

Water Dynamics in Conifer Logs in Early Stages of Decay in the Pacific Northwest, U.S.A.

Abstract

Water dynamics in decaying conifer logs of four species (*Abies amabilis* [Pacific silver fir], *Pseudotsuga menziesii* [Douglas-fir], *Thuja plicata* [western red cedar], and *Tsuga heterophylla* [western hemlock]) were studied in the Coast Range of Oregon. Measurements were made of throughfall, leachate, runoff, and absorption for logs during their 6th through 8th year of decay. During this period 47-70% of the throughfall landing on the logs evaporated, 18-35% flowed through the log and leached out, 3-29% ran off the surface, and absorption accounted for 3-11%.

Together absorption and evaporation intercepted 60% of the throughfall impacting the logs. Although the second year of the study had twice as much precipitation as the first, the partition of the fluxes was essentially identical. Direct measurement of the changes in log weight allowed calculation of water stores and the evaporative component; the latter proved to be the largest fraction of the water balance, with the majority of losses during the cool, wet, winter period.

Introduction

Water balance is important to understanding decomposition, nutrient cycling, and transfer of materials from decomposing organic matter (Harmon et al. 1986). Although early investigations measured aspects of water dynamics related to forest fuels and fire behavior (Fosberg 1971, Clark 1989), the ecological influence of water dynamics in woody detritus is poorly understood. Decomposition in forests has been shown to be limited by either very moist or very dry conditions (Hinds et al. 1965, Agee and Huff 1987, Progar et al. 2000). Changes in the water balance of woody detritus effect microclimates, and thereby biodiversity (Setälä and Marshall 1994, Rambo and Muir 1998). Beyond the direct effect that moisture content has controlling the rate of decomposition of woody detritus, the flow of water over and through coarse woody debris (CWD) influences the export of nutrients via leaching (Yavitt and Fahey 1985, Matson et al. 1987). Leachates from woody detritus can affect soil biology through input of nutrients (Spears et al. 2003).

Quantitative observation of the rainfall interception, water stores, and evaporation in forest canopies have resulted in predictive models of this system (Rutter et al. 1971, Rutter et al. 1975, Rutter and Morton 1977), but new methods are

improving our understanding of these processes (Klaassen et al. 1998). Researchers modeling the mechanisms of water balance and hydrology in forested ecosystems require similar quantification of the role of woody detritus to fully understand these systems (Nijssen and Lettermaier 1997, Unsworth et al. 2004, Waichler et al. 2005). Measurement of the water dynamics of individual logs may be scaled up to model forest stand or watershed level processes more accurately.

We previously examined water dynamics in conifer logs during the early stages of decomposition (1-8 years) and found between 20 and 30% of the water impacting the log surface was either absorbed or evaporated (Harmon and Sexton 1995), an amount that influences the overall retention of water in forests. For example, in some Pacific Northwest old-growth forests where CWD may cover over 25% of the forest floor, evaporation of the magnitude we observed would be responsible for the loss of 2-5% of the water entering the system even in wet, cool conditions (Harmon and Sexton 1995). The water loss through evaporation was primarily associated with winter wetting and drying cycles and not the summer drought, as we had earlier hypothesized.

Here, we re-examined flow of water and stores in logs in a more controlled experimental setting. Direct measurement of evaporation is difficult; however, measurement of all other inputs, outputs, and stores allowed calculation of the evaporative component in the water balance of these

¹Author to whom correspondence should be addressed.
E-mail: jay.sexton@oregonstate.edu

logs. During prior work it appeared that winter evaporation of available surface moisture exceeded summer evaporation, which is moderated by dry surface layers with less available moisture. Our main objective was to determine if the non-drought evaporation flux was indeed as large, or larger, than that occurring during the summer drought. Secondary objectives were to characterize species differences in water balance, and to investigate the change in water dynamics and water stores within logs over the annual cycle.

Study Area

This study was conducted on Oregon State University's McDonald Research Forest in the Coast Range Mountains of western Oregon. The maritime climate is characterized by cool, moist winters and warm, dry summers. Climate records from the Corvallis Water Bureau meteorological station, 7 km to the west at about the same elevation, indicate average precipitation of 1700 mm per year and mean annual air temperature of 10.2 °C (NCDC 1971-2000 Monthly Normals). We placed the study logs within an even-aged, closed canopy Douglas-fir forest approximately 75 years old. The elevation of the study site was approximately 200 m, with an eastern aspect, and a slope of less than 10%.

The study logs were collected from the H.J. Andrews Experimental Forest, approximately 100 km southeast of this study area, and were part of an ongoing long-term experiment on log decomposition. This decomposition experiment used four species common to this region: *Abies amabilis* (Pacific silver fir), *Pseudotsuga menziesii* (Douglas-fir), *Thuja plicata* (western redcedar), and *Tsuga heterophylla* (western hemlock). The trees had been felled in 1985, with logs between 45 and 60 cm in diameter, with complete bark cover, selected and cut into 5.5 m sections. Tree age was not determined during log selection, although all trees were of similar diameter and had grown in similar forest stands. These logs had spent 6 years, in ground contact, decomposing beneath old-growth Douglas-fir forest within the H. J. Andrews Experimental Forest. In the fall of 1991 two log sections approximately 50 cm in length were cut from a single log of each of the four species and transported to the McDonald Research Forest. The Pacific silver fir, Douglas-fir, and western redcedar log sections varied in diameter between 45 and

50 cm, while the western hemlock sections were slightly larger, averaging 60 cm.

These two log sections do not constitute species replicates, as they were cut from the same individual organism. The measured variation between the two sections per log reflects the variability in the surface and sub-surface details of the two log sections and does not account for potential variability within each species.

Methods

Water Flow Measurement

The logs' cut ends were sealed with molten paraffin to reduce the transfer of water across this surface. Each log was supported horizontally about 60 cm above the forest floor on two wooden "A" frames attached to the cut faces of the logs with large nails. Each "A" frame had been thoroughly coated with water sealant to minimize the moisture content changes within the frames.

We constructed the water collection apparatus (Figure 1) from sheets of low-density polyethylene (LDPE). The bottom collector was a sheet of this plastic cut in a trapezoidal shape and sealed along the horizontal midline on each side of the log using silicon rubber sealant and nails. This shape allowed the sheet to hang lower at one end, facilitating drainage. LDPE crescents were sealed into the pendent arch of the bottom collector and a bead of silicon sealant was run up the edge of the sheet from the tip of the crescent to the point of attachment to the log to guide draining water into the collection area. The lowest point of the collector was pierced with a plastic drain fitting attached to tubing that drained the leachate into a 20-L reservoir.

We constructed the surface runoff collector from a second sheet of LDPE cut to the same shape but slightly larger than the bottom collector. It was attached to the log at the same point as the bottom collector with nails driven through rubber laboratory stoppers to maintain a 2-cm space between the two collector sheets. This sheet was also closed off with LDPE crescents and a silicon bead in the same manner described above and drained into a separate reservoir. The drain tube from the bottom collector passed through a hole in the runoff collector and this passage was sealed with silicon sealant to prevent leakage from the runoff collector. Plastic sheeting was attached to

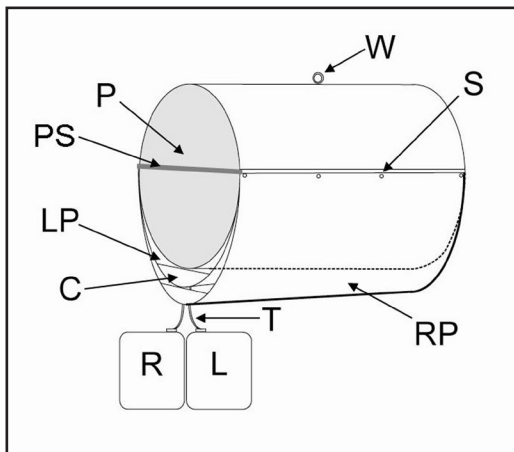


Figure 1. Diagram of Collection Apparatus. The central cylinder of the diagram is the log section, with cut ends (P) sealed with molten paraffin, and an eyebolt (W) mounted at the point of balance on the upper surface, for lifting and weighing the entire assembly with a block and tackle and spring scale. For visibility wooden "A" frame legs attached to the cut surfaces and plastic sheeting attached (at PS) along the horizontal of the mid-line cut are not shown.. A sheet of low-density polyethylene (LDPE) was attached to the log surface with nails and sealed with silicon, along the horizontal mid-line of the exterior surface of the log section to form the leachate collection panel (LP). A slightly larger LDPE sheet forming the run-off collection panel (RP), was attached with nails along the same area but offset two cm radially from the log surface with rubber stopper spacers (S). The ends of both pendent LDPE sheets were closed with LDPE crescents (C) attached with silicon. Drain fittings were sealed at the lowest point of both LDPE sheets and connected with tubing (T) to collection reservoirs for run-off (R) and leachate (L).

the cut faces of the logs to shield the ends of the water collectors from rain splash.

To measure throughfall (the portion of precipitation which penetrates the canopy) we placed four collectors among the experimental logs to estimate the amount of incident throughfall. Each was made from a LDPE laboratory funnel with an opening 20 cm in diameter. The funnel was attached to a wooden stake driven into the ground and tubing drained the funnel into a 20-liter reservoir.

Each log received a heavy screw eye attached at the center of the upper surface of the log (Figure 1). This allowed the log to be suspended from a weighing tripod erected over each log during weighing. A block and tackle attached to a spring

scale, with a capacity of approximately 230 kg, was used to raise each log and measure its weight. The total weight of the individual frame and collection apparatus of each log was known and subtracted from the gross weight to give a net weight equal to the unencumbered log.

The weights of the logs were recorded once per month to determine change in moisture content. At the same time the weight of each reservoir was recorded and then the reservoir was emptied. During months of heavy precipitation the weights were taken twice a month to avoid the overflow of the water collection reservoirs.

Throughfall was partitioned into the fraction absorbed and retained within the logs, that which leached through the logs, that which ran off the bark surface, and that which evaporated to the atmosphere. Evaporation was calculated by mass balance knowing all other components of the water flux and changes in water stores. Summer weight loss is primarily evaporation of water stores accumulated during the wet winter and this commonly exceeds throughfall during periods of low precipitation.

Log Density Measurements

Log density was determined at the start and end of the study to calculate the dry mass of the logs and the loss of mass occurring during the study. In this study cross-sectional samples were cut from the study logs and their dimensions and total wet weight were recorded. Proportionally representative subsamples were dried at 55 °C to calculate the moisture content which was used to calculate oven dry weight of the entire log. Separate densities were calculated for the bark and the wood, and these were weighted by the proportions each of these constituents contributes toward the entire log, to arrive at a total log average density. The proportion of each tissue within a log was measured from color photographic slides of log cross-sections by means of reverse-projection digitizing.

Maximum Field Moisture Determination

The maximum potential moisture content for undecayed and decayed tissues of each species was determined by submersing samples (approximately 100 cm³) under water for 1 month. 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.

Calculations

Field moisture content was calculated by measuring the volume of the bark and wood of each log and multiplying by the densities measured at the start and end of this experiment to arrive at a dry mass for each log. The rate of density change was assumed to be linear throughout the experimental period. The mass of water within each log was estimated as the total mass of each log (corrected for the mass of the attached apparatus) minus the log dry mass. Field moisture content was calculated using the mass of water divided by the dry mass of the log expressed as a percent.

The periods of maximum drying and wetting observed during the study were chosen for the calculation of drying-rate and wetting-rate constants. The rate-constant calculation was based on an exponential function,

$$Y_t=Y_0\ e^{-kt}$$

where Y_t is the moisture content at time t , Y_0 is the moisture content at the beginning of the period, and k is the drying or wetting rate-constant for the log (in day^{-1}).

Linear regressions were calculated with leachate volume and evaporation volume as dependent variables and canopy throughfall as the independent variable. Regressions were calculated with the Y-intercept as zero and a simple linear model with an $\alpha = 0.05$. The lack of true replication minimized the usefulness of statistical analysis in this preliminary study.

Results

Water Stores

A strong seasonal pattern of drying during summers and recharging water stores during winter, with some lags, was apparent (Figure 2). Loss of water stores via evaporation continued at a fairly constant rate from April through October. Water stores were recharged throughout the winter and reached their maximum in early April just before

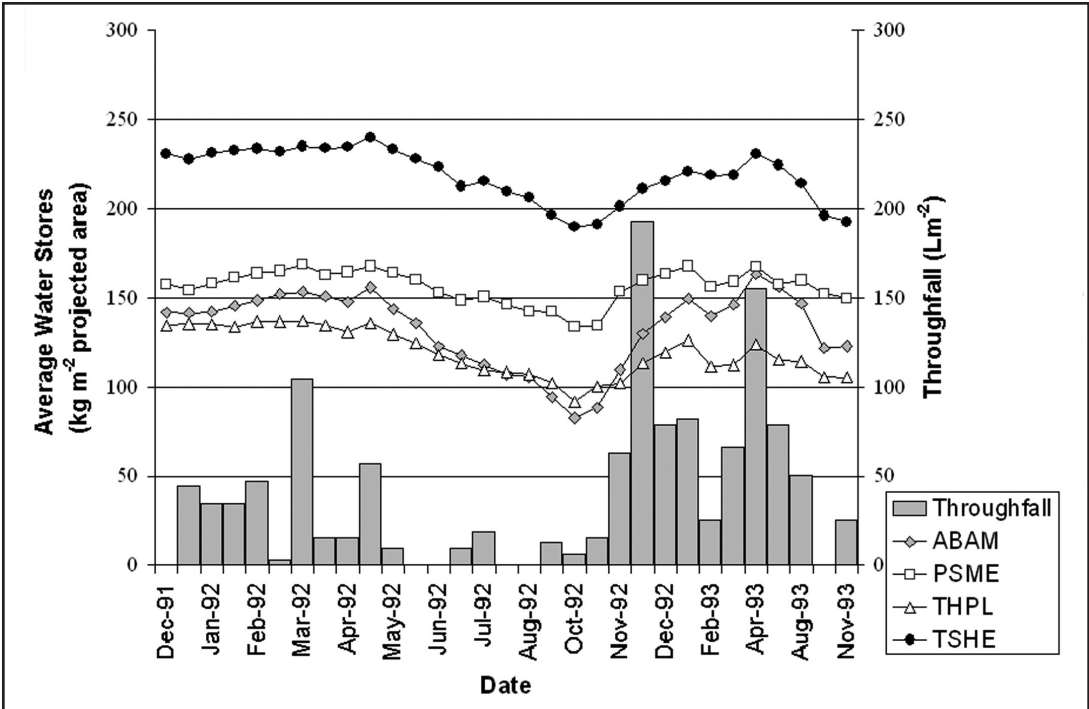


Figure 2. Average water stores (kg m^{-2} ; left vertical axis) of projected surface area of decaying logs and throughfall (L m^{-2}) plotted through time. Two measurements were made from different sections of the same log for *Abies amabilis* (ABAM), *Pseudotsuga menziesii* (PSME), *Thuja plicata* (THPL), and *Tsuga heterophylla* (TSHE).

the beginning of the drying period. Periods of low precipitation during the winter produced noticeable losses in water stores even during periods of cool temperatures.

Water stores varied between species with western redcedar being the least variable and western hemlock the most variable. To compare seasonal changes between species changes can be expressed relative to the minimum stores for each species. Water stores within logs varied by up to 97% of the minimum in Pacific silver fir, and to a lesser amount in the other species, with the least variable being a 25% seasonal change from the minimum in Douglas-fir. At the time scale of our measurement intervals, averaging 19 days during the water partition study, the seasonal trends of summer drying and winter wetting were relatively smooth with few irregularities despite a 2-fold variation from month to month in throughfall volume.

Winter maximum water stores displayed a field moisture content of 161% in Pacific silver fir,

108% in western redcedar, and 134% in western hemlock; well below the maximum potential moisture contents calculated for these same species at this stage of decay (Harmon and Sexton 1995). The maximum field moisture content of Douglas-fir reached 114% during the winter of 1993, which closely approached the potential maximum of 119%.

Water Flows

During the period of this study evaporation was the dominant process averaging approximately 55% of the water budget of all four species (Figure 3). In all species except western redcedar, leaching was the next most important pathway accounting for 26% of the water flow. Western redcedar was apparently more effective in shedding water, with runoff averaging 27% in this species as compared 8% in the other three species. Absorption was a more dynamic process showing gains and losses of water stores, but for the purposes of throughfall partitioning only the absorptive weight gain was considered. On average, absorption accounted for 3 – 11% of the input water total.

There was a correlation between the volume of throughfall and the average volume of leachate for each species, although regressions for individual logs were even more closely correlated. In all but one individual log the r^2 of the individuals exceeded the r^2 of the average of that species, for example, the

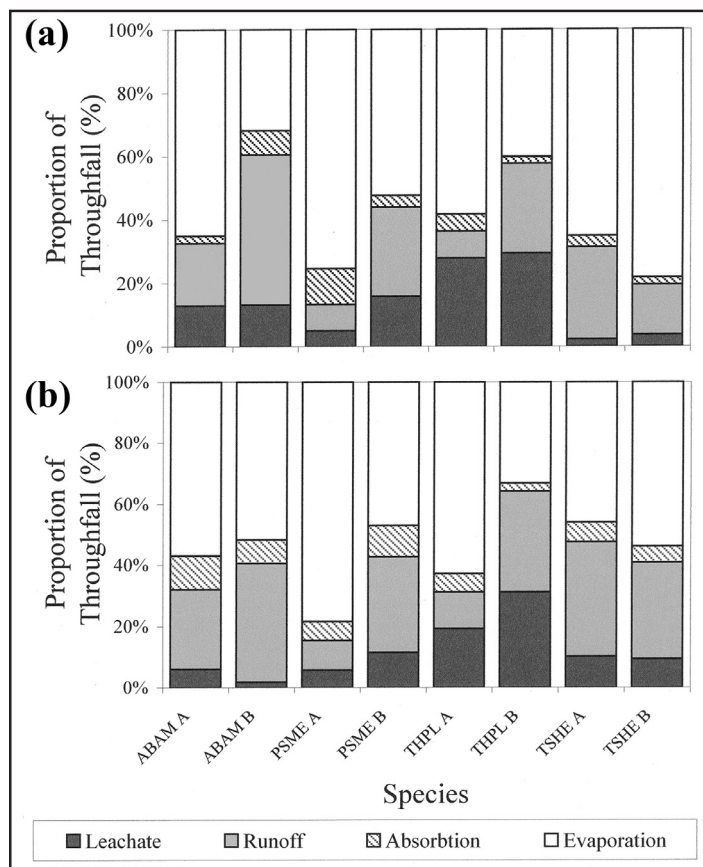


Figure 3. Partition of throughfall water for four species (ABAM = *Abies amabilis*, PSME = *Pseudotsuga menziesii*, THPL = *Thuja plicata*, and TSHE = *Tsuga heterophylla*) of decomposing logs among measured absorption, runoff, and leachate, and calculated evaporation. Two sections taken from the same log for each species are shown. Two winters of precipitation were examined: (a) December, 1991 - June 1992 (377 mm throughfall) and (b) July 1992 - April 1993 (718 mm throughfall). The time period in 1991-1992 received below average precipitation, whereas the time period 1992-1993 received above average precipitation.

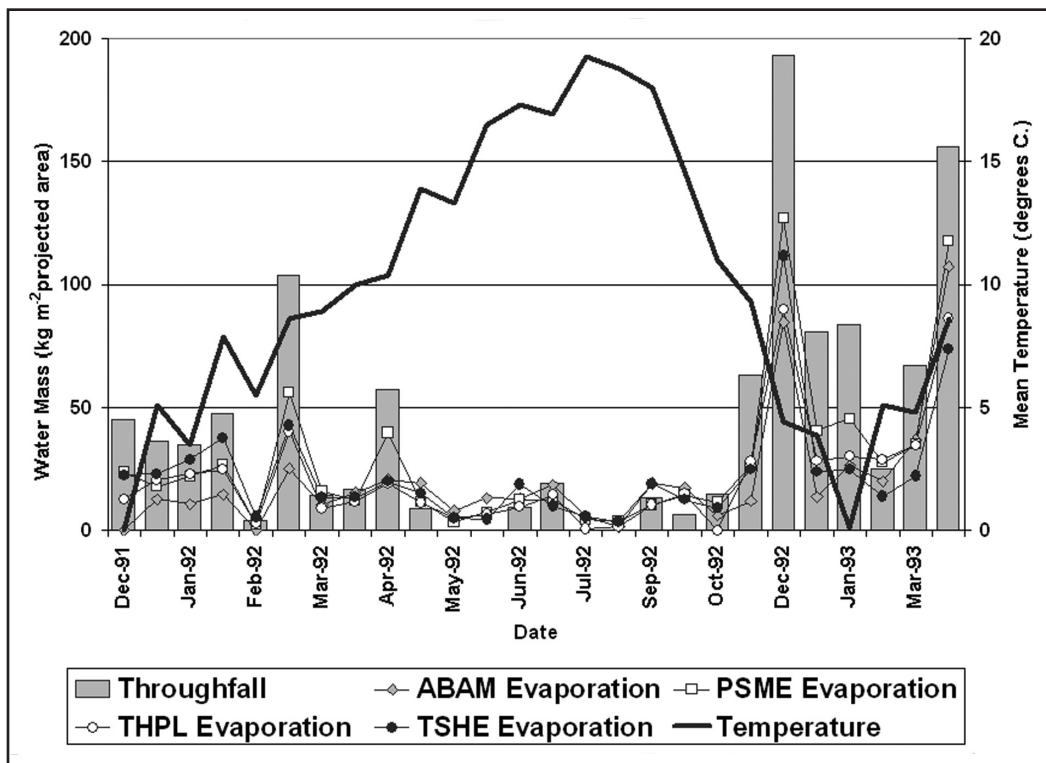


Figure 4. Average evaporated water mass (kg m^{-2}) and throughfall (kg m^{-2}) estimated by measurement period (approximately two weeks) through time. Two measurements were made from different sections of the same log for *Abies amabilis* (ABAM), *Pseudotsuga menziesii* (PSME), *Thuja plicata* (THPL), and *Tsuga heterophylla* (TSHE). Mean Temperature (right vertical axis) was measured at nearby Corvallis Water Bureau meteorological station 7 km to the west, at about the same elevation. Mean temperature is the mean of the daily maximum and minimum temperatures recorded for that day.

individual r^2 for western redcedar logs were 0.62 and 0.91 ($df=21$, $p<0.05$) while the species average regression was 0.53 ($df= 21$, $p<0.05$).

Examination of the seasonal pattern of evaporation indicates that the vast majority of evaporation occurred during the cool, wet winter season (Figure 4). Over the course of the study 80 % of the evaporation occurred during periods when the mean temperature was 10°C or below. Evaporation had strong correlation with throughfall volume with a range of r^2 values of 0.72 – 0.94 ($df =24$, $p<0.05$) when measurements were averaged by species. Evaporation was also correlated to mean temperature, but this variable explained only 5 – 19% of the variation in evaporation rates.

Drying and Wetting Rates

Drying and wetting rate-constants calculated during the period of maximum observed changes

indicate that the rate of drying and wetting are 2-3 fold greater for the more decayed Pacific silver fir logs than for those of the other three species (Table 1). Drying and wetting rate-constants were similar in magnitude. The half-time to dry completely under conditions similar to those observed during this study would range from 113 days for Pacific silver fir to 246 days for western redcedar.

Discussion

This study demonstrates the important role coarse woody debris plays in intercepting throughfall. Combined absorption and evaporation accounted for 60% of the throughfall contacting CWD, and in forests with large amounts of the forest floor covered by CWD (e.g., 25% of ground surface) this could account for as much as 15% of total throughfall. Forest canopy interception of rainfall can divert 10-50% of precipitation (Klaassen et al.

TABLE 1. Rate-constants for periods of maximum observed drying and wetting periods of four conifer species.

Species	Drying-rate constant (day ⁻¹) ^a	Wetting-rate constant (day ⁻¹) ^b
<i>Abies amabilis</i>	0.0061	-0.0087
<i>Pseudotsuga menziesii</i>	0.0041	-0.0034
<i>Thuja plicata</i>	0.0028	-0.0028
<i>Tsuga heterophylla</i>	0.0034	-0.0021

^aDrying-rate measured during a period of 35 days between 8/18 and 9/22, 1992 with a mean temperature of 16.5 °C and throughfall of 0.0 cm.

^bWetting-rate measured during a period of 49 days between 10/23 – 12/11, 1992 with a mean temperature of 6.4 °C and throughfall of 25.6 cm. Two measurements were made from two sections of the same log for each species.

1998) and so this potential additional interception of throughfall by CWD is substantial.

We initially expected that the majority of evaporative losses would occur during the summer drought. One factor that may limit the drying rate for logs in extended droughts is that as the surface layers become dry they may provide a protective layer that slows the transfer of water from the inner layers to the atmosphere. In earlier studies heartwood moisture content remained almost constant while sapwood varied some and bark moisture was highly responsive to drying conditions (Harmon and Sexton 1995).

We observed large amounts of throughfall captured by, and evaporated from, CWD during the cool wet winters of the Pacific Northwest. Studies of the interception and evaporation of water stores in forest canopies have shown that while evaporation is low during rainfall events, it rapidly increases immediately after rainfall ceases (Rutter and Morton 1977), and although evaporative potential is greater in the warm dry summer there is little water available to evaporate from surfaces (Klaassen et al. 1998). Evidently the light intermittent winter rainfall, typical of the study area, provides optimal conditions for water interception and evaporation by forest canopies and CWD.

The water dynamics we observed in this study was more heavily influenced by evaporation than in our earlier study (Harmon and Sexton 1995). However, this might be expected because throughfall at this study site averaged about one

third (550 mm vs. 1530 mm) of that during the previous study. Moreover, mean annual air temperatures were slightly higher (9.0 °C vs. 11.3 °C), which would likely increase evaporation. The experimental apparatus elevating the logs and providing more surface exposure also could have contributed to a higher rate of evaporation. Periods of higher volumes of throughfall did not appear to greatly change the water partitioning observed. The throughfall volume recorded during the second winter of this study was 190% of that recorded during the first winter. Despite this variation, the partitioning of flows was comparable.

Comparison with the drying rates calculated during our earlier study reveal that drying rates during wetter conditions are much lower than those calculated during this study. Whole log drying rate-constants (day⁻¹) from the earlier study are 0.0014, 0.0018, 0.0022, and 0.0017 for Pacific silver fir, Douglas-fir, western redcedar, and western hemlock as compared to 0.0061, 0.0041, 0.0028, and 0.0034 for these same species in this study. As previously mentioned, throughfall during the prior study in the Cascade Range was 2-4 times the volume encountered during this study. Shorter drying periods and more frequent wetting likely explain this difference.

Throughfall is spatially variable primarily due to canopy geometry. The specific study area was selected because the land surface was relatively flat and the forest had a uniform canopy. The four throughfall collectors were positioned among the study logs, and the collectors and study logs were placed beneath areas of average canopy, midway between neighboring trees. Our results did not indicate that any individual log or throughfall collector received atypical amounts of throughfall. Nevertheless, the throughfall impacting individual logs was partitioned between leaching, run-off, absorption, and evaporation in idiosyncratic patterns dependent on the surface and sub-surface characteristics of the individual logs. It is to be expected that different log species, log position and orientation, decay state, size, and other features would affect the water dynamics of woody debris. Future studies with replication for individual species and environmental conditions will further our understanding of variation in water dynamics.

In the current study, the ranking and proportion of leaching versus run-off was similar to that

observed previously. In both studies run-off was equal to or less than leaching except for western redcedar, a species in which run-off exceeds leaching. Our prior study, with 2-4 times the throughfall, found a higher proportion of run-off which suggests that larger throughfall inputs reduce the time in which evaporative conditions exist leading to greater water run-off. This result parallels the effect others have reported in studies of forest canopy water storage, where increased precipitation intensity decreases interception and increases throughfall (Rutter and Morton 1977). Absorption was not measured in the first study but it seems likely that the water store gains and losses would be similar to that measured in this study.

Although all the logs in this study were chronologically the same age, they were at different points along the decay continuum by virtue of the decay resistance of each species. Pacific silver fir, Douglas-fir, western redcedar, and western hemlock logs had lost 31%, 21%, 6%, and 15% of their original mass, respectively, at the time this study was conducted. Because of this, the most decayed species, Pacific silver fir, was more permeable and allowed a higher proportion of throughfall to pass through the log as leachate. The seasonal change of water stores in Pacific silver fir had more amplitude in part because of this increased permeability that resulted in much higher rates of wetting and drying. Earlier research has indicated that wood of lower density may dry faster (Harmon and Sexton 1995).

Literature Cited

- Agee, J. K., and M. H. Huff. 1987. Fuel succession in a western hemlock/Douglas-fir forest. *Canadian Journal of Forest Research* 17:697-704.
- Clark, J. S. 1989. Effects of long-term water balances on fire regime, north-western Minnesota. *Journal of Ecology* 77:989-1004.
- Fosberg, M. A. 1971. Climatological influences on moisture characteristics of dead fuel: theoretical analysis. *Forest Science* 17:64-72.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133-302.
- Harmon, M. E., and J. Sexton. 1995. Water balance of conifer logs in early stages of decomposition. *Plant and Soil* 172:141-152.
- We focused on logs in the early stages of decomposition, but in most forests there is a mix of CWD decay classes with an average age greater than that of those observed here. Logs in more advanced stages of decay are likely to gain and release water stores faster, if the characteristics of Pacific silver fir, the most decayed species in this study, are indicative. This characteristic of more decayed logs, as well as their greater water storage capacity suggests an increased importance of more decayed logs as buffers in stand scale water dynamics. Several other factors effect the water dynamics of coarse woody debris as decay progresses; these include increased wood permeability, fragmentation and loss of water-shedding bark cover, increased contact with the soil as logs settle, infiltration by live plant roots, and changes in moss cover. Further studies of the water dynamics of logs in later stages of decay are necessary to fully understand the role CWD plays in forest hydrology. Additionally, studies examining the effects of diameter, orientation, ground contact, and surface mosses and lichens would facilitate more complete understanding of the role woody debris plays in forest water dynamics.

Acknowledgements

The authors wish to thank Toni Hoyman and Lige Weedman for field assistance, and the McDonald-Dunn Forest of Oregon State University for providing a site for this work. This research was made possible by NSF Long Term Ecological Research Program (DEB-0218088).

- Hinds, T. E., F. G. Hawksworth, and R.W. Davidson. 1965. Beetle-killed Engelmann spruce—its deterioration in Colorado. *Journal of Forestry* 63:536-542.
- Klaassen, W., F. Bosveld, and E. de Water. 1998. Water storage and evaporation as constituents of rainfall interception. *Journal of Hydrology* 212: 36-50.
- Matson, K. G., W. T. Swank, and J. B. Waide. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. *Canadian Journal of Forest Research* 17:712-721.
- Nijssen, B., I. Haddeland, and D. P. Lettenmaier. 1997. Point evaluation of a surface hydrology model for BOREAS. *Journal of Geophysical Research* 102:29367-29378.
- Progar, R. A., T. D. Schowalter, C. M. Freitag, and J. J. Morrell. 2000. Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon. *Oecologia* 124:426-431.
- Rambo, T. R., and P. S. Muir. 1998. Bryophyte species associations with coarse woody debris and stand age in Oregon. *Bryologist* 101:366-376.

- Rutter, A. J., K. A. Kershaw, P. C. Robins, and A. J. Morton. 1971. A predictive model of rainfall interception in forests. I. Derivation of the model from observations in a plantation of Corsican pine. *Agricultural Meteorology* 9:367-384.
- Rutter, A. J., A. J. Morton, and P. C. Robins. 1975. A predictive model of rainfall interception in forests. II. Generalization of the model and comparison with observations in some coniferous and hardwood stands. *Journal of Applied Ecology* 12:367-380.
- Rutter, A. J., and A. J. Morton. 1977. A predictive model of rainfall interception in forests. III. Sensitivity of the model to stand parameters and meteorological variables. *Journal of Applied Ecology* 14:567-588.
- Setälä, H., and V. G. Marshall. 1994. Stumps as a habitat for *Collembola* during succession from clear-cuts to old-growth Douglas-fir forests. *Pedobiologia* 38: 307-326.
- Spears, J. D., H., S. M. Holub, M. E. Harmon, and K. Lajtha. 2003. The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A. *Canadian Journal of Forest Research* 33:2193-2201.
- Unsworth, M. H., N. Phillips, T. Link, B. J. Bond, M. Falk, M. E. Harmon, T. M. Hinckley, D. Marks, and K. T. Paw U. 2004. Components and controls of water flux in an old-growth Douglas-fir–western hemlock ecosystem. *Ecosystems* 7:468-481.
- Waichler, S. R., B. C. Wemple, and M. S. Wigmosta. 2005. Simulation of water balance and forest treatment effects at the H. J. Andrews Experimental Forest. *Hydrological Processes* 19:3177-3199.
- Yavitt, J. B., and T. J. Fahey. 1985. Chemical composition of interstitial water in decaying lodgepole pine bole wood. *Canadian Journal of Forest Research* 15:1149-1153.

Received 8 June 2007

Accepted for publication 18 December 2008