments. The volume of large coarse fragments was estimated by eye to an accuracy of about ±10%. Samples were air dried and sieved to remove coarse fragments larger than 2 mm. Bulk densities were corrected for coarse fragments before standing crops of nutrients were calculated.

Log sampling and density estimation

In July and October 1976 we collected 91 samples from 40 Douglas-fir logs in the stand (Means *et al.* 1985). Our goal was to sample all kinds of decaying Douglas-fir wood. All datable logs (boles or bole sections over 10 cm in diameter) were sampled, except some recently fallen logs because datable logs of this age were relatively common. Lengths, end diameters, and center diameters of long logs were recorded for volume estimation. The following techniques were chosen to sample all types of fallen decaying Douglas-fir wood. If the log contained sections of different decay classes, a sample was taken from each section. If end diameters differed by 25% or more, samples were taken near each end; otherwise, samples were taken near the center of the log. Different types of rot (brown rot, white rot), as well as solid wood, were collected from the heartwood and sapwood (when distinguishable).

The moisture content of each sample was estimated as wet weight minus dry weight (70°C) (Means *et al.* 1985 describe methods more completely). After drying to a constant mass, each sample was dunked in water, and sample volume was estimated as volume of water displaced plus volume of water absorbed. When fragile samples were broken, dry weight and volume were determined on intact subsamples that were possibly denser than the original total sample. Water probably flowed rapidly in and out of the large voids in some highly decayed samples, resulting in underestimates of volume and overestimates of density.

In January 1978 we collected 72 additional samples from 30 logs in the eastern portion of the stand, selecting sample sites on logs using the same criteria as before. These logs were also measured for volume determination. Heartwood, sapwood, and the different types of rot were sampled separately. Samples were handled very carefully to minimize breakage. Wet volumes were determined by measuring samples in the field or by water displacement of samples enclosed in plastic bags that were drawn tightly around each sample by a vacuum. Dry volumes were also determined by displacement of similarly enclosed samples, and water content was determined.

Data from these 72 samples were used to correct the densities of the first 91 samples for shrinkage upon drying and for overestimation of density caused (as described above) by the use of intact, denser subsamples and by the occurrence of voids in the very old samples. (See Means *et al.* 1985 for a detailed description of these corrections.) Densities were also corrected for ash content, as determined during wood chemistry analysis.

Decay class 5 logs were oval in cross section and usually had several characteristics from which we made inferences about their decay processes. Because class 5 logs were found set in troughs in the mineral soil, which gave some support to their sides, we inferred that fragmentation of material off the sides was less common than for decay class 4. Circular rings were usually visible, indicating that plastic deformation had been minimal. The top was usually covered with forest floor material draped continuously in a blanket form over the sides and onto the mineral soil. This indicated that fragmentation of pieces off the top was minimal. Rings were truncated at the top, indicating (in combination with the previous point) that wood volume was lost by mineralization (which we are attempting to measure with density loss), and this occurred at the wood – forest floor interface. Since we could not sample rings that had decayed completely, our estimates of field density did not reflect total loss due to mineralization. Spatial variation of decay processes within logs promises to be an interesting area for future work.

TABLE 1. Decay-class age (mean residence time) and physical characteristics of Douglas-fir logs by decay class

Decay class	Decay-class age (years)[a]	No. of logs measured	Length (m)	Diameters (cm)[b]		Surface area (m^2)	Volume (m^3)	Biomass (Mg)
				Large end	Small end			
1	7 (2,16)	13	40 (7)	103 (9)	39 (7)	94 (17)	24.0 (5)	10.1 (2.0)
2	17 (3,16)	16	42 (4)	113 (6)	39 (5)	102 (9)	26.0 (3)	8.3 (1.1)
3	33 (5,28)	30	21 (2)	74 (5)	45 (4)	42 (5)	7.8 (1.3)	2.1 (0.4)
4	82 (9,19)	25	16 (2)	57 (4)	37 (3)	23 (4)	3.4 (1.0)	0.76 (0.21)
5	219 (18,15)	16	7 (1)	50 (4)	40 (5)	11 (2)	1.2 (0.3)	0.22 (0.05)

NOTE: Standard errors are in parentheses.
[a] Standard error is followed by sample size in parentheses.
[b] The means of horizontal and vertical diameters were used when log ends were not circular.

TABLE 2. Wood density and concentrations of the acid-detergent-soluble fraction (ADSF), lignin, cellulose, and ash in Douglas-fir logs and in the forest floor

Substrate and decay class	Wood density (mg/cm^3)[a]	Carbon constituent analysis				
		No. of samples	ADSF (mg/g)[b]	Cellulose (mg/g)[b]	Lignin (mg/g)[b]	Ash (mg/g)
Douglas-fir logs						
1	416 (18,22)	10	270 (15)	383 (28)	341 (38)	7 (2)
2	317 (20,29)	14	254 (16)	332 (16)	410 (28)	4 (1)
3	274 (14,22)	35	217 (9)	329 (19)	448 (21)	6 (1)
4	224 (23,11)	13	169 (16)	269 (43)	558 (53)	4 (3)
5	187 (16,12)	19	165 (19)	159 (23)	672 (35)	4 (1)
Forest floor		3	421 (20)	157 (4)	422 (16)	147 (4)

NOTE: Standard errors are in parentheses.
[a] Standard error is followed by sample size in parentheses. The densities of decay classes 3, 4, and 5 are based on the second group of 72 samples.
[b] ADSF, cellulose, and lignin are presented on an ash-free basis.

To account for this loss of volume, we multiplied the average density of decay class 5 wood by 0.431 (SE 0.018, variance 0.013 054), the average height:width ratio from 40 other class 5 logs (Means *et al.* 1985). The only use of this corrected density was to calculate volumetric concentrations of nutrients and carbon constituents, to examine gains and losses with advancing decay. It was not used to calculate standing crops. Variances for volumetric concentrations that were corrected for volume loss in this way were calculated as the variance of a product (Mood *et al.* 1974, p. 180).

Chemical analyses

Only the 91 log samples collected in 1976 were analyzed chemically. Carbon constituents were determined following the methods of Van Soest (1963) and Goering and Van Soest (1970). These methods distinguish an acid-detergent-soluble fraction (ADSF), cellulose, lignin, and ash (by muffle furnace ashing of the ash–lignin complex). ADSF includes labile carbon constituents, such as hemicellulose and protein (Van Soest 1966), as well as more refractory constituents, such as uncomplexed phenols. Carbon was determined by dry combustion using a LECO model 12 carbon analyzer (Nelson and Sommers 1982).

Nitrogen, P, and cations (K, Ca, Mg, Na) were determined using standard methods by the Central Chemical Laboratory, USDA Forest Service, Corvallis, Oregon. Nitrogen was determined by the micro-Kjeldahl method (Jackson 1958). After perchloric acid digestion, P was determined by molybdate reduction (Olson and Sommers 1982), and cations were determined by atomic absorption spectrophotometry. Lanthanum oxide was added for Ca and Mg determinations to minimize interference.

Water content, carbon constituents, and elements in logs were expressed on a dry weight basis (mg/g) and after having been multiplied by wood density, on a volumetric basis (mg/cm^3).

Ovendry (70°C) weight and ash-free weight (500°C) were recorded for forest floor samples, then nutrients (C, N, P, K, Ca, Mg, Na) and carbon constituents were determined as for logs. Forest floor nutrient concentrations and organic matter were calculated on an ash-free basis.

Soil N and C were determined as for logs, and soil organic matter was determined by the Walkley–Black method (Nelson and Sommers 1982). Available P was determined by extraction with dilute acid fluoride (the Bray method), followed by analysis using a molybdate–vanadate reagent (Olson and Sommers 1982). Cations (K, Ca, Mg, Na) were determined by atomic absorption spectrophotometry after extraction with 1 M KCl. Total soil P was determined from the same micro-Kjeldahl digest as for soil N, followed by P determination on a Technicon Autoanalyzer.

Estimation of standing crops

Volume, projected area, and total surface area were calculated for all sampled logs and those on the intensive study plots. Volume and total surface area were calculated for class 1 through 4 logs as the frustum of a cone and for class 5 logs as the frustum of a cone with an ellipsoidal cross section. Biomass of each measured log and partial log was calculated as volume times density for that decay class.

Densities for western hemlock were taken from Graham (1981). Densities for other species were calculated, for each decay class, as the density of Douglas-fir in that decay class (this study) multiplied by the ratio of the density of sound wood (United States Forest Products Laboratory 1974) of the other species to sound wood of Douglas-fir.

Log biomass by decay class was estimated by two different methods. The first was the line intercept method, originally developed for inventorying forest fuels (Van Wagner 1968). Species, diameter, and decay class were recorded for each log encountered on twenty-five

TABLE 3. Water in wood samples taken from decaying Douglas-fir logs at different times of the year, and water content of logs

Decay class	July 1976 (% of dry wt.)	October 1976 (% of dry wt.)	January 1978 (% of dry wt.)	All dates combined		Water content per log (L)
				% of dry wt.	mg/cm^3	
1	75 (4,2)	168 (53,8)	85 (9,12)	114 (21,22)	440 (60,22)	10 681 (13)
2	216 (108,2)	165 (40,12)	178 (50,15)	175 (31,29)	450 (40,29)	11 904 (16)
3	201 (33,11)	178 (25,24)	267 (25,22)	217 (16,57)	540 (30,57)	4 240 (30)
4	234 (43,10)	156 (83,3)	269 (35,11)	241 (26,24)	500 (50,24)	1 711 (16)
5	264 (25,9)	155 (41,7)	325 (22,12)	263 (20,28)	470 (30,28)	559 (16)

NOTE: Standard error is followed by sample size in parentheses; sample size (number of logs) only is given for water content per log.

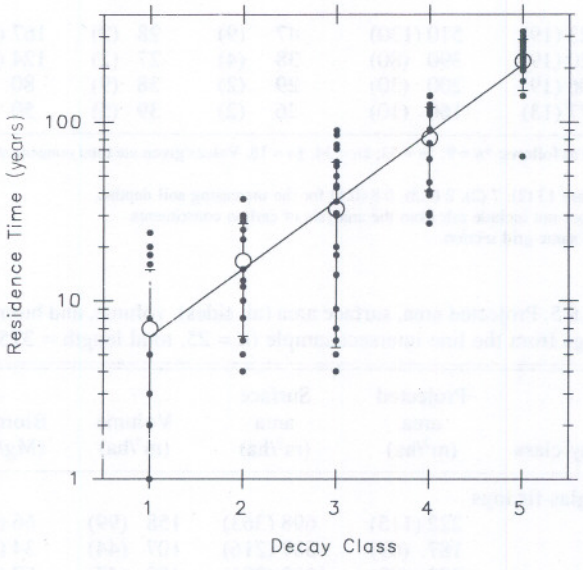

FIG. 1. Residence time (RT) on the forest floor versus decay class for all dated Douglas-fir logs. The open circles with standard error bars are mean residence times. The regression line (RT = 2.60 $e^{(0.8779\,DC)}$, S_{xy} = 0.986, n = 94), weighted by 1/(variance of the decay class), accounts for 70% of the weighted variance and shows the linear relationship. Note that the mean residence times lie very close to this line.

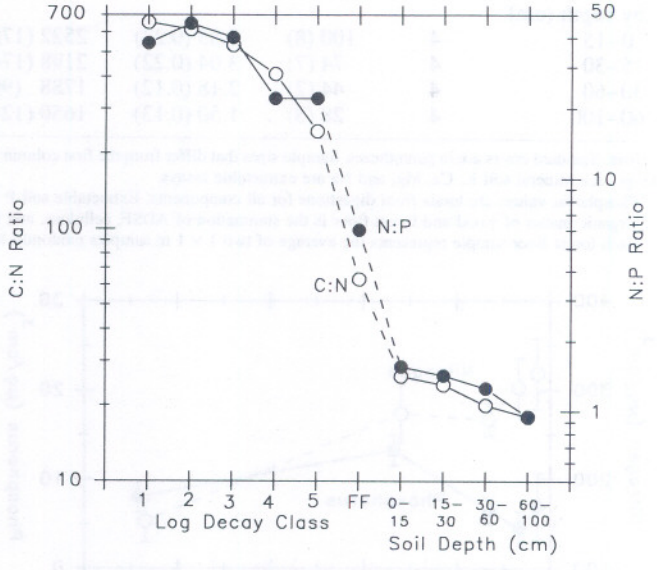

FIG. 2. C:N and N:P ratios, using total P, for Douglas-fir logs in the five decay classes, forest floor (FF), and mineral soil.

15 m long, randomly oriented transects, systematically spaced in the western part of the stand. Volume per hectare by species and decay class was computed by standard methods from log diameters (Van Wagner 1968), and biomass was calculated using the densities mentioned above.

In the second method, biomass of logs in each decay class was summed for each of the four intensive plots and an average was computed for the stand.

To estimate snag biomass, the top diameter was estimated from the bottom diameter and height, assuming a taper of 1:50 (Grier and Logan 1977). Snag surface area and volume were calculated as right frustums of a cone (Husch *et al.* 1982). Biomass for all species was estimated from the volume and decay class density for logs of that species, as described above. Snag surface area, volume, and biomass were summed over the western portion of the stand and divided by 2.325 ha to get areal estimates.

Results and discussion

Physical characteristics of logs

Length, large-end diameter, surface area, volume, and biomass of individual logs all showed a progressive decrease from decay class 1 to 5 (Table 1); the more highly decayed logs were smaller. This probably has two causes. (*i*) The average size of logs reaching the forest floor has increased with time; decay class 1 and 2 logs died more recently and were larger trees. (*ii*) Smaller logs and portions of logs may decay more rapidly; the smaller ends of large logs were often a more advanced decay class than the large ends.

The apparent time for a log to progress from one decay class to the next increased exponentially as decay class increased, so the relationship between decay class and mean residence time is linear in a semilogarithmic graph (Fig. 1).

Density loss

A rapid drop in density occurs between decay classes 1 and 2, followed by a more gradual decrease to class 5 (Table 2). Density at decay class 4, with a mean residence time of 82 years, is one-half the regional value for sound wood (450 mg/cm^3, United States Forest Products Laboratory 1974). The slow decomposition of these logs (mineralization rates of 0.006 25 and 0.007 01 per year, Means *et al.* 1985) probably has several causes. First, they are a poor substrate for growth of decay organisms. The C:N ratio for decay class 1 logs is quite high (over 600, Fig. 2) in contrast with, for example, the C:N ratio of 146 for the least decayed boles in an eastern mixed oak woodland (Lang and Forman 1978). Douglas-fir wood contains dihydroquercetin, known to inhibit

TABLE 4. Element concentrations in Douglas-fir logs, forest floor, and mineral soil

Substrate	No. of samples	C (mg/g)	N (mg/g)	P (μg/g)[a]	K (μg/g)	Ca (μg/g)	Mg (μg/g)	Na (μg/g)	Organic matter (mg/g)[b]
Douglas-fir logs by decay class									
1	10	521 (7)	0.84 (0.14)	22 (12)	135 (29)	701 (214)	42 (16)*	8 (4)	993 (2)
2	14	534 (5)	0.87 (0.06)	19 (9)	90 (19)	484 (101)	49 (7)	18 (6)	996 (1)
3	35	538 (6)	1.01 (0.07)	25 (6)	117 (14)	536 (92)†	58 (6)‡	19 (13)	994 (1)
4	13	551 (9)	1.34 (0.18)	62 (8)	118 (26)	1253 (214)	120 (20)	47 (5)	996 (3)
5	19	562 (4)	2.30 (0.34)§	105 (21)§	127 (23)§	3006 (512)	291 (44)	34 (5)§	993 (1)
Forest floor	3[c]	416 (4)	8.74 (0.74)	1410 (100)	1370 (80)	6880 (780)	1730 (170)	580 (50)	853 (4)
Mineral soil by depth (cm)									
0–15	4	100 (8)	3.85 (0.22)	2522 (175)	123 (19)	510 (130)	47 (9)	28 (2)	167 (17)
15–30	4	74 (7)	3.04 (0.22)	2198 (174)	120 (19)	390 (80)	38 (4)	27 (2)	124 (14)
30–60	4	44 (2)	2.18 (0.12)	1788 (90)	106 (19)	200 (30)	29 (2)	38 (9)	80 (5)
60–100	4	28 (3)	1.50 (0.13)	1650 (124)	77 (13)	160 (10)	26 (2)	39 (5)	50 (6)

NOTE: Standard errors are in parentheses. Sample sizes that differ from the first column are indicated as follows: *$n = 9$; †$n = 33$; ‡$n = 34$; §$n = 18$. Values given are total concentrations except, that mineral soil K, Ca, Mg, and Na are extractable assays.

[a] Phosphorus values are totals from digestions for all components. Extractable soil P values (SE) are 13 (2), 7 (2), 2 (0.5), 0.8 (0.1) for the increasing soil depths.

[b] Organic matter of wood and forest floor is the summation of ADSF, cellulose, and lignin and does not include ash from the analysis of carbon constituents.

[c] Each forest floor sample represents the average of two 1 × 1 m samples randomly located in the same grid section.

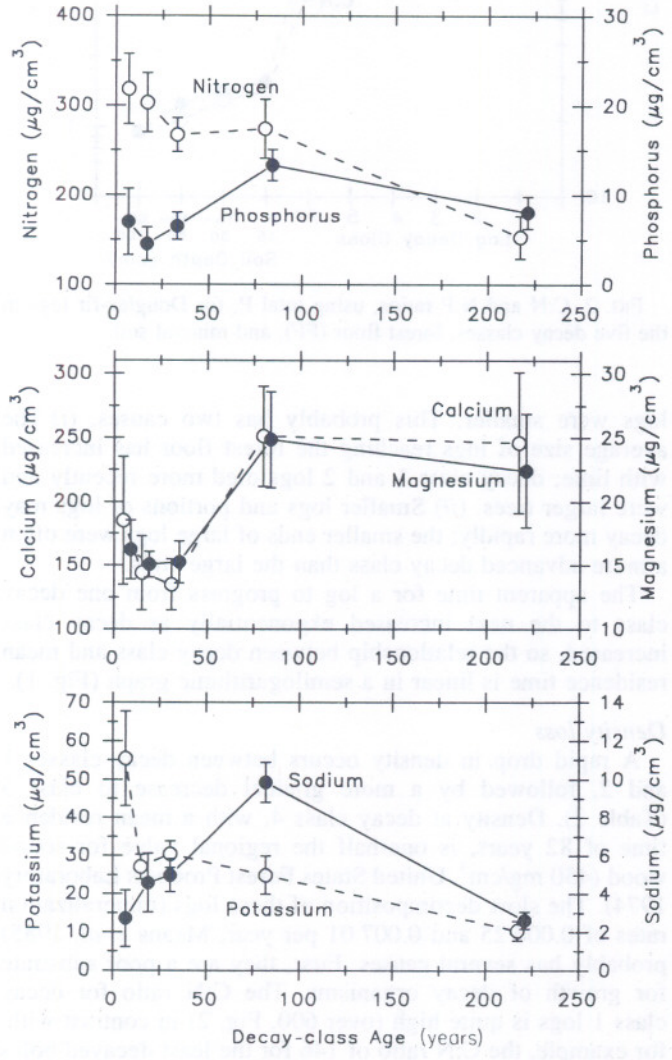

FIG. 3. Change in volumetric concentrations (±1 SE) of nutrients in decaying wood of Douglas-fir logs over time.

TABLE 5. Projected area, surface area (all sides), volume, and biomass of logs from the line intersect sample ($n = 25$, total length = 375 m)

Decay class	Projected area (m^2/ha)	Surface area (m^2/ha)	Volume (m^3/ha)	Biomass (Mg/ha)
Douglas-fir logs				
1	222 (115)	698 (363)	158 (99)	66 (41)
2	187 (69)	587 (216)	107 (44)	34 (14)
3	383 (93)	1202 (291)	189 (47)	52 (65)
4	309 (85)	971 (266)	142 (45)	32 (10)
5	16 (16)	49 (49)	5 (5)	1 (1)
Total	1116 (178)	3506 (229)	603 (118)	185 (44)
Logs of all species				
1	299 (127)	938 (398)	171 (102)	71 (42)
2	251 (79)	790 (250)	123 (48)	39 (15)
3	469 (98)	1474 (308)	228 (53)	62 (14)
4	441 (94)	1384 (295)	194 (48)	43 (11)
5	116 (46)	365 (144)	40 (17)	7 (3)
Total	1576 (160)	4952 (503)	756 (112)	222 (42)

NOTE: Standard errors are in parentheses.

decomposition of Douglas-fir heartwood (Scheffer and Cowling 1966). Also, it contains significant amounts of lignin (341 mg/g in decay class 1 wood, Table 2).

A second reason for their slow decay is probably the long time period required for colonization by microorganisms and invertebrates of boles up to 1 m or more in diameter (Table 1). Third, decomposition may be retarded to varying degrees by high water content throughout the year (Table 3).

Changes in density and chemistry reflect changes caused by mineralization but not those caused by fragmentation of small pieces off logs (Harmon *et al.* 1986).

Water content

In the winter and midway through the summer, water concentration was higher in more decomposed wood, but in the late fall no clear trend was evident (Table 3). Highly

TABLE 6. Number, basal area, surface area (all sides), volume, and biomass of snags on the whole stand

Decay class	No./ha	Mean diameter (cm)	Mean height (m)	Basal area (m^2/ha)	Surface area (m^2/ha)	Volume (m^3/ha)	Biomass (Mg/ha)
Douglas-fir snags							
1	2	102	20	2	101	31	13
2	2	120	42	2	184	51	16
3	14	114	20	15	854	237	65
4	54	76	4	28	576	128	29
Total	72	85	8	47	1716	446	122
Snags of all species							
1	8	47	12	2	167	40	16
2	2	98	34	2	184	51	16
3	27	74	14	17	932	245	67
4	72	69	4	32	710	150	33
Total	109	69	8	53	1993	485	132

TABLE 7. Element and organic matter capital in logs, snags, forest floor, and mineral soil

Substrate	C (Mg/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)	Na (kg/ha)	Organic matter (Mg/ha)	Percent of total detrital capital
Douglas-fir logs by decay class[a]									
1	34.3	55	1.45	8.91	46.3	5.02	0.53	66 (41)	8
2	18.3	30	0.65	3.06	16.5	1.67	0.61	34 (14)	4
3	29.1	53	1.30	6.08	35.7	3.64	0.99	52 (13)	7
4	17.6	43	1.98	3.78	40.0	3.84	1.50	32 (10)	4
5	0.5	3	0.13	0.18	3.0	0.29	0.04	1 (1)	0
All	99.7	183	5.51	22.01	141.5	14.45	3.68	185 (44)	23
Logs of all species[a]								222 (42)	28
Snags of all species								137	17
Forest floor[b]	31.4 (3.7)	662 (132)	108 (7)	102 (9)	538 (106)	141 (32)	45 (6)	55 (6)	7
Mineral soil[c]									
0–15	56.6 (3.2)	2 213 (114)	1426 (73)	71 (10)	278 (52)	27 (4)	16 (1)	95 (6)	12
15–30	45.3 (1.8)	1 942 (61)	1371 (66)	77 (11)	231 (31)	24 (3)	20 (2)	78 (4)	10
30–60	60.3 (2.5)	3 055 (113)	2480 (230)	143 (17)	278 (23)	40 (1)	52 (9)	112 (5)	14
60–100	51.1 (1.2)	2 853 (104)	3030 (208)	139 (10)	308 (21)	48 (3)	75 (11)	95 (5)	12
0–100	213.4 (1.1)	10 063 (168)	8307 (548)	430 (44)	1094 (76)	138 (4)	163 (14)	380 (2)	48
Total detrital capital								793	100

NOTE: Standard errors are in parentheses.
[a] Based on the organic matter capital estimated by the line intercept method.
[b] Each forest floor sample represents the average of two 1 × 1 m samples randomly located in the same grid section. $n = 3$.
[c] Depths given in centimetres. $n = 4$.

decayed logs are common sites for establishment and growth of tree species, such as western hemlock in the Pacific Northwest (Harmon and Franklin 1989; Christy and Mack 1984). Logs are probably an important source of water during the summer drought because even logs in advanced stages of decay contain hundreds of liters of water (Table 3).

Nutrient content

Concentrations of all elements, except C and K, increase markedly through the decay classes (Table 4). The C:N and N:P ratios decrease markedly, indicating the relative enrichment in N over C and in P over N (Fig. 2) with increasing decay. Similar trends in these ratios were found by Sollins *et al.* (1987). The C:N ratio shows no evidence of leveling off as logs decay, but the N:P ratio apparently stabilizes near 20 in logs.

There are four patterns of change in element content in these logs, shown on a volumetric basis in Fig. 3 so that increases and decreases represent, respectively, net gains and losses with advancing decay. Nitrogen and K are lost throughout decomposition. Most N loss occurs during later stages of decay, while most K loss occurs very early. Sodium accumulates in early stages of decay and then is lost by decay class 5. Phosphorus, Ca, and Mg show a slight decrease or little change in early stages of decay and a net increase from decay class 3 to class 4. Of these three elements, only P shows a decrease to class 5. The initial net losses of elements (Fig. 3) are related to the decrease in density (Table 2) and, for K, to a fairly large drop in concentration (Table 4).

Area, volume, and biomass of logs and snags

Table 5 presents the area, volume, and biomass of logs estimated by the line intersect method. For the intensive plot

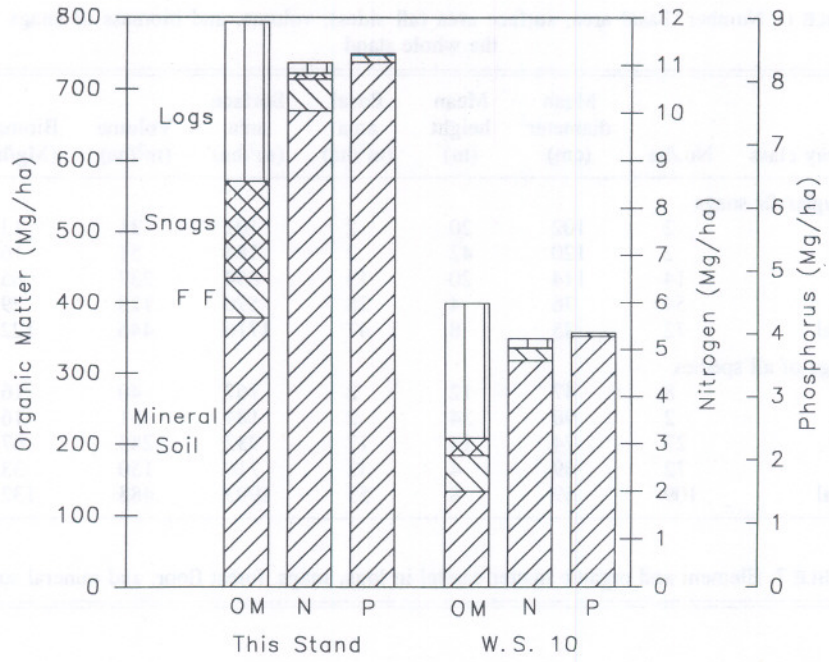

FIG. 4. Comparisons of organic matter (OM), N, and P in this stand and another old-growth Douglas-fir stand (W.S. 10) in the H.J. Andrews Experimental Forest. Nitrogen and P in wood of species other than Douglas-fir were estimated using the concentrations in Douglas-fir logs of the same decay class. FF, forest floor.

FIG. 5. Relative frequency of solid wood, white rot, and brown rot in Douglas-fir log samples. Solid wood was not necessarily undecayed but could not be identified as white or brown rot by macroscopic characteristics. Sample sizes for decay classes 1–5 are 10, 14, 34, 13, and 20, respectively.

method (table omitted to save space), totals for Douglas-fir logs over all decay classes of the projected area (1272 m^2/ha), total surface area (4100 m^2/ha), volume (681 m^3/ha), and biomass (197 Mg/ha), as well as the totals for all species (1652 m^2/ha, 5237 m^2/ha, 792 m^3/ha, 217 Mg/ha, respectively), agree closely with those in Table 5, increasing our confidence in these estimates. Values for individual decay classes, however, are probably less reliable because some differ greatly between the two methods. Most logs that were identified were Douglas-fir. All sampled and dated class 5 logs were identified as Douglas-fir, so the majority of these logs that were not identified were probably Douglas-fir. Logs in the more advanced decay classes were common, but because of their smaller size and lower density, they made up a lower proportion of the volume and biomass (Table 5). This was especially true of class 5 logs.

Projected areas indicate that about 15 to 17% of the forest floor is covered by logs. Log biomass in this stand, 222 Mg/ha, is high compared with most temperate forests, although it falls in the reported range of 1–490 Mg/ha for forest stands (Harmon *et al.* 1986).

There were relatively few snags in decay classes 1 and 2 (Table 6). This is consistent with data of Cline *et al.* (1980) and Raphael and Morrison (1987), showing snags remain in early decay stages less time than in more advanced stages. Diameter and height generally decrease as snags decay, while the per-hectare contributions to basal area, surface area, volume, and biomass generally increase with decay class. Biomass of snags (137 Mg/ha) is higher than that of all but one of the 33 stands reported by Harmon *et al.* (1986). The surface area of all sides of logs and snags together equals 69% of the area of the stand. A large area of coarse woody debris is available for interchange with the environment and biota.

Forest floor and mineral soil

Concentrations of all elements but C are much higher in the forest floor than in logs (Table 4), while the C:N and N:P ratios are much lower (Fig. 2), reflecting the greater concentrations of N and P in litter that includes a larger amount of foliage. Concentration of cellulose is lower in the forest floor than in logs, while that of lignin is intermediate and that of ADSF is higher than in even decay class 1 logs (Table 2). Microbial biomass is likely higher in the forest floor than in logs (note the much lower C:N and N:P ratios in forest floor, Fig. 2) and may, in part, account for higher ADSF in the forest floor. A significant portion of the microbial biomass would probably be extracted with our hot (>100°C reflux for 1 h) acid (0.5 M H_2SO_4) detergent (2%) soluble fraction (ADSF).

Carbon, N, organic matter, total and extractable P, and most cations show the expected decrease with depth in the mineral soil (Table 4). All are present in significant amounts at 60–100 cm depth, except extractable P. The C:N and N:P ratios

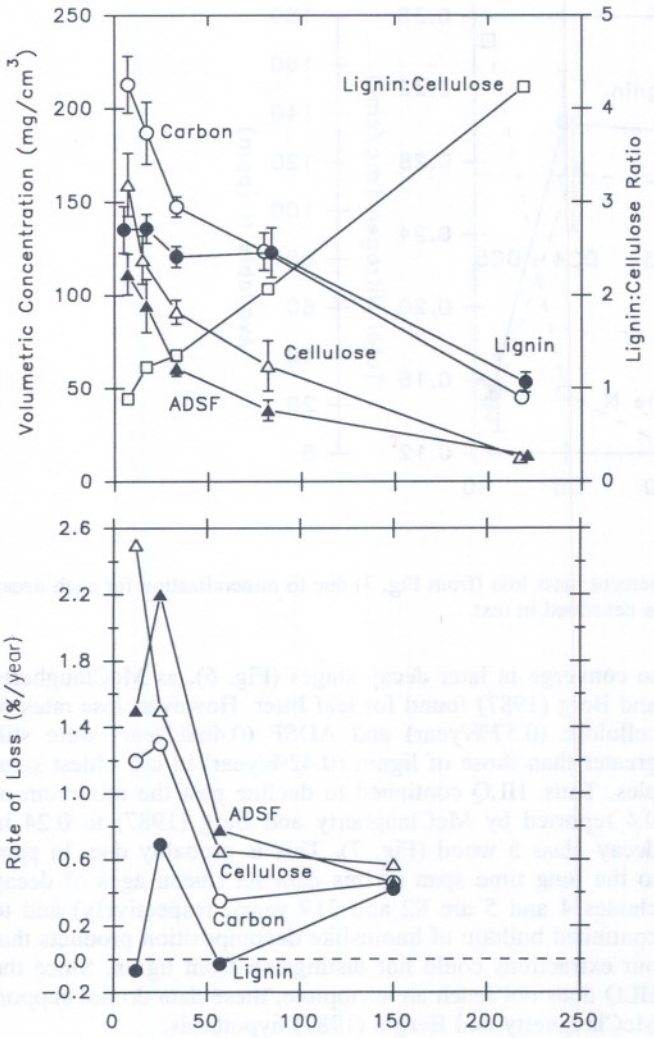

FIG. 6. Change in volumetric concentrations (±1 SE) of carbon, lignin, cellulose, and ADSF in wood of Douglas-fir logs over time and rates of loss caused by mineralization of these constituents from one decay class to the next (e.g., decay class 1 to decay class 2).

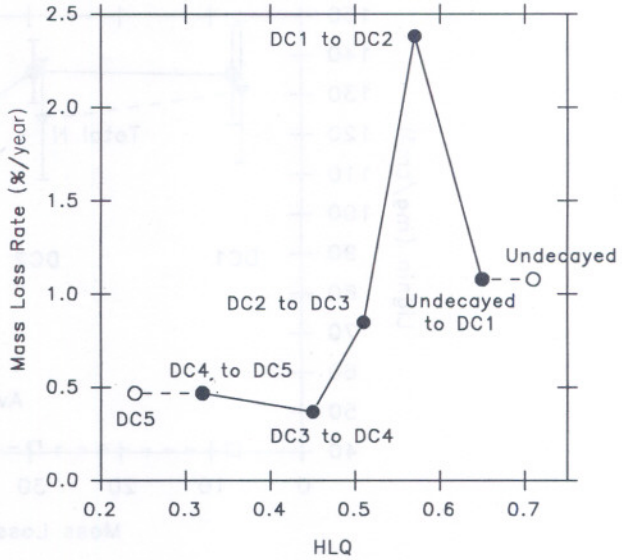

FIG. 7. Mass loss between decay classes (DC) versus HLQ (holocellulose (hemicellulose + cellulose) to lignocellulose (lignin + hemicellulose + cellulose) quotient). HLQ plotted is the mean for each pair of decay classes, except that HLQ's for DC5 and undecayed wood are plotted at the mass loss rates for adjacent data points; density of undecayed Douglas-fir wood (450 mg/cm^3) used to calculate mass loss rate for "Undecayed to DC1" is from United States Forest Products Laboratory (1974).

near the soil surface are lower than for any other aboveground detrital component and decrease with depth (Fig. 2). The similarity of the trends of these ratios is striking and may reflect close links between the responsible processes.

Detrital capital

Almost half the total detrital organic matter is in the top 100 cm of mineral soil, and almost half of this is in the top 30 cm (Table 7). Logs form the next largest portion of detrital capital, over one-quarter of the total, and coarse woody debris (logs and snags) makes up 45%. The reserves of N, P, K, Ca, Mg, and Na in logs are small compared with those of the forest floor and mineral soil (Table 7) because of their low concentrations (Table 4).

This 450-year-old stand had a large amount of detrital biomass (793 Mg/ha). Detrital organic matter, N, and P were about twice those of another old-growth Douglas-fir stand in the Andrews Experimental Forest with comparable data (Fig. 4). Only a few old-growth *Sequoiadendron giganteum* (Lindl.) Buchholz and Douglas-fir stands, and young stands with large amounts of logs and snags carried over from the previous stand, have comparable or greater coarse woody debris biomass (Harmon *et al.* 1986). It had high detrital biomass, probably because it was productive. Total aboveground biomass of live trees was 1174 Mg/ha, basal area was 100 m^2/ha, and main canopy tree height averaged 45 m (unpublished data on file at the Forestry Sciences Laboratory, Corvallis, Oregon).

Carbon compounds and types of rot

As mineralization progresses, lignin concentration increases, while ADSF and cellulose concentrations decrease (Table 2). This is paralleled by the increasing frequency of brown rot, relative to white rot and solid wood (Fig. 5). The amounts of all carbon compounds drop with advancing decay (Fig. 6). Initially cellulose and ADSF are lost more rapidly than lignin, but by decay class 5 rates of loss of all became more similar (Fig. 6).

The mineralization rate of this wood is not constant. Loss of carbon is most rapid during the early stages of decomposition (Fig. 6), which are dominated by white rots (Fig. 5) that degrade both lignin and cellulose (Boyce 1961). Carbon loss proceeds more slowly during later stages of decay, when lignin is the most common carbon constituent and brown rots that preferentially decompose cellulose (Boyce 1961) dominate. The lignin:cellulose ratio (Fig. 6) increases continuously throughout decay. This is probably caused by preferential degradation of cellulose and by accumulation of humuslike decomposition products (Clark and Paul 1970; Stevenson 1982) that our chemical analyses could not distinguish from lignin.

Ryan *et al.* (1990) report that the forage fiber technique we used gives higher values for ADSF (extractives) and lower values for cellulose than the technique developed in the forest

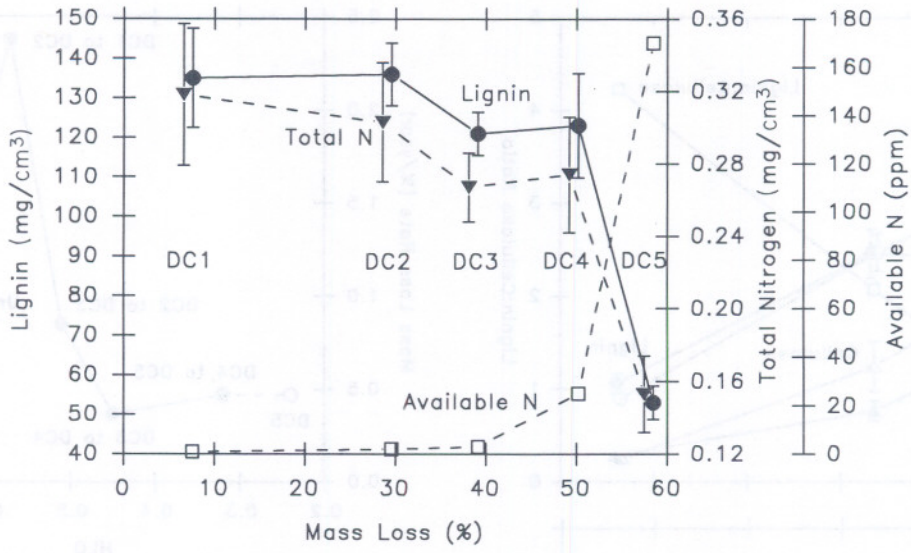

FIG. 8. Lignin, total nitrogen (±1 SE), and estimated available N over percent mass loss (from Fig. 7) due to mineralization for each decay class. Available N was estimated for our logs from Sollins *et al.* (1987) as described in text.

products field. Both techniques have been commonly used in decomposition research. Our values for ADSF, cellulose, and lignin can be converted approximately to those expected from the forest products technique using regressions in Ryan *et al.* (1990), if readers desire to make comparisons.

Control of mineralization rate by lignin

Decomposition rates of forest litter components are generally thought to be controlled by C substrate quality, nutrient limitations (especially N), and environmental factors. McClaugherty and Berg (1987) present data in which leaf litter apparently approaches a nearly constant holocellulose (hemicellulose + cellulose) to lignocellulose (lignin + hemicellulose + cellulose) quotient (HLQ) of 0.4 to 0.5 in later stages of decay. They hypothesize that HLQ reaches an asymptote because the holocellulose remaining in later decay stages is closely complexed (physically and chemically) with lignin, so both are lost at similar rates. In early stages of decay holocellulose that is not closely complexed with lignin may decay more rapidly (McClaugherty and Berg 1987). Our data provide an opportunity to test this hypothesis for wood decay.

To calculate HLQ we estimated hemicellulose as follows, because we did not separate hemicellulose from other ADSF constituents. We assumed that loss rates for cellulose and hemicellulose were equal for two reasons. First, we found that the decay rates (*k*-values, Olson 1963) for hemicellulose (0.27/year) and cellulose (0.26/year) which we calculated from data for Scots pine (*Pinus sylvestris* L.) needle litter, from Berg *et al.* (1982), were very similar. Second, both cellulose and hemicellulose are polymers of cyclic carbohydrates. We assumed an initial value of 170 mg/g for hemicellulose in undecayed Douglas-fir (mean of two values for hemicellulose from Browning 1975) and decreased it by the cellulose loss rate for each period between decay classes, to estimate hemicellulose for each decay class. Hemicellulose makes up the bulk of ADSF in our data, based on the assumed initial value of 170 mg/g.

Cellulose and ADSF were lost more rapidly than lignin from these logs in early decay stages, and loss rates tended to converge in later decay stages (Fig. 6), as McClaugherty and Berg (1987) found for leaf litter. However, loss rates of cellulose (0.57%/year) and ADSF (0.46%/year) were still greater than those of lignin (0.42%/year) in our oldest samples. Thus, HLQ continued to decline past the minimum of 0.4 reported by McClaugherty and Berg (1987) to 0.24 in decay class 5 wood (Fig. 7). This is probably due, in part, to the long time span of this data set (mean ages of decay classes 4 and 5 are 82 and 219 years, respectively) and to continued buildup of humuslike decomposition products that our extractions could not distinguish from lignin. Since the HLQ does not reach an asymptote, these data do not support McClaugherty and Berg's (1987) hypothesis.

The lignin component we extracted from advanced decay stages is chemically altered by decomposition processes and includes humified material from microbial and soil animal activities (Russell 1973; Stevenson 1982). Future studies would benefit from long-term data sets and separate identification of lignin from decomposition products, using methods similar to those of Nordén and Berg (1990).

Protection of cellulose and hemicellulose by lignin may still be an important control on mineralization rate on these logs. The increase of brown rots in advanced stages of decay probably causes a decrease in holocellulose that is not complexed closely with lignin. This would reduce the decomposition caused by brown rots that do not readily use lignin, and may in part cause the decrease in carbon loss rate (Fig. 4). Future comparisons of enzyme activity rates with loss rates of these compounds may shed light on possible protection of more labile compounds by lignin and humified carbon compounds (Sinsabaugh *et al.* 1991).

The higher mass loss rate from decay class 1 to decay class 2 (Fig. 7) probably reflects, in part, the relatively rapid (Harmon *et al.* 1986) sapwood decomposition rate (which we did not estimate separately) from DC1 to DC2, and the time required for colonization of large logs by decay organisms (Kimmey and Furniss 1943). It may also reflect our choice of an initial density (450 mg/cm^3, United States Forest Products Laboratory 1974) that is lower than that of the narrow-ringed wood of these old-growth trees.

Control of N release

The C:N ratio declined from 620:1 in decay class 1 to 244:1 in decay class 5, while total N concentrations increased from 0.84 mg/g to 2.3 mg/g (Table 4). This pattern is found in studies where there is immobilization of N in microbiota due to low N availability (Frankland 1974; Russell 1973). Loss of N paralleled loss of lignin (Fig. 8), similar to the pattern observed by Berg and McClaugherty (1987). Our results agree with theirs in that no net release of N occurred until decomposition of the recalcitrant lignin fraction had started.

The main increase in available N occurs at the same time as the largest net release of N and decrease in lignin content (Fig. 8). To estimate available N we assumed the relationship in Sollins *et al.* (1987, Fig. 7A, also in the western Cascades), between residence time of Douglas-fir logs on the forest floor and available N held for our logs, and used this to estimate available N for each decay-class age. In our logs, as in decaying leaf litter (Berg and McClaugherty 1987), lignin is a better predictor of the onset of net N release than the C:N ratio. Net N release begins at a C:N ratio of about 411:1, which is much higher than the upper value of 80:1 reported for leaf litter (Berg and McClaugherty 1987). We also found that net N loss occurred after about 44% mass loss had occurred, similar to the pattern observed by Berg and McClaugherty (1987).

Acknowledgements

Paul C. MacMillan was supported by National Science Foundation (NSF) grant DEB-74-20744A02 to the Coniferous Forest Biome and by a grant from the Hanover College Research Committee. In addition this work was supported by NSF grants DEB-76-21402, DEB-7706-075, and DEB-80-04652. Mark Harmon, Tom Sabin, and Phil Sollins provided valuable reviews.

Bartels, R., Dell, J.D., Knight, R.L., and Schaefer, G. 1985. Dead and down woody material. *In* Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 1—Chapter narratives. Chap. 8. *Edited by* E. Reade Brown. USDA Forest Service, Pacific Northwest Region, Portland, Oreg. pp. 171–186.

Berg, B., and McClaugherty, C. 1987. Nitrogen release from litter in relation to the disappearance of lignin. Biogeochemistry, **4**: 219–224.

Berg, B., Hannus, K., Popoff, T., and Theander, O. 1982. Changes in organic chemical components of needle litter during decomposition. Long-term decomposition in a Scots pine forest. I. Can. J. Bot. **60**: 1310–1319.

Boyce, J.S. 1961. Forest pathology. 3rd ed. McGraw-Hill Book Co., New York.

Browning, B.L. 1975. The composition and chemical reactions of wood. *In* The chemistry of wood. Chap. 3. *Edited by* B.L. Browning. Robert E. Krieger Publishing Co., Huntington, N.Y. pp. 57–101.

Christy, E.J., and Mack, R.N. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. J. Ecol. **72**: 75–91.

Clark, F.E., and Paul, E.A. 1970. The microflora of grassland. Adv. Agron. **22**: 375–435.

Cline, S.P., Berg, A.B., and Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. **44**: 773–786.

Cornaby, B.W., and Waide, J.B. 1973. Nitrogen fixation in decaying chestnut logs. Plant Soil, **39**: 445–448.

Frankland, J.C. 1974. Decomposition of lower plants. *In* Biology of plant litter decomposition. Vol. 1. *Edited by* C.H. Dickinson and G.J.F. Pugh. Academic Press, New York. pp. 3–36.

Franklin, J.F., and Waring, R.H. 1980. Distinctive features of the northwestern coniferous forest: development, structure, and function. *In* Forests: fresh perspectives from ecosystem analysis. *Edited by* R.H. Waring. Oregon State University Press, Corvallis. pp. 59–85.

Goering, H.K., and Van Soest, P.J. 1970. Forage fiber analysis (apparatus, reagents, procedures, and some applications). U.S. Dep. Agric. Agric. Handb. 379.

Graham, R.L.L. 1981. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Ph.D. thesis, Oregon State University, Corvallis.

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.

Grier, C.C., and Logan, R.S. 1977. Old-growth Douglas-fir communities of a western Oregon watershed: biomass distribution and production budgets. Ecol. Monogr. **47**: 373–400.

Harmon, M.E., and Franklin, J.F. 1989. Tree seedlings on logs in *Picea–Tsuga* forests of Oregon and Washington. Ecology, **70**: 48–59.

Harmon, M.E., Franklin, J.F., Swanson, F.J., *et al.* 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133–302.

Harmon, M.E., Ferrell, W.K., and Franklin, J.F. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. Science (Washington, D.C.), **247**: 699–702.

Husch, B., Miller, C.I., and Beers, T.W. 1982. Forest mensuration. 3rd ed. Ronald Press, New York.

Jackson, M.L. 1958. Soil chemical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.

Kimmey, J.W., and Furniss, R.L. 1943. Deterioration of fire-killed Douglas-fir. Tech. Bull. U.S. Dep. Agric. No. 851.

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, **61**: 1460–1473.

Lang, G.G., and Forman, R.T.T. 1978. Detrital dynamics in a mature oak forest: Hutchenson Memorial Forest, New Jersey. Ecology, **59**: 580–595.

Larsen, M.J., Jurgenson, M.F., and Harvey, A.H. 1978. N_2 fixation associated with wood decayed by some common fungi in western Montana. Can. J. For. Res. **8**: 341–345.

MacMillan, P.C. 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. Can. J. For. Res. **18**: 1353–1362.

Maser, C., and Trappe, J.M. 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-164.

McClaugherty, C., and Berg, B. 1987. Cellulose, lignin and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. Pedobiologia, **30**: 101–112.

McFee, W.W., and Stone, E.L. 1966. The persistence of decaying wood in the humus layer of northern forests. Soil Sci. Soc. Am. Proc. **30**: 512–516.

McKee, A., Laroi, G., and Franklin, J.F. 1982. Structure, composition, and reproduction behavior of terrace forests, South Fork Hoh River, Olympic National Park. *In* Ecological research in national parks of the Pacific Northwest. *Technical Coordinators*: E.E. Starkey, J.F. Franklin, and J.W. Matthews. Forest Research Laboratory, Oregon State University, Corvallis. pp. 22–29.

Means, J.E., Cromack, K., Jr., and MacMillan, P.C. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Can. J. For. Res. **15**: 1092–1098.

Mood, A.M., Graybill, F.A., and Boes, D.C. 1974. Introduction to the theory of statistics. 3rd ed. McGraw-Hill, New York.

Neitro, W.A., Binkley, V.W., Cline, S.P., *et al.* 1985. Snags (wildlife trees). *In* Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 1—Chapter narratives. Chap. 7. *Edited by* E. Reade Brown. USDA Forest Service, Pacific Northwest Region, Portland, Oreg. pp. 129–169.

Nelson, D.W., and Sommers, L.E. 1982. Total carbon, organic carbon, and organic matter. *In* Methods of soil analysis. Part 2. Chemical

and microbiological properties. Chap. 29. 2nd ed. *Edited by* A.L. Page, R.H. Miller, and D.R. Keeney. American Society of Agronomy, Soil Science Society of America, Madison, Wis. pp. 539–579.

Nordén, B., and Berg, B. 1990. A non-destructive method (solid state ^{13}C NMR) for determining organic chemical components of decomposing litter. Soil Biol. Biochem. **22**: 271–275.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology, **44**: 322–331.

Olson, S.R., and Sommers, L.E. 1982. Phosphorus. *In* Methods of soil analysis. Part 2. Chemical and microbiological properties. Chap. 24. 2nd ed. *Edited by* A.L. Page, R.H. Miller, and D.R. Keeney. American Society of Agronomy, Soil Science Society of America, Madison, Wis. pp. 403–430.

Raphael, M.G., and Morrison, M.L. 1987. Decay and dynamics of snags in the Sierra Nevada, California. For. Sci. **33**: 774–783.

Russell, E.W. 1973. Soil conditions and plant growth. Longman, Inc., White Plains, N.Y.

Ryan, M.G., Melillo, J.M., and Ricca, A. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. Can. J. For. Res. **20**: 166–171.

Scheffer, T.C., and Cowling, E.B. 1966. Natural resistance of wood to microbial deterioration. Annu. Rev. Phytopathol. **4**: 147–170.

Silvester, W.B., Sollins, P., Verhoeven, T., and Cline, S.P. 1982. Nitrogen fixation and acetylene deduction in decaying conifer boles: effects of incubation time, aeration, and moisture content. Can. J. For. Res. **12**: 646–652.

Sinsabaugh, R.L., Antibus, R.K., and Linkins, A.E. 1991. An enzymatic approach to the analysis of microbial activity during plant litter decomposition. Agric. Ecosyst. Environ. **34**: 43–54.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon. Can. J. For. Res. **12**: 18–28.

Sollins, P., Grier, C.C., McCorison, F.M., *et al.* 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecol. Monogr. **50**: 231–285.

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

Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology, **69**: 1689–1702.

Stevenson, F.J. 1982. Humus chemistry: genesis, composition, reactions. John Wiley and Sons, Inc., New York.

Triska, F.J., and Cromack, K., Jr. 1980. The role of wood debris in forests and streams. *In* Forests: fresh perspectives from ecosystem analysis. *Edited by* R.H. Waring. Proc. 40th Annu. Biol. Colloq. (Oreg. State Univ.). pp. 171–190.

United States Forest Products Laboratory. 1974. Wood handbook: Wood as an engineering material. U.S. Dep. Agric. Agric. Handb. 72. [Revised.]

Van Soest, P.J. 1963. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. J. Assoc. Off. Agric. Chem. **46**: 829–835.

Van Soest, P.J. 1966. Nonnutritive residues: a system of analysis for replacement of crude fiber. J. Assoc. Off. Anal. Chem. **49**: 546–551.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. For. Sci. **14**: 20–26.