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Water balance of conifer logs in early stages of decomposition*

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Abstract

Seasonal and long-term changes in the water balance of conifer logs during the first 8 years of decomposition were studied in an old-growth *Pseudotsuga/Tsuga* forest in the Oregon Cascade Mountains. Measurements were made of the moisture content of outer bark, inner bark, sapwood, and heartwood and of the flow of water into and out of logs of four species (*Abies amabilis*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*). After the logs had decomposed from 1 to 2 years, 38–47% of the canopy throughfall landing upon them ran off the surface, 29–34% leached from the bottom, and 21–30% was absorbed and evaporated. After 8 years of decomposition, water entering and then leaching from logs increased 1.3 times while runoff decreased a similar amount. The proportion of water stored by and evaporated from logs in this study indicates that in old growth forests they may intercept 2–5% of the canopy throughfall to the forest floor and that, even in early stages of decomposition, they may affect the hydrological cycle of Pacific Northwest old-growth forests.

Introduction

The water balance of logs and other forms of coarse woody debris may strongly influence ecosystem functions (Harmon et al., 1986); for example, moisture strongly affects decomposition (Carpenter et al., 1988; Harmon and Chen, 1991; Harmon et al., 1987). In cool, humid climates such as those found in the Pacific Northwest, decomposition can be extremely slow, leading to large accumulations of coarse woody debris (Agee and Huff, 1987; Grier and Logan, 1977; Grier, 1978). Extremely dry environments may also reduce decomposition, most notably that of standing dead trees (Hinds et al., 1965). Moisture not only determines the decomposition rate but also the amount of fuel available for combustion (Brown et al., 1991; Fosberg, 1971; Sandberg and Ottmar, 1983). Also, the flow of water over and through coarse woody debris results in a significant flux of carbon and nutrients into and out of logs (Matson et al, 1987; Yavitt and Fahey, 1985).

Although the interception of water by forest floors has been considered in many hydrological calculations, the effects of coarse woody detritus has not (Sollins et al., 1980). In ecosystems such as those in the Pacific Northwest where in old-growth forests the forest floor may be covered more than 25% by coarse woody debris, the interception value may be significantly underestimated. Despite the many ways water affects processes occurring in coarse woody debris, and therefore its effect on ecosystems, water balance of woody detritus has seldom been studied. Boddy (1983) examined the seasonal patterns of branch wood moisture in a deciduous forest and, as might be expected, moisture contents were highest during winter when precipitation recharged moisture and evaporation was low. She found that moisture content of decaying hardwood species at saturation decreased with density, a relationship that has also been demonstrated for sound wood (Peck, 1953). Although bark cover or thickness is often assumed to influence drying rates (Sollins et al., 1987), Boddy did not find significantly faster drying in barkless branches. Brackebush (1975) summarized a 19-year record of moisture content in coarse woody material during the fire season in Rocky Mountain forests.

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Moisture content decreased with decreasing size, exposure to sunlight, and suspension off the ground. As with Boddy's study of smaller material, moisture content was highest in early summer, decreased during the summer despite occasional rain, and began to recharge in the fall.

Our study, made each season during the first 8 years of log decomposition, is part of a large long-term investigation of the decomposition and nutrient cycling of 50-cm-diameter logs that was established in 1985 at the H J Andrews Experimental Forest, near Eugene, Oregon (Harmon, 1992). To date, the logs have been examined for initial tannin, phenolic and pentane extractive chemistry (Kelsey and Harmon, 1989), fungal colonization and foodweb structure (Carpenter et al., 1988; Schowalter et al., 1992), patterns of nitrogen fixation (Griffiths et al., 1993), and nutrient exports by fungal sporocarps (Harmon et al., 1994). Additionally, data on patterns of decay colonization, seasonal respiration rates, mass loss, nutrient concentrations, and leaching rates are also being gathered. As moisture content influences many of these processes, it seemed that understanding changes over time in the water balance of downed logs would be crucial to understanding their effect on other parts of the ecosystem. Unlike previous studies of changes in the water balance of conifer logs, this one examines not only changes in their moisture content but also the water flow into and out of them. We considered these components: input by canopy throughfall, water running off the upper log surface, water absorbed and later leached from the bottom of the log, and water absorbed and later evaporated.

Materials and methods

Study area and background sampling

This study was conducted at six old-growth forest sites within the H J Andrews Experimental forest in the Cascade Mountains of Oregon (Harmon, 1992; Harmon et al., 1994). Sites were selected to represent typical old-growth forests in the mid-elevational range from 530 to 1150 m. Slopes at all sites were less than 10%. The general climate is maritime and wet (McKee and Bierlmaier, 1987). Mean annual air temperatures range from 8.0° to 9.9°C and mean annual precipitation from 207 to 232 cm at the six sites (Harmon, 1992). Soils are deep well-drained Typic Dystrochrepts (Griffiths et al., 1993). (For more site details and fuller description of the larger study, see Harmon 1992, available from the senior author).

The 24 logs used in this portion of the study were some of 530 logs of the larger study of log decomposition previously mentioned. Live, healthy trees of four species common to the area *Abies amabilis*, (Pacific silver fir), *Pseudotsuga menziesii* (Douglas-fir), *Thuja plicata* (western redcedar), and *Tsuga heterophylla* (western hemlock) were felled in 1985 and cut into 5.5 m lengths. After yarding, the log were trucked to the six sites (each approximately 10 ha in area) and were placed on the forest floor with a mobile loader. Cross-sections were removed from each end of each log for determining initial volume, density, moisture content and nutrient content of four tissues – outer bark, inner bark, sapwood, and heartwood (Carpenter et al., 1988; Griffiths et al., 1993; Harmon, 1992). Log volume was calculated from length, end diameters, and midlength diameter by means of Newton's formula (Harmon, 1992). Surface area was calculated from diameters and length with the assumption that logs were frustums of cones. The fraction of logs composed of the various tissues was measured from a color photographic slide of each cross-section by means of reverse-projection digitizing (Harmon, 1992).

Sampling moisture content

In 1986–1992, one log of each species at each site was sampled in September primarily for measuring annual changes in tissue density. In 1986–90, five cross-sections were removed annually from each log sampled, and in 1991–92, two more cross-sections were removed from each of the same logs. For each year's sampling, the density and field moisture content of outer bark, inner bark, sapwood, and heartwood was measured (Griffiths et al., 1993; Harmon, 1992). Density was estimated by cutting blocks of the various tissues from the cross-sections, measuring the external dimensions for calculating volume, and determining the oven dry weight at 55°C.

Moisture content of logs lying on the forest floor (field moisture content) was also determined between May 1986 and November 1988 from one log of each species that was kept intact at each of the six sites. Samples were taken at roughly monthly intervals to give seasonal trends rather than the annual trends revealed by cross-section sampling. Wood samples were extracted from these logs with an increment corer (3-mm diameter) and were placed in sealed plastic straws. Two bark samples were removed from each log by hammering a corer (2-cm diameter) into the log until the bark layer could be removed. The bark samples were wrapped in plastic until laboratory processing. All holes created by the sampling were sealed with silicone rubber caulking. In the laboratory, wood samples of each species were separated into sapwood and heartwood. Bark samples of all species except *Abies* were separated into inner and outer bark layers. *Abies* bark was kept intact as the separation of bark into distinct layers was extremely difficult. Wet weight of the samples was determined to the nearest 0.001 g before and after drying for 4 days at 55°C.

The maximum potential moisture content for undecayed and decayed tissues of each species was determined by submersing samples (approximately 100 cm^3) under water for 1 month (heartwood samples absorbed water slowly). As the maximum potential moisture content of samples was dependent upon density, a range of samples from sound to extremely decayed was tested for each log species. Decayed samples were from the cross-sections taken from logs in 1992 after 7 years of decomposition.

Field moisture content was calculated as mass of water divided by mass of dry material in each sample. The mass of water contained within entire logs was calculated by multiplying the mass of each tissue type by the field moisture content of each layer. The mass of each tissue type was calculated from the average volume of tissues for each species and the average density for each species, tissue, and time of field moisture sampling. Densities for each year were adjusted in the fall. As seasonal respiration data indicate that $> 90\%$ of the decline in density occurs between July and September (Carpenter et al., 1988), there is little error in water stores resulting from an annual density adjustment. The maximum potential moisture content was estimated from tissue-specific regressions with density as the independent variable. The maximum potential water stores were calculated by multiplying the maximum potential moisture content by the mass of each tissue type. Total log density was calculated for each year by dividing the total mass of all tissue types by the total log volume.

Water flows 1986–1989

Water collectors were installed in 1986 for one log of each species at each site. Three flows of water were measured: canopy throughfall, runoff from the tops of the logs, and leachates from the bottom. Canopy throughfall and bottom leachate flows were measured for all species, runoff flows from the tops of logs for only one species at each site. Canopy throughfall collectors were galvanized steel triangles (collection area 900 cm^2) placed next to each log. Bottom collectors, two aluminium sheets approximately 0.5 m long attached parallel to the ground on opposite sides of each log, caught and channelled leachate water dripping from the lower surface of a log into a galvanized steel triangle. So that runoff would not enter these collectors, their tops were sealed with silicone rubber. The projected area of the bottom collectors was approximately 2500 cm^2 (actual area was recorded for each log). Runoff water from the top half of each log was diverted to a side collector attached above the bottom collector. Catchment area for these side traps was approximately half that of the bottom collectors. Water diverted into the collectors was stored in 20-L plastic jugs, and the volume was measured at intervals of 2 weeks to 1 month. As runoff was not measured on all logs during this sampling period, the relationship between runoff and canopy throughfall for logs with runoff collectors was used for estimating the runoff from all logs.

Water flows 1991–1993

After a hiatus in 1990, new collectors that allowed a longer collection period before storage capacity was exceeded were installed in 1991 on the logs used in 1986–1989. For each log, there were separate collectors for canopy throughfall, runoff, and leachates. The throughfall collector was a plastic funnel with an area of 317 cm^2 that was placed next to each log. Side collectors for runoff from the tops of logs were plastic trays that had been cut in half for sampling a 25-cm log length. The side collection area ranged from 488 to 768 cm^2. Leachate collectors were flexible, corrugated plastic pipe (12.5-cm diameter) cut longitudinally into thirds and attached around the bottom half of each log. The pipes were lined with plastic film so leachate would not collect in the corrugated ridges. Water was channelled into a plastic funnel similar to those used in throughfall collections. As with the collectors used in 1986–1989, the tops of leachate collectors were sealed so that runoff was unable to enter. The leachate collector area ranged from 577 to 740 cm^2. Water volume moving through the collectors was measured from that stored in 20-L jugs at two of the sites during 1991–1993. At the other four sites, it was measured from the throughfall collectors at each sampling time. The proportion of water running off the sides and leaching out the bottom at those sites was periodically sampled in order to develop a water-flow model for each log (see Statistical-analysis section). Total runoff and leachate flows were then estimated from throughfall flows for the logs at those sites with log-specific models. The proportion of water absorbed and evaporated (A + E) was estimated as the difference between the volume of canopy throughfall (T) and the sum of leaching (L) and runoff (R): $A + E = T - L - R$.

Statistical analysis

Linear regressions were calculated with leachate volume and runoff volume as dependent variables and canopy throughfall volume as the independent variable. Because preliminary tests indicated that the Y-intercept did not differ significantly from zero, regressions were calculated with the Y-intercept as zero.

The model used to estimate flows was therefore of the form: $Y = B_1X$, where Y is the flow to be estimated, X is canopy throughfall, and B_1 is the regression coefficient. A simple linear model was used, as polynomial models often predicted more leachate and runoff flow than canopy throughfall.

To test whether log species had a significant effect on the proportion of leachate and runoff, the regression coefficients (B_1) for each log were used as the dependent variables in an analysis of variance. As these regressions are linear and have a Y-intercept of zero, the regression coefficients represent an estimate of the mean proportional flow of leachate or runoff. This test was performed separately for each observation period (1986–1989, 1991–1993) with a single factoral experimental design.

Drying rates of the four tissue types were estimated by selecting periods when moisture contents decreased, then regressing the natural logarithm of moisture content against the length of the drying period. Differences in the drying rates of species of log and tissue type were tested with the rates of drying for 3–4 periods as the dependent variable in a two-way ANOVA. Regression analysis was used to test whether drying rate was a function of mean temperature for the different drying periods.

Polynomial regression analysis with time and the square of time as independent variables was used to test the significance of long-term trends in sapwood moisture content and log water stores. Each log species was examined separately in these tests.

Analysis of variance was used to compare the moisture contents of inner and outer bark individually for the three species that provided separate samples of those layers. In order to eliminate seasonal change, sample time was used for blocking moisture content in a randomized complete-block design.

A three-way analysis of variance tested the effect of log species, tissue type, and time of log exposure to decay on maximum potential moisture content. The experimental design was a randomized, complete factorial.

The mean annual rate of decomposition of tissue types and entire logs was estimated by means of regression, with the natural logarithm of mean density as the dependent variable and time of log exposure to decomposition as the independent variable. All statistical tests were performed with PC-SAS (SAS Institute Inc., 1985).

Results

Moisture content

The seasonal and long-term patterns of field moisture content varied greatly among tissue types (Figs. 1–2). The heartwood of all four species was stable, with little seasonal variation in moisture content during 1986–88 or 1989–93 (Fig. 1), indicating no absorption of water even after 8 years of exposure to precipitation. Heartwood probably remains unimportant to log water balance until extensive decomposition of this layer has started.

The inner and outer bark layers showed seasonal fluctuations in field moisture content, the highest values in late winter and the lowest in late summer (Fig. 2). These seasonal changes followed the pattern of precipitation at the H J Andrews meterological station (Bierlmaier and McKee, 1989). Analysis of variance indicated that inner bark of *Pseudotsuga*, *Thuja*, and *Tsuga* logs was always significantly ($p < 0.01$) moister than outer bark (ranges 63–206% and 20–95%, respectively). The mixed inner and outer bark of *Abies* fluctuated seasonally as well (field moisture content range: 52–135%).

Sapwood showed the most complicated temporal patterns of moisture content, having both seasonal cycles and a long-term drying trend during 1986–88 (Fig. 1). Seasonal cycles in field moisture content were not as evident in sapwood as in outer and inner bark (Fig. 2), and during some periods of precipitation, sapwood moisture content did not increase, which may indicate that water was unable to infiltrate the sap-

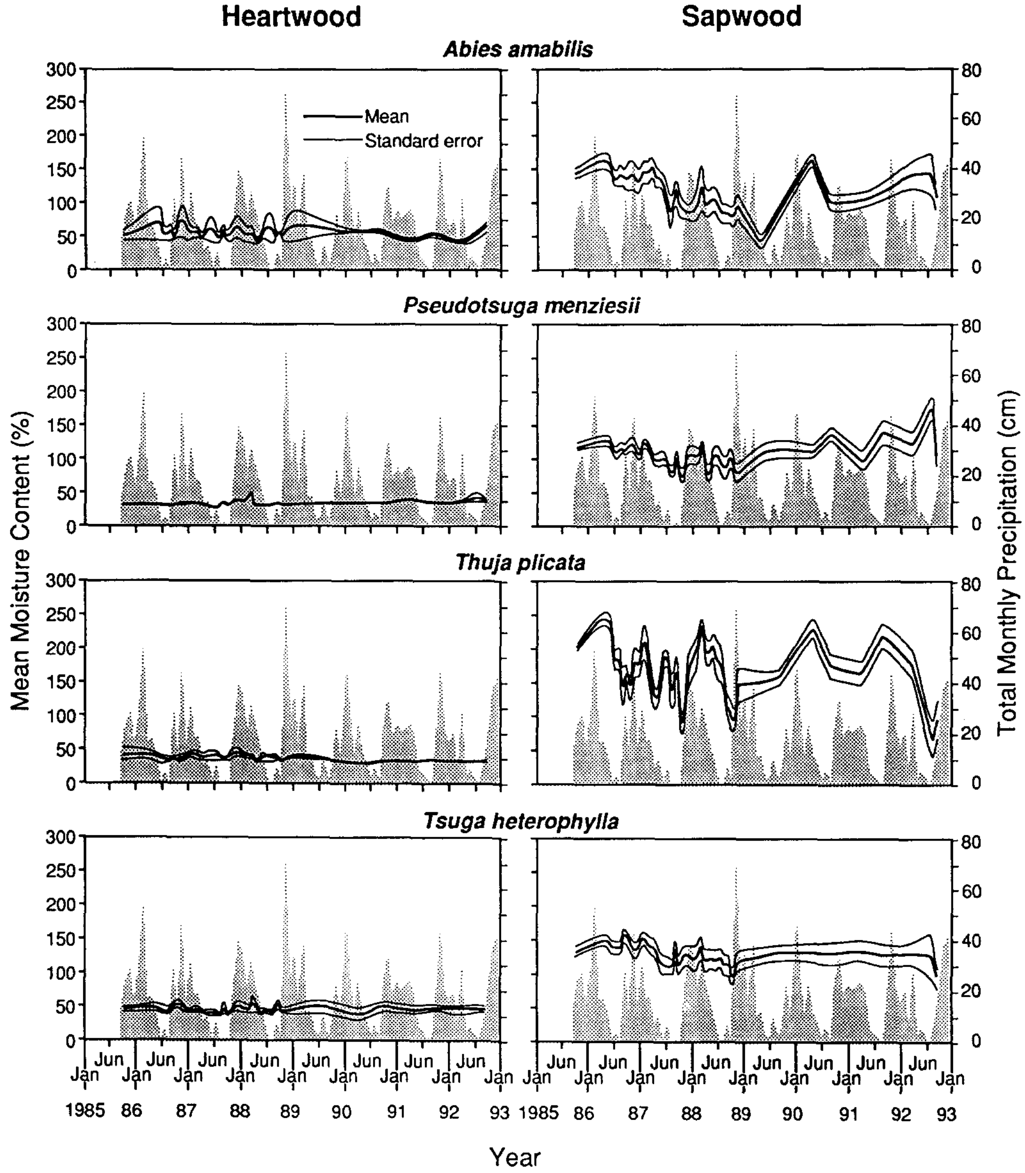

Fig. 1. Mean moisture content of heartwood and sapwood in conifer logs of four species, and monthly precipitation during the first 8 years of decomposition. Monthly sampling was conducted until September 1988. Precipitation data, shown as a gray histogram, is from the Primary Meterological Station, H J Andrews Experimental Forest (Bierlmaier and McKee, 1989). (Original data is available from the senior author).

wood readily. The overall drying trend, which regression analysis indicated was highly statistically significant ($p < 0.01$) for all species except *Thuja* during 1986–88, may have also been caused by poor infiltration of water into relatively sound sapwood. There is evidence that as decomposition proceeded during 1989–93, the field moisture content of *Abies* and *Pseudotsuga* sapwood increased. Regression analysis indicates the 1986–93 data for *Abies* and *Pseudotsuga* had a highly significant ($p < 0.01$) polynomial trend: sapwood moisture content decreased the first 4 years and then increased. *Thuja* showed a similar long-term pattern, but the relationship was not significant. *Tsuga* sapwood moisture content initially decreased and then appeared stable between 1989–93, although the overall trend was not significant.

The rate of drying differed significantly among tissues in all species of log (Table 1). Drying rates

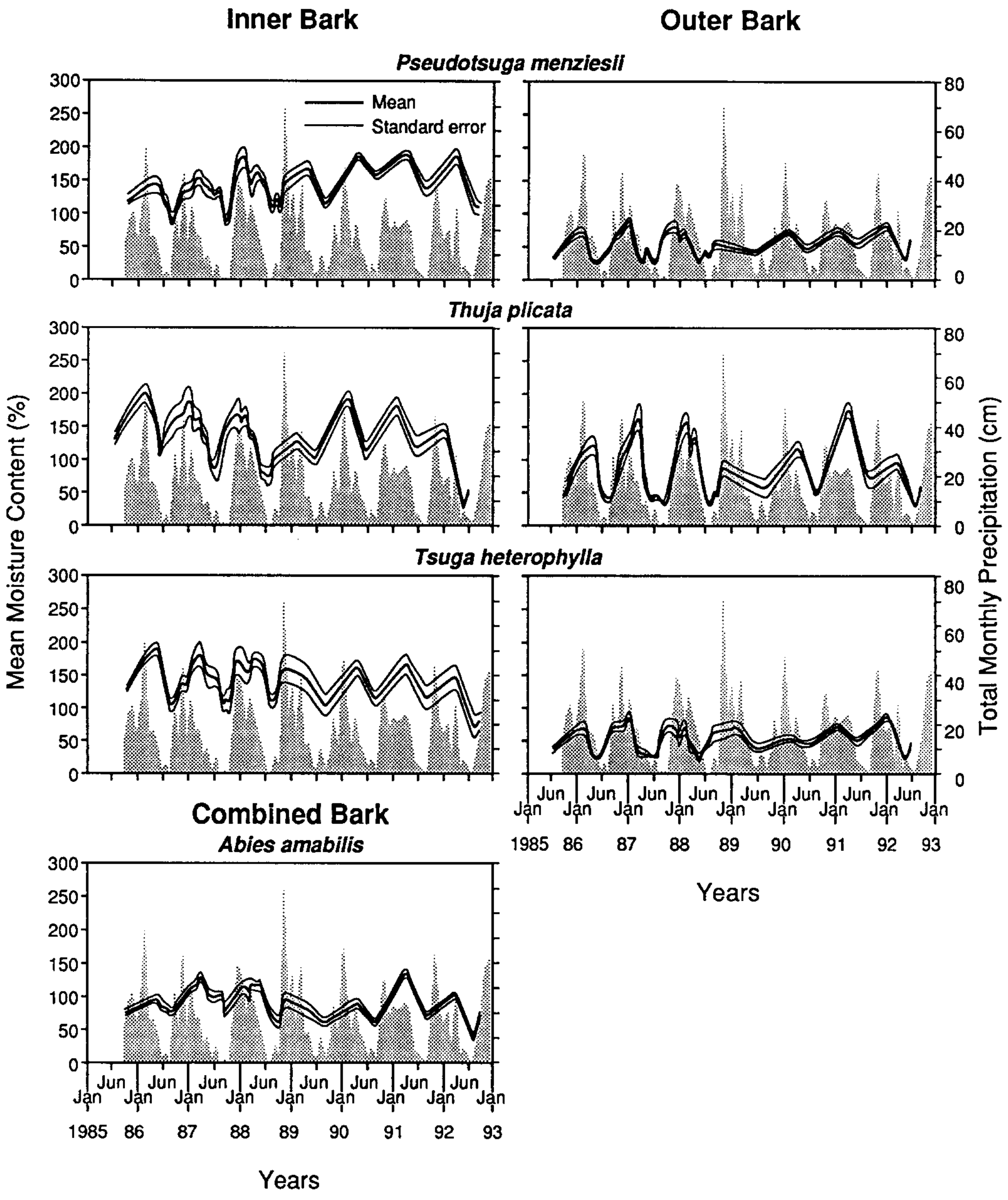

Fig. 2. Mean moisture content of outer and inner bark of conifer logs of four species and monthly precipitation during the first 8 years of decomposition. The outer bark and inner bark of *Abies amabilis* were difficult to separate, hence they were combined. Monthly sampling was conducted until September 1988. Precipitation data, shown as a gray histogram, is from the Primary Meterological Station, H J Andrews Experimental Forest (Bierlmaier and McKee, 1989). (Original data is available from the senior author).

appeared to be functions of the degree of exposure, on the order outer bark > inner bark > sapwood. Drying of outer bark and sapwood also differed significantly among species. The rate for outer bark appeared to be inversely related to bark density; *Thuja* bark (density 0.32 g cm^{-3}) dried faster than *Pseudotsuga* and *Tsuga* bark (density 0.44 g cm^{-3}). Differences in sapwood drying rates among species appeared to be related to thickness; *Thuja* sapwood (mean thickness 2.2 cm) dried 4 times faster than *Tsuga* sapwood (mean thickness 7.9 cm).

Regression analysis indicated that rates of drying for outer and inner bark increased significantly ($p < 0.01$) with temperature; however, the relationships are of limited quantitative use as light precipitation during some of the 3-4 week drying cycles may

Table 1. Drying rates of sapwood and outer and inner bark of logs of four conifer species[a]

Species	Drying-rate constant (day^{-1})[b]		
	Outer bark	Inner bark	Sapwood
Abies amabilis	0.0052 (0.0019)[c]		0.0025 (0.0007)
Pseudotsuga menziesii	0.0109 (0.0012)	0.0048 (0.0003)	0.0023 (0.0007)
Thuja plicata	0.0168 (0.0014)	0.0054 (0.0004)	0.0056 (0.0003)
Tsuga heterophylla	0.0123 (0.0003)	0.0047 (0.0013)	0.0015 (0.0006)

[a] Mean and standard error ($n = 3$).
[b] Based on exponential decay function $Y_t = Y_0e^{-kt}$, where Y_t is the moisture content at time t, Y_0 is the initial moisture content, and k is the drying-rate constant.
[c] Outer and inner bark combined.

Table 2. Maximum potential moisture content (%) of bark and wood of four conifer species before (1986) and after (1992) 7 years of decomposition[a]

Species	Outer bark			Inner bark			Sapwood			Heartwood		
	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	N
Sound material (Sept. 1986)												
Abies amabilis	147	(2)	7	NA			160	(9)	7	97	(3)	7
Pseudotsuga menziesii	97	(4)	14	250	(19)	12	120	(5)	7	95	(4)	7
Thuja plicata	160	(11)	7	269	(7)	7	270	(9)	7	146	(7)	7
Tsuga heterophylla	138	(5)	7	245	(6)	7	127	(3)	7	97	(3)	7
Decayed material (Sept. 1992)												
Abies amabilis	166	(28)	5	NA			367	(32)	15	294	(19)	25
Pseudotsuga menziesii	102	(14)	5	173	(3)	5	189	(12)	16	85	(3)	17
Thuja plicata	177	(6)	5	239	(11)	5	312	(22)	15	146	(7)	22
Tsuga heterophylla	95	(7)	5	206	(16)	5	195	(12)	15	154	(9)	31

[a] S.E. = standard error, N = number, NA = not applicable.

have led to underestimates. Moreover, the temperature range was limited (6°–20°C) because extended drying periods were warm periods. Despite these shortcomings, it was clear that even when temperatures were low (6°C), the drying rate of outer and inner bark exceeded 0.008 and 0.0027 day^{-1}, respectively. At these rates, a week without precipitation could lead, respectively, to 5% and 2% stored-water loss in bark layers. While these amounts may seem to be insignificant, such repeated short-term losses during cool periods may mean considerable water loss over the year.

The maximum potential moisture content differed significantly between first and last measurement time (Table 2) and among species and tissue types. Analysis of variance inicated highly significant interactions of species X tissue type, species X time, and tissue type X time. This complex pattern is probably caused largely by the different decreases in density of the various tissue types over the 1986–92 period; for example, in sapwood of all four species, the maximum mois-

Table 3. Statistically significant ($p < 0.05$) regressions between density of tissue type and maximum potential moisture content[a], all species combined

Tissue	B_0	B_1	r^2	N
Heartwood	972	5.37	0.80	96
Inner bark	605	2.61	0.66	26
Sapwood	834	4.18	0.86	62
All types	726	4.08	0.60	219

[a] Regressions were of the form $Y = B_0e^{-B_1X}$, where Y is maximum moisture content (%) and X is tissue density (g cm^{-3}).

Table 4. Relationship of canopy throughfall volume to leachate and runoff volume

Measurement period; Species	Leachate/throughfall ratio			Run-off throughfall ratio		
	Mean	Standard error	N	Mean	Standard error	N
1986–88						
Abies amabilis	0.301	0.040	6	0.455		1
Pseudotsuga menziesii	0.344	0.033	6	0.335	0.147	2
Thuja plicata	0.296	0.022	6	0.339		1
Tsuga heterophylla	0.319	0.025	6	0.396	0.031	2
All species	0.315	0.015	24	0.376	0.044	6
1991–93						
Abies amabilis	0.500	0.024	6	0.250	0.092	6
Pseudotsuga menziesii	0.378	0.048	6	0.242	0.071	6
Thuja plicata	0.337	0.072	6	0.442	0.035	6
Tsuga heterophylla	0.499	0.020	6	0.216	0.053	6
All species	0.428	0.026	24	0.288	0.072	24

ture content increased as decay progressed and density declined. During the first 8 years of decomposition, changes in sapwood density were largest in *Abies* ($k = -0.071$ year^{-1}), but similar for the other three species ($k = -0.036$ to -0.042 year^{-1}). In heartwood, the pattern was more complex: in species subject to heartwood decay (*Abies* and *Tsuga*) maximum potential moisture content increased; in those with decay-resistant heartwood (*Pseudotsuga* and *Thuja*) maximum potential moisture content remained constant. Regression analysis indicated that heartwood decay was fastest in *Abies* ($k = -0.033$ year^{-1}) and intermediate in *Tsuga* ($k = -0.009$ year^{-1}). There was no significant decrease in heartwood density of *Pseudotsuga* or *Thuga* during the first 8 years. As has been found for sound sapwood (Peck, 1953), a significant negative exponential relationship was found between sapwood and heartwood density and maximum potential moisture content regardless of state of decay (Table 3). A highly significant, but weaker relationship was also found for inner bark, which was the tissue type with the fastest decay rates, ranging from 0.059 year^{-1} in *Tsuga* to 0.128 year^{-1} in *Thuja*. Interestingly, no significant relationship appeared between outer bark density and maximum moisture content, perhaps because the density did not change greatly over the time period examined. Regression analysis indicated *Thuja* and *Tsuga* outer bark had significant ($p < 0.05$) decay over this period with rates of 0.021 and 0.017 year^{-1}, respectively. *Pseudotsuga* did not show a significant change in outer bark density.

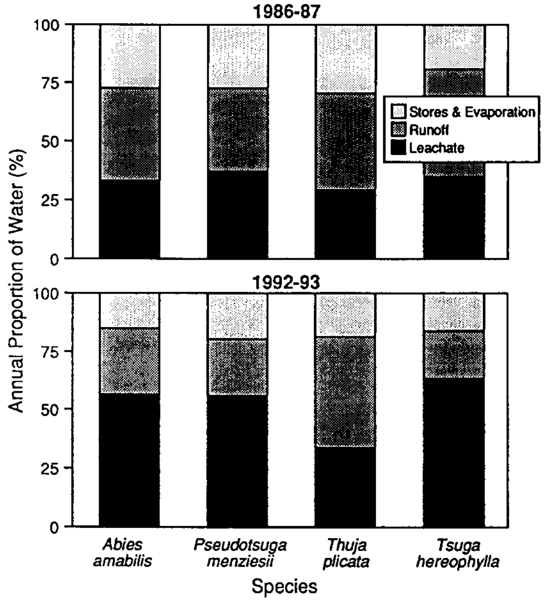

Fig. 3. Annual proportion of leaching, runoff, and storage and evaporation in four species of conifer logs after 1 and 8 years of decomposition. Total canopy throughfall landing on the logs was estimated to be 1,568 and 1,499 liter m^{-2} log in years 1 and 8, respectively.

Water flows

Correlations between the volumes of leachates and canopy throughfall were highly significant for both 1986–88 and 1991–93. Although species-level regressions were highly significant, the coefficient of determination was greatly increased when regressions were calculated for individual logs. For *Pseudotsuga*, for example, the r^2 for species-level regression was 0.58 over 1991–93; r^2 for individuals ranged from 0.75–0.98. The variability among individuals is larger than that among species. Analysis of variance with the proportion of water flowing as leachate as the dependent variable and species as the independent variable showed no significant differences among species for 1986–88. However, differences among species in ratios of leachate to canopy throughfall were significant ($p < 0.05$) in the 1991–93 period, *Abies* and *Tsuga* having higher ratios than *Pseudotsuga* and *Thuja* (Table 4).

The proportion of canopy throughfall leaching through logs increased substantially between 1986–88 and 1991–93 (Table 4), on average, 1.3 times. For some logs, the increase was even more dramatic. The increase was probably caused by the increased decay of the inner bark and sapwood layers during the 8 years the logs have been studied; both layers have lost 25–63% of their initial mass.

For both the 1986–88 and 1991–93 periods, correlations between the volumes of throughfall and runoff were highly significant. As with leachate, there was much log-to-log variation. Analysis of variance of the 1991–93 ratios indicated no significant difference among species. On average, 1.3 times more water ran off during 1986–88 than during 1991–93. In some cases this decrease was dramatic: one log had a runoff-to-throughfall ratio of 0.45 in 1986–88 and 0.08 in 1991–93. Such changes probably resulted from increased decay of underlying layers, as surface roughness and moss and litter cover did not change appreciably.

The water balance of logs changed substantially over the observation period, with a greater amount of rainfall leaching through logs and a smaller proportion running off their tops as decay progressed (Fig. 3). The proportion of water absorbed and then evaporated during the two observation periods appears to have decreased slightly for all the species.

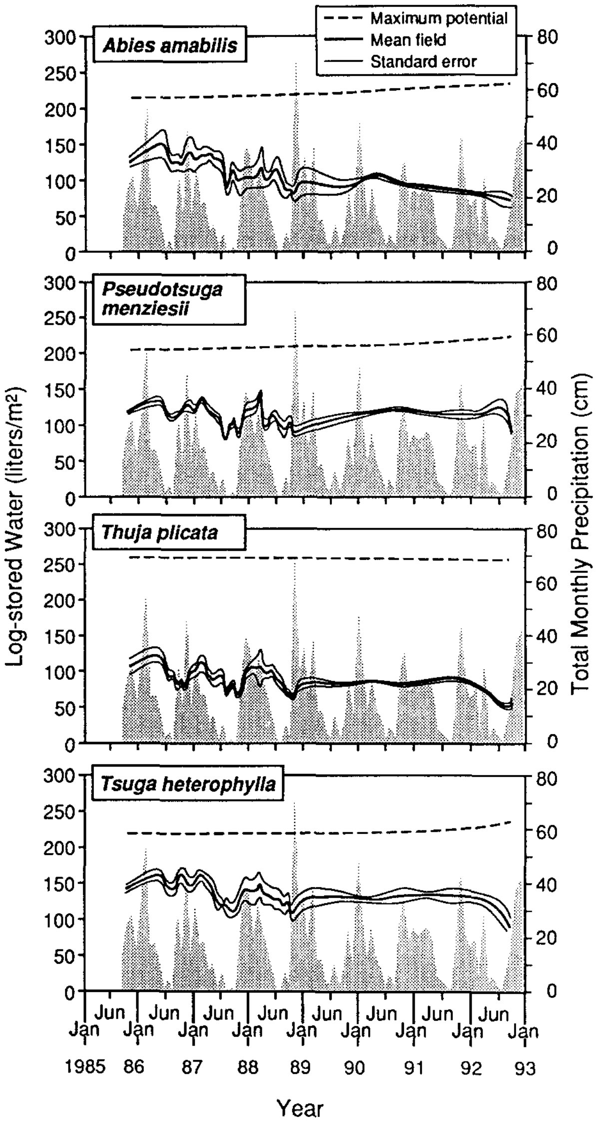

Fig. 4. Mean waterstores in four species of conifer logs during the first 8 years of decomposition. Precipitation data, shown as a gray histogram, is from the Primary Meterological Station, H J Andrews Experimental Forest (Bierlmaier and McKee, 1989). (Original data is available from the senior author).

Water stores

The overall pattern for all four species over 1985–92 was one of reduced water stores with increased decay (Fig. 4). Maximum water volume in logs of all four species appeared in the spring of 1986 (140–160 L m^{-2} projected area). Regression analysis of the 1986–88 trend indicated significant decline in water stores for all four, probably resulting from the steady decline in sapwood moisture during that time. Water stores in *Abies*, *Thuja*, and *Tsuga* logs showed continuing decline over all 8 years of decomposition. In contrast, *Pseudotsuga* logs significantly increased water stores over 1989–93.

The long-term trends in water stored do not necessarily reflect changes in moisture content. Sapwood moisture content of *Abies* logs increased between

1989–93, whereas water stores decreased because of a large decrease in sapwood density that reduced the absolute volume stored.

Actual water stores in the field were 30–50% lower than maximum potential stores estimated from measurements of density and maximum potential moisture content of the various tissues in the laboratory (Fig. 4). The differences stem, in part, from the fact that the heartwood layer did not absorb much water during the 8 years; the greatest difference between observed and maximum potential storage was related to the proportion of heartwood in logs. Other factors may also be at play; however, actual stores generally declined while the maximum potential store increased slightly with increasing decay, indicating that water may be unable to enter the log system despite the fact that decay increases potential storage capacity. The mean log density, for example, has decreased at an annual rate of 0.057, 0.024, 0.015, and 0.018 year^{-1} for *Abies*, *Pseudotsuga*, *Thuja*, and *Tsuga*, respectively.

Seasonal variations in stored-water volume was evident during 1985–88, the maximum in late winter being 20–80 L m^{-2} greater than the minimum in the late summer (Fig. 4). Seasonal fluctuations were less evident during 1989-92 as the late fall sample time allowed some recharge of the bark layers. Summing the decreases in stores over the 1986–87 and 1987–88 periods shows that a minimum of 80–165 and 59–86 L m^{-2}, respectively, evaporated from logs. The water-balance estimates, however, indicate that evaporative losses from logs ranged between 300–515 L m^{-2} and 230–380 L m^{-2} in 1986–87 and 1987–88, respectively. The 1986–87 estimates are likely too low because the rapid drying of bark during short periods without precipitation may have led to considerable water loss from logs. The exact cause for the difference in estimates cannot be resolved without a shorter time resolution and without temperature-specific drying rates.

Discussion

As log decay proceeded, the importance of pathways of water flow changed markedly. Initially almost half of the water landing on logs ran off the top. A surprisingly large proportion (29–34%), however, entered logs and leached from the bottom even after 1 year of decay. It is unlikely this water actually flowed through the logs, as the underlying wood was quite sound. There is evidence that during this early period the sapwood was unable to absorb water during winter. The most likely pathway for leachate flow during the first year was the inner bark layer, but with increasing decay, the sapwood became capable of absorbing and transporting water.

The decreasing proportion of water running off the surfaces of logs by year 8 was unexpected, given that their surface roughness and moss and litter cover were similar to that of logs in the first year of decay. The differences may be due to an increase in the density of insect galleries breaching the outer bark; however, that does not appear to be the case as there were already 280–310 galleries m^{-2} in *Pseudotsuga* and *Tsuga* logs and 50–100 m^{-2} in *Abies* and *Thuja* logs in the first year (Zhong and Schowalter, 1989). Despite the difference in gallery density, the proportion of water runoff did not differ significantly among log species. Another factor explaining the decreasing proportion of runoff may be the increasing wood decay. By decreasing density, decay allows wood to store a larger proportion of water (Boddy, 1983; Peck, 1953), and by decreasing wood strength, it leads to the development of cracks that serve as macropores in which water may be rapidly transported from the surface. It is possible that a large amount of water was transported through the bark in the first year but was unable to penetrate the underlying sound wood.

The volume of water apparently lost via evaporation from logs was 2–6 times higher than that estimated from changes in log moisture content during the extended summer drought, indicating that considerable evaporation may occur in other periods, most likely by short-term wetting and drying of the outer and inner bark. Our estimates of drying rates for outer and inner bark indicate that even under cool conditions the bark can dry rapidly.

The large proportion of water stored and evaporated from logs in this study indicates that fallen trees may have important implications for the hydrologic cycle in old-growth Pacific Northwest forests. It is currently estimated that an old-growth canopy intercepts 15% and the forest floor only 1% of precipitation (Rothacher, 1963; Sollins et al., 1980). A rough estimate of stand-level forest-floor interception was made with the assumption that older logs have the same balance of storage, runoff, and leachates as the decayed logs in our study. The range in log projected area in old-growth forests of this region is 10–25% (Harmon et al., 1986), so if logs intercept 20% of the canopy throughfall, a rough stand-level estimate of forest-floor interception in an old-growth forest would be 2–5%. Even that may be an underestimate, as in the most advanced stages of decay, wood can absorb up to 3.5 times its dry weight in water (Sollins et al., 1987).

The large volume of water flowing into and through logs in early stages of decay means that organic matter and nutrients may be transferred to the forest floor even during the early stages of decomposition. Preliminary data on dissolved organic carbon and nitrogen concentrations in bulk solutions for both periods evaluated in this study indicate that 0.30–0.45% of the initial carbon and 0.99–1.86% of the initial nitrogen may have been transferred out over the first 8 years (Harmon et al., 1994). The mass of organic matter and nitrogen annually transferred from logs increased at least 10- and 16-fold, respectively, over the 8-year period. This change is due not only to an increase in leachate concentrations, but also to the greater proportion of water flowing into and subsequently leaching out of logs. The long-term implications of these flows are unknown; however, given their relatively low pH (5.4) and high organic content, the potential exists to alter the properties of the underlying soil (Yavitt and Fahey, 1985).

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