Dynamics of large woody debris in streams in old-growth Douglas-fir forests

G. W. LIENKAEMPER AND F. J. SWANSON

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

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Transfer of large woody debris (>10 cm diameter) from old-growth Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco) forests into five first- to fifth-order stream reaches (drainage areas of 0.1 to 60.5 km²) has ranged from 2.0 to 8.8 Mg·ha⁻¹·year⁻¹ in 7- to 9-year study periods. Amounts of large debris in these streams range from 230 to 750 Mg·ha⁻¹, with generally lower values in larger channels. The addition of woody debris is widely scattered in time and space and comes mainly from single trees rooted away from the streambank. We infer that wind is a major agent for entry of wood into these streams. Downstream movement of debris is strongly related to length of individual pieces; most pieces that moved were shorter than bankfull width.

Introduction

The transfer of large woody debris from forests to streams is a major link between terrestrial and aquatic ecosystems. In the past decade logs have been recognized as an important structural component of streams in forested mountainous areas and a source of nutrients for aquatic biota (Swanson et al. 1976, 1982; Bilby and Likens 1980; Triska 1984; Triska et al. 1982, 1984). Large pieces of wood form important elements of fish habitat by creating pools and providing cover (Bustard and Narver 1975; Bisson and Sedell 1984; Lestelle and Cederholm 1984). Woody debris structures also retain fine particulate organic matter which serves as habitat and nutritional resources for some groups of aquatic invertebrates (Triska et al. 1982; Speaker et al. 1984).

Logs are a conspicuous feature of many forested streams. The amount of woody debris in streams strongly reflects the structure, composition, and history of the adjacent forest. The highest reported quantities of woody debris (660 Mg/ha) are found in streams draining basins of less than 1000 ha and flowing through old-growth coastal redwood (Sequoia sempervirens (D. Don) Endl.) stands in north coastal California (Keller et al. 1986). Streams of similar size flowing through other types of old-growth coniferous forests in northwestern North America contain 100 to 300 Mg/ha (Harmon et al. 1986).

Despite the large quantities and biological importance of wood in aquatic ecosystems, especially in creating fish habitat, there has been little study of the mechanisms and rates of delivery and redistribution. The importance of estimating recruitment of large woody debris to streams has increased as land managers have begun to manage streamsid stands for long-term production of large woody debris for streams. Knowledge of debris stability is critical to managers charged with maintaining stream crossings and road networks.

Movement of pieces of wood has been observed by periodic surveying of mapped channel sections (Swanson et al. 1976; Megahan 1982; Toews and Moore 1982) and by relocating marked pieces (Bilby 1984). Swanson et al. (1976) and Keller and Tally (1979) used dendrochronologic analysis of trees growing on downed trees and of stems damaged by falling trees to measure the residence time of logs in streams. These studies revealed that many large conifer logs have remained in place in small streams for a century or more.

Here we report the first, long-term, direct observations of wood input and redistribution in streams. This study of the dynamics of woody debris in streams is based on 7 to 9 years of observations in five stream reaches in old-growth Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco) forests. This is part of an interdisciplinary, ecosystem-scale examination of forest-stream interactions, but this discussion is limited to analysis of log input and redistribution in mountain streams.

Study sites

The study sites are in the H. J. Andrews Experimental Forest, Willamette National Forest, Oregon (Fig. 1). Sites were selected to represent a range of stream sizes in old-growth forests. Other stream ecology and riparian vegetation research is underway at several of these sites. The study area, located about 70 km east of Eugene, Oregon, is typical of central western Cascade Range environments (Zobel et al. 1976; Swanson et al. 1980). The streams drain a steep, forested landscape underlain by Tertiary volcanic rocks. The five study stream reaches represent a range of channel sizes (Table 1). Channels are steep and boulders >1 m in diameter are common in the bed and along the banks. Dense forests of 400- to 500-year-old Douglas-fir, western hemlock (Tsuga heterophylla (Raf.) Sarg.), and western redcedar (Thuja plicata Donn ex D. Don) extend downslope to the banks of even fifth-order streams. Tree heights of 70 m and diameters of 2 m are common. Human disturbance in the reaches has been minimal except along lower Lookout Creek where nearby logging and road construction at distances of 20 to 180 m on one side of the channel have limited

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the source of wood and possibly increased potential for windthrow in the uncut forest adjacent to the stream.

Streams carry flood flows during autumn and winter (Harr 1981). Average annual precipitation is about 2500 mm. Continuously recording stream gauges have been operating for more than 30 years on two of the study streams. During our period of observation, instantaneous peak discharges at watershed 2 ranked as the 6th (3075 L/s) and 10th highest peak discharges between 1950 and 1984 occurred in the period of this study.

Methods

Channel mapping

Stream channels were mapped in 1975, 1976, or 1977 (Table 1) to illustrate the distribution of individual logs and debris accumulations. Channels were mapped at a scale of 1:118 with a rangefinder and a leveling rod to locate pieces of debris and boundaries of channel units (Swanson et al. 1976). Changes in log position and the rate of introduction of new logs were determined annually at Mack Creek and upper Lookout Creek and less frequently at the other sites. Minor changes were noted on the maps from the previous year, but major changes in the structure of debris accumulations or channel geometry required complete remapping of the reach. Logs were not tagged; recognition of individual pieces from year-to-year was based on shape, location, and distinctive distinguishing characteristics of debris pieces. Some pieces of woody debris may have fallen into the wider channels and floated downstream before sampling, but this is likely to be balanced by input of material floated in from upstream areas.

Amount of woody debris

Woody debris, here referred to as logs ≥10 cm in diameter and ≥1.5 m in length, was measured and mapped in and adjacent to the stream channel. The diameter at each end and the length of the piece were recorded for pieces within the bankfull channel, as defined by channel banks and lack of rooted trees. Root wads were not included in the calculation of log volume. Bank-full stream width was measured at regular intervals along each study reach. Mean width calculated from these measurements and length of the study reach were used to determine the area of each study section.

Determinations of amount of large woody debris included material ≥10 cm in diameter located within the bankfull channel. The volume of each piece was calculated using the formula for the frustum of a paraboloid:

\[ V = \frac{\pi(D_1^2 + D_2^2)L}{8} \]

where \(D_1\) and \(D_2\) are the diameters at each end and \(L\) is the length. This equation is the product of the average diameter of the two ends and piece length. Total volume of all pieces of woody debris divided by the sampled area yielded the volume per unit area, excluding root wads. An assumed average specific gravity of relatively undecayed conifer wood (0.4 Mg/m³) was multiplied by volume per unit area to estimate standing crop.

Debris delivery to streams

Study areas were examined in the autumn to determine the annual delivery rate of logs. New material was noted on the maps and each piece tallied and measured. Delivery of logs was inventoried in terms of (i) the number of occurrences of input (an occurrence could involve all or part of one tree or more than one tree), (ii) the number of trees from which pieces were derived, and (iii) the number of pieces delivered to the channel. Mass of material delivered per unit area was calculated and divided by the period of observation to estimate an annual rate of delivery.

Each of the inventory factors has different implications. The number of trees involved in delivering woody debris depends on structural characteristics of a stand as well as on the agents of delivery. The frequency of tree fall is an important aspect of stand dynamics. The stream channel responds to the number and size of pieces that result from delivery and related breakage.

Results

Amount of large woody debris

The amount of large woody debris was measured during the first year of monitoring at each study site (Table 2). Values ranged from 92 Mg/ha at lower Lookout Creek to 300 Mg/ha at watershed 2. These quantities were typical of those measured in other streams of similar size flowing through mature coniferous forests in the Pacific Northwest, but less than in coastal redwood forests (Harmon et al. 1986). Amounts of large woody debris in the streams generally decreased from small to large channels.

Debris delivery

Source location and agents of delivery

Rooting locations of trees that were sources of wood entering stream channels set limits on interpretation of the agents of delivery. Portions of 38 trees entered the study reaches during the sample period (Table 3). Twenty-five of these trees (66%) were growing in areas not subject to bank erosion and accounted...
for 69% (136.4 m³) of the volume added. In these cases, wind, possibly coupled with stem or root decay, was a probable delivery agent. Thirteen trees, or about 34% of the total number and 31% (61.3 m³) of the volume added, grew adjacent to the stream. Bank cutting may lead to delivery of logs to streams, but we believe that lateral cutting of these high-gradient channels is very limited. Trees growing in the stream bank may be particularly prone to falling into a channel even without bankcutting. Instability imposed by the asymmetry of the rooting environment of a stable streambank and the tilt of trees growing into the open canopy space above streams could result in a high susceptibility of large trees to windthrow.

Large woody debris entering steep, narrow channels of watershed 2 and watershed 9 originated entirely in areas not influenced by the stream channel, with the exception of one tree rooted at the streambank. In intermediate-sized channels of upper Lookout Creek and Mack Creek, added material originated at a variety of sites equally distributed between areas at and away from the stream banks. At the lower Lookout Creek site all but one occurrence of wood introduction involved trees originating at the stream edge. In these cases bank erosion was probably a major factor. Two trees rooted away from the streambank accounted for the bulk of the wood volume delivered at this site. No input by landslides occurred at the study sites in the period of observation, but they have been important in other parts of the basin.

**Temporal variation of delivery**

Entry of woody debris to the stream is highly variable from year to year. For several years at each site no new wood entered the study area (Table 3). At most sites a single tree contributed a large proportion of the total volume of material that entered the stream during the 7- to 9-year study periods. For example, in watershed 9 a single tree that fell into the stream in 1980 accounted for 75% of the total volume delivered to the channel during the 8-year period. In another instance, two trees that fell during 1982 into lower Lookout Creek represented 70% of the total volume that entered this reach. In 1977, 82% of the 9-year total volume that entered the upper Lookout Creek reach and 69% of the total volume at Mack Creek entered in 1978. No new material entered the lower Lookout Creek reach during the first 3 years of monitoring, but fresh wood has been added every year since 1980. Some of this woody debris input may have been influenced by windthrow from the edge of a 1980 clearcut 200 m down valley.

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**Table 2.** Estimates of the amount and input rates of woody debris for each study site; mass values are based on bulk density = 0.40 g cm⁻³ (see text for discussion)

<table>
<thead>
<tr>
<th>Study site</th>
<th>Amount of woody debris</th>
<th>Input rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Volume (m³ ha⁻¹)</td>
<td>Mass (Mg ha⁻¹)</td>
</tr>
<tr>
<td>Watershed 9</td>
<td>500</td>
<td>200</td>
</tr>
<tr>
<td>Watershed 2</td>
<td>750</td>
<td>300</td>
</tr>
<tr>
<td>Mack Creek</td>
<td>570</td>
<td>228</td>
</tr>
<tr>
<td>Upper Lookout Creek</td>
<td>340</td>
<td>136</td>
</tr>
<tr>
<td>Lower Lookout Creek</td>
<td>230</td>
<td>92</td>
</tr>
</tbody>
</table>

**Table 3.** Frequency and volume of woody debris delivery at each study site: watershed 9 was surveyed once between 1977 and 1982; watershed 2 once between 1977 and 1981

<table>
<thead>
<tr>
<th>Study site</th>
<th>Watershed 9</th>
<th>Watershed 2</th>
<th>Mack Creek</th>
<th>Upper Lookout Creek</th>
<th>Lower Lookout Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>O T P V</td>
<td>O T P V</td>
<td>O T P V</td>
<td>O T P V</td>
<td>O T P V</td>
</tr>
<tr>
<td>1975</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1976</td>
<td>Mapping</td>
<td>Mapping</td>
<td>Mapping</td>
<td>Mapping</td>
<td>Mapping</td>
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<td>1977</td>
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<td></td>
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<tr>
<td>1978</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1979</td>
<td>3 3 9 6.3</td>
<td></td>
<td>2 2 7 0.9</td>
<td>0 0 0 0</td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1981</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1982</td>
<td>3 3 3 0.4</td>
<td>1 1 5 1.2</td>
<td>2 2 8 5.8</td>
<td>2 2 2 4.1</td>
<td>1 1 2 8 82.0</td>
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<tr>
<td>1983</td>
<td>4 0 0 0</td>
<td>1 1 2 1.8</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
<td>2 2 2 4 2</td>
</tr>
<tr>
<td>1984</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>6 6 12 6.7</td>
<td>4 4 15 5.7</td>
<td>10 10 43 39.9</td>
<td>10 12 21 30.3</td>
<td>5 6 12 115.1</td>
</tr>
</tbody>
</table>

Note: Table headings: O, number of occurrences of woody debris delivery; T, number of trees; P, number of pieces; V, volume in m³.

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**Table 4.** Frequency, volume, and breakage of added woody debris by decay class

<table>
<thead>
<tr>
<th>Decay class</th>
<th>No. of trees</th>
<th>No. of pieces</th>
<th>Volume (m³)</th>
<th>Average pieces per tree</th>
<th>Average volume/tree (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live</td>
<td>7</td>
<td>36</td>
<td>143.4</td>
<td>5</td>
<td>4.0</td>
</tr>
<tr>
<td>1</td>
<td>6</td>
<td>17</td>
<td>5.9</td>
<td>3</td>
<td>0.4</td>
</tr>
<tr>
<td>2</td>
<td>12</td>
<td>24</td>
<td>38.7</td>
<td>2</td>
<td>1.6</td>
</tr>
<tr>
<td>3</td>
<td>13</td>
<td>26</td>
<td>9.7</td>
<td>2</td>
<td>0.4</td>
</tr>
<tr>
<td>Total</td>
<td>38</td>
<td>103</td>
<td>197.7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Stage of decomposition and breakage of logs

Woody debris entering the stream channel was classified according to a modification of the Fogel et al. (1972) decay class system. Logs in decay class 1 had intact bark, twigs of less than 3 cm diameter, and wood with no decay stains. Logs in decay class 2 had lost twigs and some bark and sapwood was soft. Logs in decay class 3 were only partially intact with sloughing bark and red-brown wood. Trees or portions of trees that were living when they fell were also noted.

Freshly killed trees made up 73% of the volume but only 18% of trees added at all sites during the study (Table 4). Decay class 2 made up 19% of the volume, and classes 3 and 1 accounted for 5% and 3%, respectively. Freshly killed trees broke into the highest number of pieces (5) per tree (Table 4). The number of pieces produced per fallen tree or snag decreased slightly with increasing stage of decay.

Redistribution

The greatest redistribution of woody debris occurred in larger streams during the monitoring period (Table 5). Less than 10% of the pieces identified on the original maps were detected to have moved during the 8 years of observation at watershed 2 and watershed 9 (downstream or rotational movement of more than 1 m was easily detected). None of the material added to these streams during that period moved. Just over 10% of the pieces originally surveyed in upper Lookout Creek moved during the study period, and 24% of the material added in 9 years was redistributed. Of the debris pieces first mapped in lower Lookout Creek, 65% was redistributed between 1978 and 1984, and half of the material added during that period has moved since it was introduced.

Since Mack Creek had been mapped in detail before a high flow in November 1977 moved many pieces of woody debris, we were able to develop a detailed description of redistribution of woody material. Because the stream gauge on Mack Creek was not operational at the time of the high flow, we used data from other stream gauges and other information to estimate a return interval of 10 years. Snow conditions in the Mack Creek basin may have resulted in flows of greater return interval than in other basins in the H. J. Andrews Experimental Forest. However, the greater mobility of debris in Mack Creek during this event, relative to other study sites, may have resulted primarily from the breakup of a single debris jam; releasing pieces which triggered downstream changes. The high flow moved half of the pieces in the Mack Creek study site by 1978. None have moved since. Of the 18 pieces that fell into Mack Creek during the monitoring period before the November 1977 flow, 16 moved before 1978. Between 1978 and 1984 only 2 of 25 new pieces of wood that entered Mack Creek were redistributed.

Woody debris was transported through a 220 m long zone in Mack Creek where log movement was severely restricted at the upstream and downstream ends. A large debris jam located at the upstream end of this zone trapped material transported from farther upstream. During the high flow, water ponded behind a roadfill at the downstream end of the zone, and most of the material that moved out of the section was trapped in the resulting pond. Transported woody debris also accumulated at several areas between the upper jam and the pond.

Many pieces exported from the reach and deposited at the roadfill were recognizable by size, shape, bark pattern, and other characteristics. Their positions before high flow and distances transported could be determined from stream maps and observations of researchers familiar with the site. We relocated 70 pieces of woody debris that appeared on maps prepared before high flow (Fig. 2A). Of these, 28 pieces remained in place and 42 were transported varying distances downstream. Most of the transported pieces accumulated in the pond behind the roadfill below the study section and at the debris accumulation at the left-hand end of Fig. 2A. For example, the log that keyed the debris accumulation highlighted in black (Fig. 2A) was broken, and most of the material that accumulated behind it floated out of the section. Black, highlighted logs (Fig. 2B) show where a few pieces were deposited. Although most pieces floated into place, the streamward ends of several logs that were anchored outside the stream channel pivoted a few metres downstream, e.g., a stippled log in Fig. 2B. Some pieces were buried within major accumulations and were not tallied.

Pieces of woody debris that remained stationary were anchored in some way or were protected from high streamflow by anchored pieces. Root wads anchored five (19%) of the pieces that did not move. Another 44% were anchored on the streambank by part of their mass. The remaining 37% of the stationary pieces were protected by anchored pieces. The mean length of pieces anchored by rootwads was 15.4 m and protected pieces had a mean length of 6.0 m. The seven pieces anchored on the bank by 50% or less of their length had a mean length of 7.6 m, and the five pieces that had more than 50% of their length outside of the stream channel averaged twice that length (15.2 m).

The distance a piece moved in the November 1977 high flow depended greatly on the length of the piece in relation to bankfull width (Fig. 3). All 30 pieces moving more than 10 m were shorter than 11 m; average bankfull width was 11.9 m. Several longer pieces moved less than 10 m by pivoting or turning on points located on adjacent hillslopes.

Discussion

The locations of trees that supplied wood to the study reaches offer some insight to agents of woody debris introduction. Trees rooted at the streambank can enter the channel as a result of
Fig. 2. The November 1977 high flow redistributed a large amount of wood in Mack Creek. For example, most of the material highlighted in black (A) was washed out of the study area, but some material was redeposited at the next bend (black pieces in B). The stippled log in A broke and pivoted downstream.

Fig. 3. Unanchored logs that were shorter than bankfull width were redistributed in the November 1977 high flow at Mack Creek.

Lateral cutting by the stream. Wind and other factors, such as asymmetry of a root mass developed in the bank environment, might also lead to introduction of trees rooted at the stream margin, even in the absence of bank cutting. Lateral cutting in the study reaches appeared to be rare; the presence of 400- to 500-year-old trees along the banks indicated that channel migration has been minimal. Consequently, the large proportion of woody debris added from trees growing away from the stream channel, coupled with complex root and crown environments of streamside trees, led us to conclude that wind (perhaps predisposed by decay and other factors) has been the most prominent agent of delivery of wood to the studied stream channels. Elsewhere in the basin debris slides and earthflows have been localized sources of woody debris for stream reaches.

Amounts and delivery rates of woody debris in streams are similar to estimates of woody debris in nearby forest stands. For Douglas-fir forests similar in age to those in our sites, other studies reported values of 80–190 Mg/ha (Grier and Logan 1977; Sollins 1982; Harmon et al. 1986). Input rates to the forest floor as reported in the same studies ranged from 4.5 to 7.0 Mg·ha⁻¹·year⁻¹. Woody debris delivery rates for sites sampled in this study (2.0–8.8 Mg·ha⁻¹·year⁻¹) and standing crop estimates (92–300 Mg/ha) were similar to forest floor values. Variation in delivery rate among and within stream sites and upland forest areas is partly a result of the shortness of record.

An index of the residence time of woody debris is the "turnover time," calculated as the standing crop divided by the delivery rate (Table 2). The broad range of estimates of turnover time (12–83 years) is in part a result of the short period of record. The 9-year record, for example, is less than 10% of the time required for complete decomposition of an individual log from an old-growth tree in these streams (Swanson et al. 1976). Because of the small sample size, the introduction of only one or
two massive trees dominated the delivery of debris during the observation period for all reaches. The upper range of "turnover time" corresponds with the range of residence times estimated from dendrochronologic studies of wood in streams (Swanson et al. 1976) when the lag time until establishment of conifer seedlings on logs is considered (Fogel et al. 1972).

Length of a piece of wood is an important factor in its mobility. In the 1977 high flow in Mack Creek, shorter pieces moved farther than pieces with lengths equal to bankfull channel width or longer (Fig. 3). Swanson et al. (1984) and Bilby (1984) also found length relative to bankfull stream width to be important in judging mobility of logs in streams.

Mobility of debris pieces mapped in the study reaches was evaluated, based on the criteria of stable pieces being longer than bankfull channel width or having more than 50% of their length outside the stream channel. In small streams many pieces of wood (23-39%) were long relative to the bankfull channel width and tended to remain in place. Larger streams had a smaller proportion of pieces longer than bankfull channel width (10-18%) and shorter pieces were clumped behind longer, more stable pieces. Because type and structure of the stand supplying wood to these channels was similar at all sites, we expect that the size distributions of material entering each channel would be similar also. Consequently, the lower stability of wood in larger channels is primarily a result of greater channel width and discharge (Table 5), hence the greater ability of larger streams to transport wood.

Interpretation of mobility of debris pieces, however, is more complicated than relative size alone. A smaller proportion of pieces moved in each study reach (Table 5) than were judged to be unstable by the above criteria. Many small pieces of debris, which might be considered unstable if isolated in the stream channel, are part of accumulations of woody debris stabilized by one or more much larger pieces. Consequently, logs moved into debris accumulations by streamflow are likely to be more stable than material of similar size that is randomly located where it falls into the stream from the adjacent stand.

Mobility of debris in a channel also depends on the time since the last streamflow high enough to redistribute freshly delivered material. In Mack Creek, for example, 50% of pieces mapped in 1975 and 89% of pieces added between 1975 and 1978 were redistributed, mainly by a flow with a 10-year recurrence interval in November 1977. None of the pieces mapped in 1978 and only 2 of 25 pieces introduced since 1978 moved in the 1978-1984 period. Of the 23 pieces that entered Mack Creek since 1978 and that have remained in place, 21 are shorter than bank-full width and are susceptible to transport in the next major flow.

Physical characteristics of the stream channel greatly influence the movement of large woody debris. High streamflow can move many pieces of debris that are shorter than the width of the stream. Conversely, the same event is just as likely to deposit the debris in existing and new accumulations that are stabilized by large, long logs.

Despite the substantial movement of woody debris observed in Mack Creek, the overall distribution of debris accumulations changed little. Twelve of 14 of the largest accumulations of wood remained in place, although the arrangement of pieces changed somewhat, in part as a result of additions and losses. Persistence of these debris accumulations was described by Swanson et al. (1976) whose dendrochronologic studies showed that large stable pieces maintain accumulation sites for many decades. Based on dendrochronological evidence, all the debris accumulations in place at the time of the dramatic November 1977 high flow had remained in place through an even greater high flow in December 1964.

Change in the abundance and arrangement of large woody debris in forested stream systems is an integral part of the physical dynamics of aquatic ecosystems. Studies of these phenomena are best based on an integrated terrestrial-aquatic monitoring program involving (i) stem maps of standing live and dead trees and of downed trees that are updated annually for mortality and tree fall; (ii) stream maps of woody debris and broad-scale channel geomorphic units (e.g., pools and riffles) that are updated annually; (iii) annual checks of location and orientation of logs marked with numbered tags; (iv) annual survey of monumented channel cross sections located in part at channel features controlled by logs; and (v) annual resurvey of habitat factors (e.g., substrate type and cover). The locations of tagged pieces of debris, cross sections, and habitat survey points are referred to on stream maps. This design allows examination of the immediate and delayed effects of stand dynamics on channel geomorphology and habitat. We have undertaken such a sampling program as part of National Science Foundation sponsored Long-Term Ecological Research at the H. J. Andrews Experimental Forest.

Acknowledgments

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