Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington

PHILLIP SOLLINS

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

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At 10 locations in Oregon and Washington, tree mortality resulted in dry-matter transfer of 1.5–4.5 Mg · ha^{-1} · year^{-1} of boles and branches to the forest floor and 0.3–1.3 Mg · ha^{-1} · year^{-1} of large-diameter roots directly to the mineral soil. The first value is about the same as that reported for leaf fall in similar stands; the second value generally is smaller than that reported for fine root turnover. Results are based on measurements by the U.S. Forest Service spanning 16–46 years and areas as large as 42 ha. Values based on intervals < 10 years were highly variable and potentially misleading.

At an old-growth Douglas-fir stand in Washington, fallen boles accounted for 81 Mg/ha, standing dead for 54 Mg/ha. Density of fallen boles averaged from 0.14 to 0.27 g/cm^3 depending on decay state. Values were lower than some previously reported because (1) our sample included small-diameter fallen boles that tend to decay rapidly, and (2) we measured density with techniques that minimized compaction and shrinkage.

The decay rate at the old-growth stand, calculated indirectly by dividing bole mortality (megagrams per hectare per year) by the amount (megagrams per hectare) of fallen and standing dead woody material, was 0.028 year^{-1}. This rate, three to five times those previously calculated directly from change in density alone, was almost identical to values calculated elsewhere from change in both volume and density. Decay rates based on change in density alone include only respired and leached material and exclude the large amount of material lost in fragmentation. This study shows the value of permanent plots, undisturbed by salvage logging, for retrospective studies of decomposition, nutrient cycling, and productivity.

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À 10 endroits de l'Orégon et de Washington, la mortalité des arbres a entraîné un transfert de matière sèche à la litière forestière de 1,5 à 4,5 Mg · ha^{-1} · an^{-1} à partir des tiges et des branches et directement au sol minéral de 0,3 à 1,3 Mg · ha^{-1} · an^{-1} à partir des racines de fort diamètre. La première valeur correspond à peu près à celle rapportée pour la chute des feuilles dans des peuplements semblables; la seconde valeur est généralement plus petite que celle rapportée pour le renouvellement des radicelles. Les résultats proviennent de mesures effectuées par le Service forestier des E.U.A., sur des périodes de 16 à 46 ans et dans des superficies allant jusqu'à 42 ha. Les valeurs qui reposaient sur des périodes < 10 années étaient variables et possiblement erronées. Dans un peuplement âgé de sapin de Douglas dans le Washington, les tiges tombées représentaient 81 Mg/ha et les arbres morts debout 54 Mg/ha. La densité du bois des arbres tombés se situaient entre 0,14 et 0,27 g/cm^3 selon l'état de la pourriture. Ces valeurs sont inférieures à celles déjà rapportées du fait que (1) notre échantillonnage incluait des tiges tombées de faible diamètre dont la tendance est de pourrir rapidement et que (2) nous avons mesuré la densité avec des techniques qui minimisent le compactage et le rétrécissement.

Lorsque calculé indirectement en divisant la mortalité des tiges (megagrammes par hectare par an) par la quantité (megagrammes par hectare) de matériel ligneux mort tombé ou debout, le taux de décomposition dans le peuplement âgé était de 0,028 an^{-1}. Ce taux, de trois à cinq fois supérieure à ceux autrefois calculés directement à partir du seul changement de densité, était à peu près identique aux valeurs obtenues ailleurs et calculées à partir d'un changement de volume et de densité. Les taux de décomposition basés uniquement sur la densité n'incorporent que du matériel oxidé et lessivé et excluent une forte quantité de matériel perdu dans la fragmentation. Cette étude montre l'importance des parcelles permanentes, non modifiées par des opérations de récupération, pour des travaux en rétrospective sur la décomposition, le recyclage des éléments nutritifs et la productivité.

[Traduit par le journal]

Introduction

Input and decay of coarse woody debris (snags and fallen boles) are important processes in northwestern coniferous forests (Triska and Cromack 1980; Franklin *et al.* 1981). Tree mortality, a conspicuous feature of forest ecosystems, is difficult to measure because it is sporadic in space and time. Apparently only six studies of forest net primary productivity include mortality (Table 1), and in five of these it was measured for only 8 years or less. However, these studies suggest that mortality should not be ignored in computing net primary production, since in most instances it was comparable to or greater than leaf fall.

As part of a research project on the role of coarse

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TABLE 1. Dry-matter transfers to the forest floor from leaf fall and stem mortality

Location	Forest type	Leaf fall ($Mg \cdot ha^{-1} \cdot year^{-1}$)	Stem mortality: Input ($Mg \cdot ha^{-1} \cdot year^{-1}$)	Stem mortality: Area (ha)	Stem mortality: Time (year)	Reference
New Mexico	Aspen	1.8	0.45	3.4	5	Gosz (1980)
New Hampshire	Northern hardwoods	2.5–2.9	0.81	13.2	1	Whittaker *et al.* (1974)
Tennessee	Yellow poplar	3.6	1.1	0.04	8	Sollins *et al.* (1973)
	Mixed hardwood	3.7–4.1	0.6–1.2	24	5	Harris *et al.* (1973)
	Pine	3.4	1.9	24	5	Harris *et al.* (1973)
Oregon	Old-growth Douglas-fir	2.4	7.0	10.2	2	Grier and Logan (1977)
	Coastal hemlock–spruce (120 years old)	2.8	2.8	0.4	40	Grier (1976, 1978)

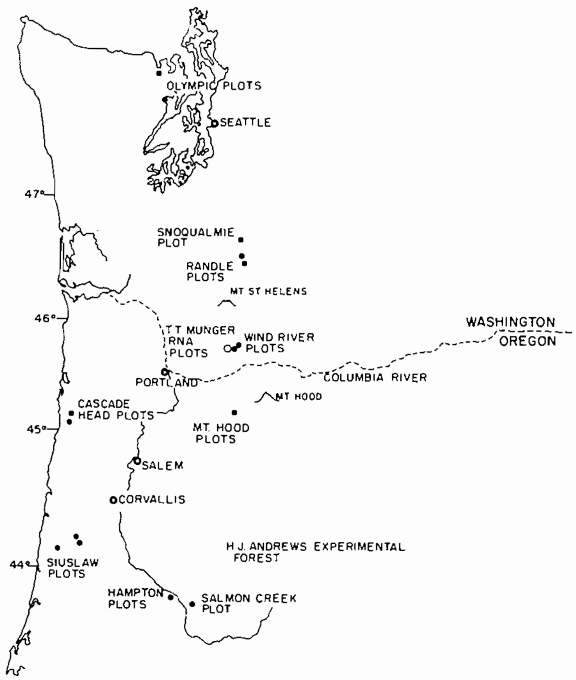

FIG. 1. Location of plots established by the U.S. Forest Service for growth and mortality studies in western Oregon and Washington National Forests.

woody debris in forests of the Pacific Northwest, we computed dry-matter input to the forest floor and mineral soil resulting from mortality at 10 locations in western Oregon and Washington (Fig. 1). We used three sets of long-term data gathered by the U.S. Forest Service Pacific Northwest Forest and Range Experiment Station (PNW Station).

In addition, at one site, an old-growth forest for which extensive data were available, we established debris plots for measuring biomass of standing and fallen coarse wood. Assuming the forest to be in steady state, we calculated a decay rate for the coarse wood which we compared with rates calculated elsewhere. Methods of characterizing and measuring the amount and transfer of coarse wood are discussed.

Methods

U.S. Forest Service data: site descriptions and sampling methods

Williamson plots

The first set of data is from plots established between 1909 and 1939 in well-stocked, young-growth stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) by the PNW Station under the direction of T. T. Munger, E. J. Hanzlik, W. H. Meyer, J. V. Hofmann, W. Peterson, and R. E. McArdle. Stands ranged in age from 42 to 97 years at time of establishment. The plots were remeasured at about 5-year intervals until 1962. Williamson (1963) summarized growth and yield of most of the plots and their status in 1962. They will thus be referred to here as the Williamson plots. Over the next decade Robert Curtis and David Bruce of the PNW Station remeasured several of them, and recently Oregon State personnel remeasured several not destroyed by logging, road building, and salvage operations. The data now span periods from 16 to 46 years and afford an unusual opportunity to gauge mortality at several Douglas-fir stands that are just now entering maturity.

The Williamson plots are distributed throughout western Oregon and Washington in the Willamette, Siuslaw, Gifford Pinchot, Mt. Hood, Olympic, and Snoqualmie National Forests (Fig. 1). They span a wide range of age, elevation, and topography (Table 2). Most were 1-acre (1 acre = 0.405 ha), square or rectangular plots on which all trees greater than 6.4 cm dbh were tagged. All plots were well stocked when established, but considerable mortality on several of them has caused yield to depart significantly from yield tables (Williamson 1963). Whether such mortality should be regarded as exceptional or normal if large areas are measured over long time periods is a question that has never properly been addressed.

Cascade Head plots

The second set of data is from a study begun in 1935 by

TABLE 2. Location and description of plots established by the U.S. Forest Service for studies of growth and mortality

National Forest and plots	Ranger district	Year estab-lished	Age at year of estab-lishment	Status (fall 1981)	Legal description: Sec-tion	Legal description: Town-ship	Legal description: Range[a]	Topographic features: Ele-vation (m)	Topographic features: Slope (%)	Topographic features: Aspect	Annual precipi-tation (cm)
Willamette											
Hampton 1,2,3[b]	Oak Ridge	1910	54	Salvage logged	19	20 S	2 E	210	0–30	N	122
Salmon Creek 1	Oak Ridge	1928	80	Unknown	14	21 S	3 E	—	—	—	—
Siuslaw											
4,5[b]	Mapleton	1911	50	Unknown	6	16 S	8 W	240	15–25	S, SW	—
6–8[b]	Waldport	1926	54	Salvage logged (one destroyed by road construction)	—	—	—	400[c]	—[c,d]	W[d]	—
9–10[b]	Mapleton	1926	65	Unknown	21,22	15 S	9 W	—	20–40	NE	—
20[b]	Waldport	1927	56	Unknown	—	—	—	—	—	—	—
Gifford Pinchot											
Randle 1–5[b]	Randle	1937	45–55	Unknown	7,8	11 N	8 E	550	0–10	S	150
7,9[b]	Randle	1927	42,48	Unknown	6	12 N	7 E	—	0–50	S to SE	—
Wind River											
4,5,90[b]	Wind River	1914,1939	72,97	Protected	13	4 N	7½ E	400–430	5–100	W, E	250
2,9[b]	Wind River	1914,1924	72,81	Logged about 1965	34	5 N	7 E	790	2–15	E to NE N to NW	—
Mt. Hood											
1–3	Zig-Zag	1930	45	Protected	23	3 S	7 E	580	60	NE to SE	250
Olympic											
1,2[b]	Quilcene	1926	51	Unknown	34	27 N	2 W	30	0–60	W to NW	130
3,4[b]	Quilcene	1926	43	Unknown	24	29 N	3 W	60	30–60	W to SW	90
Snoqualmie											
1[b]	Randle[e]	1928	42	Unknown	16	14 N	8 E	760	15–20	SW	210
Cascade Head											
1,3–10, 12–13	Hebo	1935	80–86	Protected	7,8, 15,22	6 S	10 W	240–380	0–25	S, W	330
14,41,42	Hebo	1935	62–85	Protected	21	6 S	10 W	90–120	—	—	—
T. T. Munger											
RNA	Wind River	1947	350–550	Protected	8,17, 20,21	4 N	7 E	340–625	—[f]	—[f]	230

[a]East or west of the Willamette meridian.
[b]Information (except status) after Williamson (1963).
[c]Ridgetop.
[d]Data for plot 8 only but representative of the other two.
[e]Administered by Randle District, Gifford Pinchot National Forest.
[f]Variable.

Walter H. Meyer at Cascade Head Experimental Forest near Lincoln City, Oregon, in stands that became established after the Nestucca fire of 1845. Twelve of the sixteen 1-acre plots originally established survive today. Diameter was remeasured at 5-year intervals until 1955 and then sporadically until 1975, when a continuing program of remeasurement was instituted by Jerry Franklin of the PNW Station.

The coastal sites at Cascade Head are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.). When the plots were established in 1935, aboveground biomass averaged 647 Mg/ha (SE = 42), of which 48% was hemlock and 48% spruce. Species composition varied widely among the individual plots; as much as 100% of aboveground biomass and as little as 2.5% was Sitka spruce. Plot 12 is a particularly fine stand that has been the subject of several studies. Fujimori *et al.* (1976) reported aboveground net primary production (excluding mortality) as 10.3 $Mg \cdot ha^{-1} \cdot year^{-1}$; Grier (1976) reported 13.5 $Mg \cdot ha^{-1} \cdot year^{-1}$. Grier (1978) used U.S. Forest Service data for the plot to calculate input of coarse woody debris (Table 1) and also estimated amounts and decay rate of fallen boles (see Discussion). Understory vegetation, climate, and soils are described in more detail in these papers.

At the three Douglas-fir plots at Cascade Head, Sitka spruce is largely absent. Aboveground biomass averaged 558 Mg/ha in 1935 (SE = 44), of which 91% was Douglas-fir and 7% western hemlock. Stocking of red alder (*Alnus rubra* Bong.), 16.5/ha in 1935, had decreased to 1.7/ha by 1979. No studies of the Douglas-fir plots have been published.

Thornton T. Munger Research Natural Area

The third set of data is from a study established in 1947 by William Stein, William Bullard, and Robert Steele in an area of old-growth Douglas-fir near Wind River, Washington, now known as the Thornton T. Munger Research Natural Area (RNA). The PNW Station has checked growth and mortality in this stand at 2- to 5-year intervals since the plots were established. Remeasurements continue today under Dean DeBell and Jerry Franklin. This data base is almost certainly unique in that it describes mortality over a 30-year period on an area of about 42 ha.

The stand at the T. T. Munger RNA consists primarily of Douglas-fir 350–550 years old, much western hemlock, silver fir (*Abies amabilis* (Dougl.) Forbes), grand fir (*Abies grandis* (Dougl.) Lindl.), and in one wet portion, western red cedar (*Thuja plicata* Donn.). Understory trees include hemlock, silver fir, vine maple (*Acer circinatum* Pursh.), and yew (*Taxus brevifolia* Nutt.). Western white pine, once a major component of the overstory, has all but disappeared from the stand during the past century.

Few quantitative studies have been conducted at this old-growth stand, but it appears to differ from old-growth Douglas-fir stands at the H. J. Andrews Experimental Forest some 500 km to the south. Scattered noble fir and Engelmann spruce at the T. T. Munger old-growth site indicate a colder environment, probably a result of cold-air drainage from higher land to the north. Elevation ranges from 340 to 610 m. Annual rainfall is 228 cm (King 1961); mean annual temperature is 8.9°C. In 1947, aboveground tree biomass on the T. T. Munger old-growth plots averaged 654 Mg/ha (SE = 45), whereas the most intensively studied old-growth stand at the H. J. Andrews Experimental Forest averaged 711 Mg/ha (SE = 88) (Grier and Logan 1977). Site quality of both stands averages III (King 1961; Grier and Logan 1977).

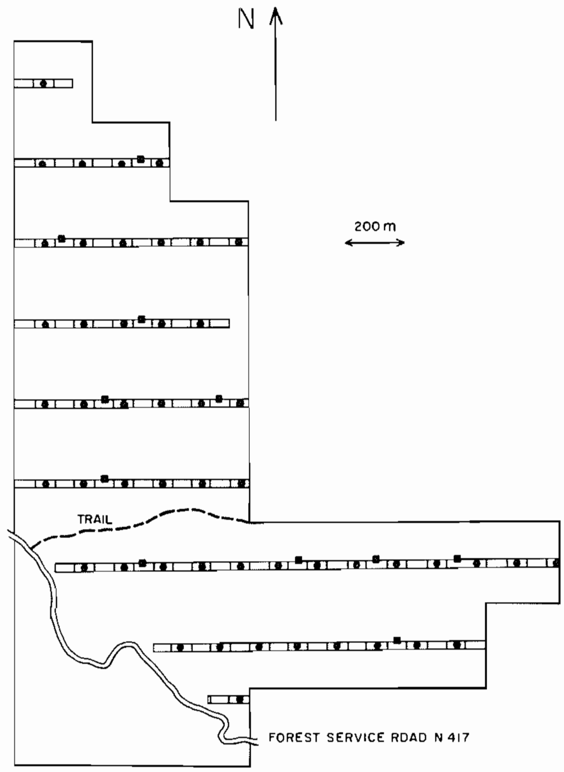

FIG. 2. Arrangement of mortality strips, growth plots (●), and coarse woody debris plots (■) at the Thornton T. Munger Research Natural Area in Washington.

During the summer of 1947, transect lines were laid out east to west, and nested, circular, growth plots were established along them at regular intervals (Fig. 2). In the outer circle of each plot (0.08 ha), all stems > 24 cm (9.5 in.) in diameter were tagged and measured, and in each inner circle (0.02 ha), all stems > 6.4 cm (2.5 in.) in diameter were tagged and measured.

Larger strips centered along each transect were checked for mortality only (not growth). Trees outside a growth plot but within a mortality strip were not tagged. Instead, when the study began in 1947, all recently fallen boles and standing dead trees (snags) > 25.4 cm diameter in the mortality strips were blazed. One year later, the diameter and species of all snags and recently fallen trees not blazed were noted.These new snags and fallen trees were then blazed and the process repeated at 2- to 4-year intervals to the present. Total area cruised was 41.6 ha.

Coarse woody debris plots: field and laboratory methods

During the summers of 1977, 1979, and 1980, my field crew and I selected at random 11 of the growth plots at the old-growth T. T. Munger site for measuring coarse woody debris. The 30 × 30 m debris plots were established west

TABLE 3. Classification scheme for fallen, large-diameter Douglas-fir (*Pseudotsuga menziesii*) boles[a]

	Class description				
Character	I	II	III	IV	V
Bark	Intact	Mostly intact	Sloughing or absent	Detached or absent	Detached or absent
Structural integrity	Sound	Sapwood somewhat decayed; heartwood mostly sound	Heartwood mostly sound, supports own weight	Heartwood rotten, does not support own weight, branch stubs pull out	None
Branch system	Current-year twigs present	Larger twigs present, branch system entire	Large branches present, longer than log diameter	Branch stubs present, shorter than log diameter	Absent
Invading roots	Absent	Absent	Sapwood only	Throughout	Throughout
Vegetation	None	Conifer seedlings germinate but do not survive	*Tsuga* <2 m height; some shrubs and mosses	*Tsuga* <15 cm dbh; smaller shrubs; moss	*Tsuga* up to 200 cm dbh; shrubs, some large; moss

[a]Based on an unpublished report by R. Fogel, M. Ogawa, and J. M. Trappe (Terrestrial decomposition: a synopsis. Internal Report 135, Coniferous Forest Biome, Corvallis, OR).

of the growth plots and north of the transect lines in order to avoid sampling within heavily traveled areas (Fig. 2). All standing and fallen dead stems > 15 cm diameter were measured and mapped. The decay state of fallen logs was classified with a system developed by R. Fogel, M. Ogawa, and J. M. Trappe, extended by P. McMillan, J. Means, K. Cromack, and P. Sollins (Table 3), and published by Triska and Cromack (1980).

Density of each log extending across the plot perimeter was measured. A cross section was removed 1 m outside the plot boundary because logs had been disturbed at the boundary during mapping and tallying. Sampling was thus proportional to occurrence over the whole area.

Cross sections from the more decayed logs (class IV and V) had previously proven difficult to keep intact (in work with P. McMillan, K. Cromack, J. Means in Oregon). We therefore measured diameter and thickness of cross sections in the field and brought whole samples to the laboratory where they were dried at 50°C to approximately constant weight and weighed. A chainsaw was used for all operations, including sampling of class IV and V logs. (Hand tools tended to catch on hemlock roots and tear the samples. A chainsaw cut cleanly and is recommended for this procedure, though chain and bar required frequent replacement.)

Snags were sampled in the summer of 1977. Because we were unwilling to fall snags on the T. T. Munger RNA, we selected reasonably stable snags whose date of death could be determined from the tally data, and we removed wedges by making nose cuts with a chainsaw. Volume and dry weight of the wedges were measured and their densities were calculated.

Calculations and results

U.S. Forest Service plots

U.S. Forest Service data for growth and mortality from the Williamson plots, Cascade Head plots, and T. T. Munger RNA plots were recoded into a single format. We then wrote a program to calculate biomass of branches, boles, and coarse roots for each tree using regression equations compiled by Gholz *et al.* (1979). For the most part, equations were based on trees similar to those in the U.S. Forest Service plots, although equations were not available for a few minor species. Summing weights of trees that died during each interval gave dry-weight tranfers resulting from mortality. In the U.S. Forest Service tally system, trees were dropped after they died. Because only death was noted, not when the tree fell, the aboveground mortality transfer is the sum of the input to both standing-dead and fallen-dead compartments.

Mean dry-matter transfer to the forest floor ranged from 1.5 to 4.5 Mg · ha^{-1} · year^{-1}, including branches, over the 16- to 46-year study periods. The grand mean

TABLE 4. Dry-matter transfers resulting from whole-tree mortality at selected locations in western Oregon and Washington. SE in parentheses[a]

National Forests and plots	Mean stand age (years)	Area sampled (ha)	No. of plots	Time period sampled (years)	Aboveground input ($Mg \cdot ha^{-1} \cdot year^{-1}$)	Branch input (%)[b]	Belowground input ($Mg \cdot ha^{-1} \cdot year^{-1}$)
Snoqualmie	57	0.2	1	29	1.70 (—)	16	0.46 (—)
Olympic	63	1.4	4	30	1.52 (0.55)	11	0.30 (0.10)
Mount Hood	66	1.2	3	42	2.48 (0.14)	9.7	0.48 (0.05)
Gifford Pinchot							
Randle	69	2.8	7	30	2.44 (0.41)	8.6	0.50 (0.09)
Wind River	102	2.0	5	36	3.50 (0.41)	7.4	0.80 (0.10)
Siuslaw	75	2.5	8	25	4.25 (1.25)	7.8	0.91 (0.30)
Willamette							
Hampton	77	1.2	3	46	1.95 (0.49)	8.2	0.40 (0.12)
Salmon Creek	87	0.4	1	16	1.80 (—)	8.9	0.38 (—)
Cascade Head							
Douglas-fir	95	1.2	3	38	2.22 (0.45)	8.6	0.43 (0.11)
Hemlock–spruce	105	4.5	11	43	3.11 (0.33)	12	0.96 (0.17)
T. T. Munger RNA							
Growth plots	450	4.1	50	30	2.95 (0.65)	9.8	0.79 (0.12)
Mortality plots	450	41.6	103	29	4.54 (0.38)	13	1.27 (0.35)

[a]Standard error based only on variation among plots.
[b]Percent of aboveground input.

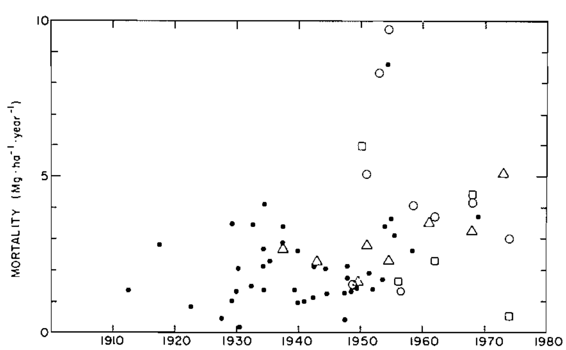

FIG. 3. Transfer to the forest floor resulting from tree mortality between 1910 and 1979 at 10 locations in western Washington and Oregon: mortality strips at the Thornton T. Munger old-growth site (○), growth plots at the Thornton T. Munger old-growth site (□), hemlock–spruce growth plots at Cascade Head Experimental Forest (△), all other Douglas-fir growth plots (●).

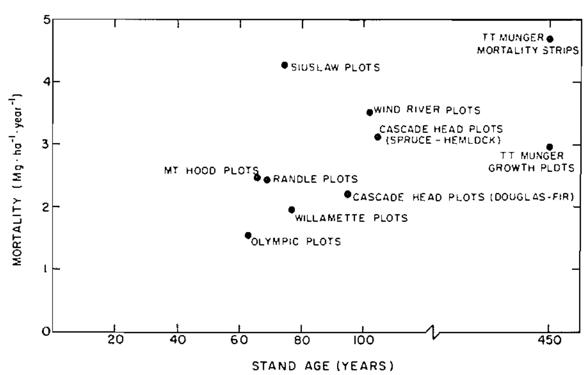

FIG. 4. Transfer to the forest floor resulting from tree mortality as a function of stand age (mortality and age averaged over the length of time each stand was studied).

for all locations was 2.7 $Mg \cdot ha^{-1} \cdot year^{-1}$ (Table 4). The data were very scattered, however, and values for individual measurement periods ranged from 0.2 to 13 $Mg \cdot ha^{-1} \cdot year^{-1}$. There was no obvious pattern with time (Fig. 3) or with stand age (Fig. 4), although many of the highest values were from the T. T. Munger old-growth site. Branches accounted for 7–16% of the transfer aboveground. Input belowground resulting from death of coarse roots ranged from 0.30 to 1.27 $Mg \cdot ha^{-1} \cdot year^{-1}$.

Debris plots

Density of logs at the old-growth T. T. Munger site ranged from a maximum of 0.5 g/cm^3 in a few freshly fallen boles to 0.05 g/cm^3 in the most decayed material. Density data were arranged first by species and decay class. Because we sampled in proportion to occurrence, some of the less prevalent species and decay classes were poorly represented. Class V logs were in general unidentifiable as to species, as were most of class IV and few of class III. All class IV logs and class III silver fir and unknown logs were grouped together (Table 5). These classs III logs generally had small diameters and punky interiors despite nearly intact

TABLE 5. Mean density (grams per cubic centimetre) of fallen and standing dead boles at the Thornton T. Munger Research Natural Area. Sample size and SE in parentheses

Species	Decay class				
	I[a]	II	III	IV	V
Douglas-fir	0.349 (2, 0.022)	0.282 (3, 0.065)	0.280 (8, 0.045)	0.211 (8, 0.031)	—
Grand fir	—	0.186 (1)	0.247 (1)	0.254 (1)	—
Western hemlock	0.439 (5, 0.024)	0.267 (1)	0.293 (1)	0.148 (1)	—
Silver fir	0.371 (2, 0.014)	0.224 (1)	0.172 (4, 0.027)	—	—
Western white pine	—	—	—	0.189 (1)	—
Unknown	—	—	0.168 (4, 0.034)	0.163 (8, 0.021)	0.138 (22, 0.008)
All class IV; class III silver fir and unknowns	—	—	—	0.182 (28, 0.013)	—
All class II; class III western hemlock, Douglas-fir and grand fir	—	0.272 (16, 0.026)	—	—	—

[a]Fresh stumps sampled in adjacent clear cut, summer 1977.

bark. Their densities were similar to class IV Douglas-fir and grand fir logs, which tended to be of large diameter. Other class III logs, mostly Douglas-fir and large-diameter hemlock, were grouped with class II. This arrangement gave means with low variances and seemed to make sense biologically (Table 5).

Mean density of snag wood was 0.34 g/cm^3 (SE = 0.02). Because of technical difficulties, only lower portions of recently dead, sound snags were sampled. Consequently, our value was biased and was too high to use as an average for all snags and stubs (stumps of disintegrated snags). Snag biomass was estimated with the assumption that partially and well-decayed snags had the same average densities as class III and IV logs (0.24 and 0.18 g/cm^3) and that stubs had the same average density as class V logs (0.14).

Densities (Table 5) and detailed measurements of each log and snag on the debris plots at the T. T. Munger old-growth site were used to calculate biomass and volume of standing and fallen dead trees by species for each plot, and from these values averages were calculated for the entire stand. Biomass of fallen logs averaged 81 Mg/ha (SE = 11) and of snags and stubs 54 Mg/ha (SE = 15). Volume of fallen logs averaged 396 m^3/ha (SE = 45) and of snags 270 m^3/ha (SE = 70).

Class I and II logs accounted for little mass or volume except for 7.9 Mg/ha contributed by a single class I red cedar log at plot 26. Log biomass decreased in the order class III > class IV > class V. Volumes in decay classes III, IV, and V were roughly equal.

Discussion

Input to the forest floor

Dry-matter transfer from living trees to standing and fallen dead trees ranged from 1.5 to 4.5 Mg · ha^{-1} · year^{-1} and averaged 2.7 Mg · ha^{-1} · year^{-1}. Gessel and Turner (1976) compiled leaf fall and litter fall data for 23 Douglas-fir stands 22–160 years old in the Pacific Northwest. Leaf fall ranged from 1.0 to 2.9 Mg · ha^{-1} · year^{-1} and total litter fall (excluding mortality) from 1.5 to 5.1 Mg · ha^{-1} · year^{-1}.

If the stands studied by Gessel and Turner are not greatly different from those we studied, then mortality is at least as important as leaf fall and can outweigh total litter fall. Moreover, mortality is highly episodic, and there will be many periods in the life of a stand during which it will be the largest term in the equation for aboveground net primary production (NPP). (Aboveground NPP is defined as the sum of net biomass increment, grazing, litter fall, and tree mortality.) If mortality is not taken into account during one of these periods, NPP estimates will be incorrect. Note that NPP is substantial in both young-growth and old-growth stands. However, in the young stands, biomass accretion accounts for much of the net productivity, whereas in the old-growth stands, detrital production accounts for most of it. Detrital production is perhaps not the most economically important component of NPP in the short term, but it may be needed to maintain current levels of soil organic matter and therefore be essential to long-term productivity.

Coarse-root death

When trees die, the dead root systems contribute to the "light-fraction" component of soil organic matter (Greenland and Ford 1964; Ford *et al.* 1969; Paul and Van Veen 1978). Transfer of coarse roots averaged 1.0 Mg · ha^{-1} · year^{-1} at the 11 locations tallied by the U.S. Forest Service, which is small compared with estimates for fine-root turnover in Douglas-fir stands, 8–13 Mg · ha^{-1} · year^{-1} (Fogel and Hunt 1979; Santantonio 1979).

At a hemlock–spruce plot at Cascade Head (plot 12), coarse-root input ranged from 0.1 to 1.9 Mg · ha^{-1} · year^{-1} over the six measurement intervals, values similar to minimum estimates of fine-root turnover at the same site of 1.2–1.5 Mg · ha^{-1} · year^{-1} provided by C. C. Grier (personal communication). Coarse-root turnover may be even more important than the comparison indicates. Unlike fine-root turnover, it is concentrated in a relatively small area of the stand. When mortality is accompanied by root throw, large volumes of soil and even parent material are raised into the air to settle later as the coarse roots decay. At the H. J. Andrews Experimental Forest (watershed 10), it appears that root throw resulted in complete turnover of the soil to a depth of 1 m every 10 000 years (Sollins *et al.* 1980; Swanson *et al.* 1982); however, this calculation was based on sketchy data. Much of the U.S. Forest Service data includes information on cause of death, therefore more accurate calculation of effects of mortality on soil turnover may be possible.

Biomass of snags and fallen logs

Our values for log and snag biomass are within the ranges reported by Franklin and Waring (1980) for a chronosequence of Douglas-fir stands from 125 to 1000+ years old. Their values for log biomass ranged from 60 to 420 Mg/ha and for snag biomass from 26 to 164 Mg/ha. Although the results of both studies appear to agree, careful comparison of densities used to convert volume to biomass is necessary because differences in these values translate proportionally into differences in biomass.

Franklin and Waring based densities primarily on values obtained from a single midelevation Douglas-fir stand at the H. J. Andrews Experimental Forest by Means *et al.* (in preparation[2]). Means *et al.* measured volumes by drying cross sections (and portions thereof) in the laboratory and immersing them in water to measure volume displaced. Some samples were placed in plastic bags to prevent water absorption during immersion. Volume of samples not placed in bags had to be corrected for water absorbed, and all volumes had to be corrected for shrinkage during drying and for compaction of the material during transport and handling. After correction, their mean densities for Douglas-fir boles of decay classes II through V were 0.30, 0.27, 0.23, and 0.21 g/cm^3. The first three values agree quite well with results in Table 5. However, our class V value was lower (0.14 g/cm^3).

The discrepancy between values for class V boles probably results from differences between methods for measuring sample volume. Means *et al.* (see footnote 2) obtained few densities less than 0.15 g/cm^3, but in our study many class IV boles, and virtually all class V, were below that value. The standard error of estimate for class V values in our study was 7% of the mean (n = 22), which indicates a consistent measurement technique, and it seems unlikely that a systematic bias was introduced. I therefore recommend that volume of class IV and V material be measured in the field rather than by water displacement.

At the hemlock–spruce plot at Cascade Head Experimental Forest, Grier (1978) reported 212 Mg/ha fallen log biomass, of which 136 Mg/ha were produced by the current stand and the remainder by the previous stand. His estimates were based on volume and density measurements of all logs in each of 10 randomly selected 2 × 15 m subplots. Densities of logs down 2–38 years, measured by water displacement of frozen samples, ranged from 0.42 to 0.32 g/cm^3, again somewhat higher than values in this study, which suggests that either compaction or water absorption occurred. Class IV material was also sampled, but density values were not reported.

Grier and Logan (1977) reported 190 Mg/ha of fallen logs at the old-growth Douglas-fir stand at watershed 10. They prepared a scale map of the logs on the 10.2-ha watershed and converted area covered by fallen logs to biomass, assuming an average log thickness of 30 cm and an average density of 0.30 g/cm^3 (C. Grier, personal communication). Class V logs were excluded on the assumption that they had been included in sampling of the litter layer and mineral soil. That Grier and Logan arrived at a value so close to ours and those of Franklin and Waring is perhaps fortuitous but shows that even rough calculations can provide a value sufficiently accurate for many purposes.

We realize that snags were not adequately sampled in this study (or other studies to date). R. L. Graham has systematically sampled snags at the H. J. Andrews Experimental Forest as part of a doctoral research program in progress at Oregon State University. Her

[2]Means, J., K. Cromack, Jr., P. C. McMillan, and A. T. Brown. Modeling change in density of old-growth Douglas-fir logs. In preparation.

density data should greatly improve our ability to estimate snag biomass.

Decay classification of fallen logs

Three summers of fieldwork have provided a basis for reinterpreting the decay classification scheme (Table 3). We now understand that the decay classes correlate well with structural, biochemical, and ecological characteristics of the logs.

Large-diameter Douglas-fir boles have deeply furrowed bark, often exceeding 12 cm thickness, which produces a distinctive decay pattern. Because of its roughness, large amounts of organic debris accumulate on the upper surface, providing a seedbed for a variety of plants. Typically, the sapwood rots first, then the bark loosens, and because of its weight, falls off. In class II logs, the bark is still intact. Seedlings germinate but rarely survive because they are unable to penetrate into the sapwood. The transition from class II to III is marked by rotting of the sapwood, which causes the bark to loosen and to slough and which also permits seedlings to establish root systems in the sapwood. Silvester *et al.* (in preparation[3]) have found that class II and III sapwood support the highest rates of N fixation. Consequently, once seedlings penetrate the bark, they may have access to a large available pool of N.

The transition from class III to class IV is marked by rotting of the heartwood until the log cannot support its own weight. Thus branch stubs can be pulled from class IV but not from class III logs. Roots ramify throughout the heartwood of class IV logs but are restricted to the sapwood in class III logs. The transition to class V, less well-defined, consists of a settling process in which the logs flatten and sink into the forest floor.

Although this decay pattern holds well for thick-barked trees, such as large-diameter Douglas-fir and Sitka spruce, it appears not to hold for thin-barked species such as hemlock and the true firs (*Abies*), or for small-diameter Douglas-fir, which tend to be thinner barked than their massive relatives. Probably because it is lighter, the thin bark remains attached and largely intact well after sapwood and heartwood have rotted. These "shell" logs support their own weight but disintegrate when stepped upon. The bark is smoother, therefore litter doesn't accumulate, and such logs seem to provide a poorer bed for seedling establishment.

The decay pattern is also different for snags, especially those of large Douglas-fir. On these the bark sloughs early in the decay sequence and falls to the ground (Cline *et al.* 1980). Often the sapwood rots and sloughs before the snag falls. The absence of bark and sapwood alters the subsequent decay pattern. Snags that fall after the sapwood has fallen away do not appear to provide good sites for seedling growth. This may also be true of fire-charred logs and snags, probably because the sapwood has been burned (see also Kaarik 1974).

Decay rate

A simple equation for the rate of change of material in a compartment is $\Delta X/\Delta t = I(t) - kX$, where X is the amount of material in the compartment, k is the decay rate constant, and $I(t)$ is rate of input. At the old-growth T. T. Munger RNA in Washington, values for both the amount in 1979–1980 and the long-term rate of input were available for 1947–1976. (To calculate input, only bole material was considered because the X value did not include branch material.) If we assume that this old-growth system is in steady state, then $\Delta X/\Delta t = 0$. If we further assume that the input rate is constant over long periods, then $k = I/X$. (This indirect method was used first by Jenny *et al.* (1949) to calculate litter decay rates in tropical and temperate regions.) Calculated this way, k for bole wood at the T. T. Munger old-growth site is 0.028/year, slower than 0.05–0.20/year for fine litter in similar environments (Fogel and Cromack 1977).

Mitchell *et al.* (1975) calculated indirectly a decay constant for American chestnut boles in North Carolina by comparing the amount of live boles standing in 1934 just before the chestnut blight with the amount of fallen chestnut boles remaining in 1971. From U.S. Forest Service tallies and biomass regression equations for similar species (Sollins and Anderson 1971), they estimated that 40.5 Mg/ha were present in 1934 and that only 11.8 Mg/ha remained in 1971 (Cromack 1973). Assuming an exponential decay pattern, they calculated a rate constant of $k = 0.031$/year, similar to our value.

At Cascade Head plot 12, Grier (1978) estimated a decay rate constant for hemlock boles that had fallen during the previous 40 years. He measured density of boles for which a tag number could be determined, and was able to estimate from U.S. Forest Service data approximately when the tree died, although not when it fell. Plotting weight remaining (density times volume) against time since death, he calculated that $k = 0.012$/year. A similar procedure was used by Means *et al.* (see footnote 2) at the midelevation old-growth Douglas-fir stand at the H. J. Andrews Experimental Forest, except ages were obtained by coring hemlocks growing on logs and by counting rings in scars formed on live trees when the logs fell. Volume change was not considered. Both their value of 0.006/year and Grier's value are much lower than those calculated indirectly at the T. T. Munger site and in North Carolina.

Comparison of these decay rates is difficult because

[3]Silvester, W. B., P. Sollins, T. Verhoeven, and S. Cline. Nitrogen fixation associated with decomposition of fallen Douglas-fir boles.

methods for determining them vary. Neither Grier nor Means *et al.* sampled logs systematically; consequently they may have undersampled small-diameter material that decays faster. Also, they measured volume by water displacement, which may cause density to be overestimated, and therefore the decay rate to be underestimated. Finally, in both this study and that of Mitchell *et al.* (1975), snags and fallen boles were considered as a single compartment in calculation of the decay rate. Snags were excluded from the study of Means *et al.* (see footnote 2), though many were on the plot. (Few were on the plot Grier studied.) Our observations at the Williamson and T. T. Munger RNA growth plots indicate that snags rarely persist in recognizable form more than about 50 years (see also Cline *et al.* 1980), whereas logs are often still identifiable as to species when 150-year-old hemlocks are growing on them. This suggests that snags decay approximately four to five times faster than fallen boles, and that a decay rate that takes snags into account should be larger than one that does not.

Despite effects of differing methodology, it is clear that k values calculated by dividing input by accumulation are larger than those calculated from density change alone. This is to be expected; only the first method accounts for material lost through fragmentation.

Lambert *et al.* (1980) made explicit the importance of fragmentation in a study of log decay at a subalpine balsam fir stand in New Hampshire. Based on density change alone, k was 0.012/year; based on both density and volume change, k was 0.030/year. They noted that the first value was lower because it included only C, H, and O lost in the respiration stream (plus small amounts of other elements leached from the wood). The difference between the values, 0.018/year, is an estimate of fragmentation, which appears to have contributed more to weight loss at their site than did respiration.

If the difference between density change and total weight loss (respiration plus fragmentation) is recognized, values obtained in the five North American studies agree well. Decay rates based on density change (respiration rates) range from 0.006 to 0.012/year. Decay rates that include fragmentation range, with one exception, from 0.028 to 0.031/year. Only the decay rate of 0.012/year (Grier 1978) based on volume and density change appears low (particularly given the mesic environment at the Oregon coast). It may be low in part because density values were generally higher than those of other studies.

Failure to account for fragmentation of logs and snags is the apparent cause of an error in the element and biomass budgets for the old-growth stand (watershed 10) at the H. J. Andrews Experimental Forest (Grier and Logan 1977; Sollins *et al.* 1980). Decay of coarse woody debris (logs and snags) at watershed 10 was calculated with a k value of 0.009/year, intermediate to values reported by Grier (1978) and Means *et al.* (see footnote 2). This rate, multiplied by a standing crop of 215 Mg/ha, gave a decay transfer of 2.0 $Mg \cdot ha^{-1} \cdot year^{-1}$ from coarse woody debris. With an input of 7.0 $Mg \cdot ha^{-1} \cdot year^{-1}$, accumulation was 5.0 $Mg \cdot ha^{-1} \cdot year^{-1}$, a high value, given the age of the stand and the likelihood that it was approaching steady state. The decay rate used is much too low. If, instead, steady state is assumed and input is divided by standing crop, the decay rate (0.033/year) agrees with values calculated indirectly at T. T. Munger RNA and Coweeta and directly at New Hampshire.

Results of this study show the value of long-term plots for retrospective studies of decomposition and productivity. Samples have been submitted for nutrient analysis; when results are complete, we will be able to fill important gaps in our understanding of carbon and nutrient transfer through the system from producers into decomposers and finally into the mineral soil. It is unfortunate that so many of the U.S. Forest Service Douglas-fir plots were destroyed by logging and salvage operations during the 1960's. It is commendable that action is being taken now to protect some of the remaining plots.

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