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Patterns of Instream Wood Recruitment and Transport at the Watershed Scale

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Abstract.—A wood budget was constructed for the Game Creek basin (132 km^2) in southeast Alaska to identify spatial and temporal controls on the abundance and distribution of large woody debris (LWD). Field measurements of wood storage, size, and age were used to estimate volumetric rates of LWD recruitment and transport. Mortality recruitment did not follow a spatial pattern and ranged from 0.1 to 8.1 m^3·km^{-1}·year^{-1} (recruitment corresponded to forest mortality rates of 0.1–2.6% per year). Wood recruitment by bank erosion increased with increasing drainage area and ranged from 1 m^3·km^{-1}·year^{-1} at the smallest drainage areas to about 16 m^3·km^{-1}·year^{-1} at 60 km^2. Bank erosion recruitment exceeded the maximum mortality recruitment at a drainage area of approximately 20 km^2 (about 10-m-wide channel). Recruitment from land-sliding was only locally significant. The contribution of fluvial transport (flux) to total LWD storage increased with drainage area to an asymptotic maximum of 50% at about 50 km^2 (about 20-m-wide channel). Mean predicted transport distances for mobile LWD over the lifetime of individual pieces ranged from about 200 m in small, jam-rich streams to about 2,500 m in larger channels with fewer jams. Fluvial transport of LWD increased interjam spacing and jam size and decreased jam age with increasing distance downstream. Constructing LWD budgets at the watershed scale has numerous geomorphic and ecological implications, including identifying spatial controls on the abundance and diversity of aquatic habitats. In addition, information on LWD budgets may be useful for determining how and where to protect LWD sources to streams.

Numerous studies have documented the positive role that large woody debris plays in riverine ecosystems. Large woody debris (LWD) creates pools (Robison and Beschta 1990; Montgomery et al. 1995; Beechie and Sibley 1997), enhances deposition of spawning gravels (Lisle 1986; Cederholm et al. 1997), boosts trophic processes (Maser and Sedell 1994; Wallace et al. 1995), and adds structural complexity (Keller and Swanson 1979; Bilby and Ward 1989). Hence, the rate at which LWD is delivered to streams is an important constraint on riverine ecology. Rates of LWD supply vary by landscape process and at different locations within a watershed (Bisson et al. 1987; Maser and Sedell 1994; Bilby and Bisson 1998). This understanding has motivated several studies of the LWD mass budget in streams. Keller and Swanson (1979) outlined a conceptual framework that qualitatively described the major input, output, and transport processes at the watershed scale. At the reach scale, Murphy and Koski (1989) made quantitative estimates of the major recruitment processes for three small streams in southeast Alaska, including LWD depletion rates. Grette (1985), McHenry et al. (1998), and Hyatt and Naiman (2001) also estimated LWD depletion rates at the reach scale. The authors are not aware of a LWD mass balance study calculated at the watershed scale.

In this paper we constructed a LWD budget using a proposed quantitative framework (Benda and Sias 1998; L. E. Benda, in press) to evaluate spatial and temporal controls on LWD recruitment rate, transport, and distribution for a sixth-order basin located in southeast Alaska. Recruitment rates of LWD were estimated for several decades with field measurements of wood storage, size, and age. Wood transport was predicted from measurements of piece size, jam spacing, and jam age by using LWD transport equations (Benda, in press). Spatial controls on wood recruitment by different input processes were explored, and estimates for bank erosion and forest mortality were derived from re-

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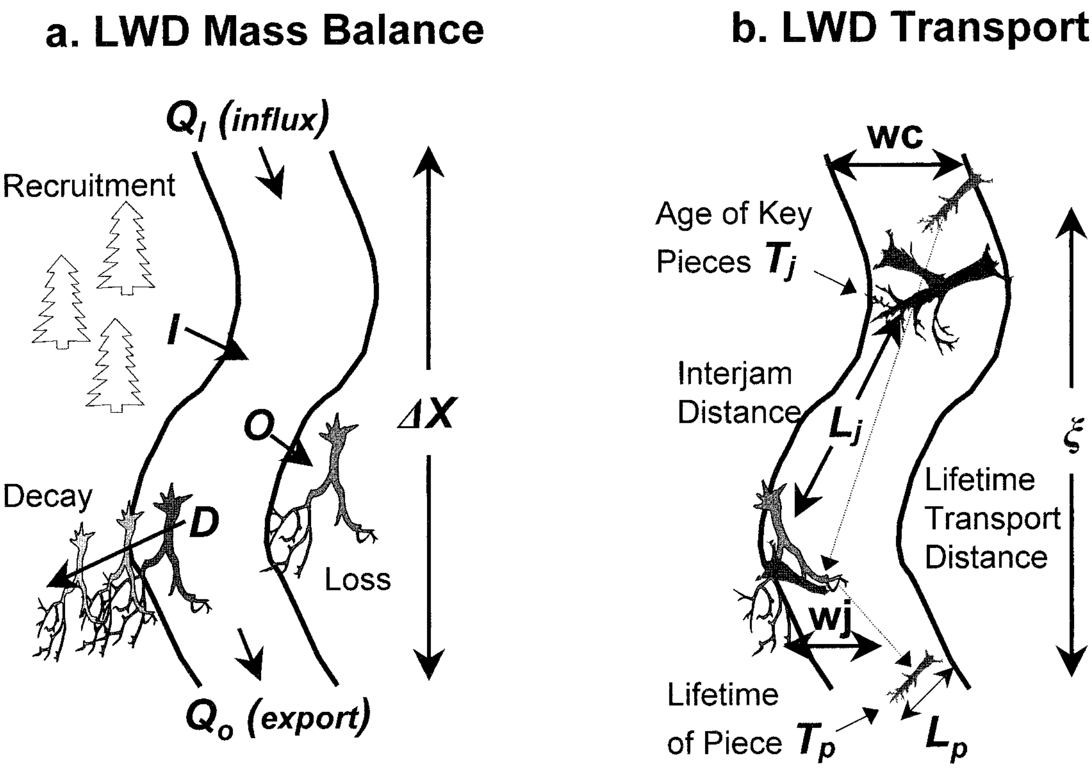


FIGURE 1.—Illustrations of variables (see text for definitions) used (**a**) in the equation for mass balance of LWD, and (**b**) in equations for LWD transport for Game Creek basin in southeast Alaska.

cruitment equations. Understanding the spatial patterns of LWD abundance across a channel network should increase our understanding of fluvial geomorphic and ecological patterns, including spatial controls on the abundance and diversity of aquatic habitats. In addition, the LWD budget provides a watershed context for resource management that may be useful for determining how and where to protect LWD sources to streams.

Principles of Wood Budgeting

Woody debris in channels has definable inputs, outputs, and residence times, and therefore its mass budget can be analyzed in an orderly and quantitative fashion. The quantitative framework for computing the volumetric mass balance of LWD is based on Benda (in revision) and Benda and Sias (1998). The mass balance of LWD is a consequence of input, output, and decay (Figure 1a):

$$\Delta S = (I\cdot\Delta x - O\cdot\Delta x + Q_i - Q_O - D)\,\Delta t, \quad (1)$$

where ΔS is a change in storage within a channel segment of some arbitrary length Δx over the time interval Δt in cubic meters per year; I is lateral wood recruitment; O is loss of wood from the active channel due to overbank deposition during flood events, abandonment of jams, and burial; D is in situ decay; and Q_i and Q_O, are fluvial transport of wood into and out of the segment. Both I and O have units of volume per unit reach-length per time, and the remaining terms (Q_i, Q_O, and D) have units of volume per time. All of these variables are functions of time and position.

Lateral wood recruitment represents five different types of supply:

$$I = I_m + I_f + I_b + I_l + I_e, \quad (2)$$

where I_m is chronic stand mortality; I_f is toppling of trees following catastrophic events (e.g., windstorms or fires); I_b is inputs from bank erosion; I_l is wood delivered by episodic landslides, debris flows, and snow avalanches; and I_e is exhumation of buried wood.

The rate of recruitment from chronic mortality (volume per unit reach-length per unit time) is expressed as:

$$I_m = (B_L \cdot M \cdot H \cdot P_m)\mathrm{NB}, \tag{3}$$

where B_L is the volume of standing live biomass per unit area, M is the rate of mortality (fraction of live biomass per unit time), H is average stand height, P_m is the average proportion of stem length that becomes in-channel LWD when a tree falls from anywhere within the riparian zone, and NB is 1 or 2 depending on whether one or both sides of the channel are forested

Wood recruitment from bank erosion varies with forest biomass, rate of bank retreat, and the proportion of tree length that can intersect a channel:

$$I_b = (B_L \cdot E \cdot P_b), \tag{4}$$

where I_b is the volumetric recruitment (volume per unit reach-length per unit time), E is the mean bank erosion rate (width per year of bank retreat on one side of the channel), and P_b is the proportion of undercut tree lengths that intersect a channel.

Transport of LWD may become significant in larger streams and rivers where an increasing proportion of wood becomes mobile. Wood transport or flux depends on several factors. Mobile pieces tend to be shorter than bankfull width (Lienkaemper and Swanson 1987; Nakamura and Swanson 1993; this study), and transport distances are limited by obstructions such as debris jams that capture mobile pieces (Likens and Bilby 1988). Transport of wood is also affected by stream power (slope and stream cross sectional area), diameter of logs, piece orientation, and the presence of root wads (Abbe 2000; Braudrick and Grant 2000). In our wood budget in Game Creek, our objective is to examine how a few landscape factors, specifically channel width, tree size, and piece size distribution, affect LWD transport at the watershed scale. Hence, we use the wood transport equations of Benda (in revision), which are described below.

In channels of sufficient depth and stream power (i.e., some fraction of LWD is mobile), wood transport over the lifetime of a piece of wood is described by

$$Q_w = I_{(x,t)} \cdot \phi_{(x,t)} \cdot \xi_{(x,t)}, \tag{5}$$

where Q_w is the volumetric transport rate (i.e., flux in volume per time) for segment x in year t; ϕ is the proportion of all recruited LWD, I having piece lengths (L_p) less than the channel width (wc); and ξ is transport distance over the lifetime of LWD (i.e., before decay and breakup). Transport distance over the lifetime of LWD (Figure 1b) is described by (for $T_p > T_j$)

$$\xi_{(x,t)} = L_{j(x,t)}(T_{p(x,t)}/T_{j(x,t)})\beta^{-1}, \tag{6}$$

where L_j is the distance between transport-obstructing jams, T_p is the lifetime of LWD in fluvial environments (individual pieces or aggregated), T_j is jam longevity (in years), and β is the transport-obstructing effectiveness of jams. All of these variables are dynamic and can vary over time, space, or both. Transport is limited to interjam spacing (L_j), and it can become a multiple of L_j when the lifetime of LWD exceeds jam longevity. In the absence of measurements on how wood transport is affected by jams, we assume β is equal to wj/wc, where wj is the width (normal to the channel axis) of the in-channel portion of the jam. Values of β less than 1 increase transport distance by increasing the effective interjam distance. The effects of flood frequency and magnitude are omitted in equation (6), based on the assumption that floods of sufficient magnitude will transport LWD a distance L_j in a time interval T_j. In equation (1), if x represents the location at the top end of a reach, then Q_i (flux into reach) is equivalent to Q_w or $I\phi_{(x,t)}$, where the contributing upstream reach has a length of $\xi_{(x,t)}$. The flux out of the reach (Q_O at the bottom) is equivalent to Q_w or $I\phi_{(x + x,t)}$, where the reach over which the mass balance is being calculated has a length of $\xi_{(x + x,t)}$.

Study Area

Game Creek is located on the northern edge of Chichagof Island (75 km southwest of Juneau) in southeast Alaska. The watershed area is 132.5 km^2 (32,753 acres) and has 241 km of perennial streams. A north-trending U-shaped glaciated valley with steep side slopes dominates watershed topography. Elevation ranges from sea level at the mouth of Game Creek to 1,033 m in the headwaters (USFS 1994). Dominant landforms include high-elevation mountain slopes (56% of area), gently sloping lowlands (22%), and valley bottoms (19%). Steep first-order channels frequently dissect hillslopes. Lowlands and valley floors are often comprised of coalescing alluvial and debris fans (USFS 1994).

Average annual precipitation ranges from 200 to 250 cm, most occurring in the fall. Maximum stream discharge occurs during the fall (October to November) with a second peak during spring (snowmelt) runoff. Low flows occur during the summer and can occur for short periods during winter cold periods. Strong winds are common during the fall and winter gale season (USFS 1994). Stream flow records are not available for

TABLE 1.—Physical characteristics of study segments in Game Creek on southeast Alaska.

Study segment	Drainage area (km^2)	Mean width (m)	Length (m)	Gradient (%)	Channel type[a]
1	0.62	3.3	607	10.0	High-gradient contained
2	0.86	3.3	288	4.3	Moderate-gradient contained
3	1.27	3.5	245	15.0	High-gradient contained
4	1.56	4.9	882	15.0	High-gradient contained
5	1.67	3.5	324	9.0	High-gradient contained
6	2.11	4.1	698	7.3	Moderate-gradient mixed control
7	2.21	4.1	341	2.3	Flood plain
8	2.46	5.0	282	1.0	Flood plain
9	3.60	7.3	846	7.3	High-gradient contained
10	4.09	6.2	1,307	3.0	Moderate-gradient mixed control
11	4.30	4.1	408	4.3	High-gradient contained
12	4.32	4.5	527	3.0	Moderate-gradient mixed control
13	4.65	5.5	466	6.0	Moderate-gradient contained
14	5.13	6.5	834	2.8	Moderate-gradient mixed control
15	5.37	5.1	535	10.4	High-gradient contained
16	5.42	6.6	583	2.5	Moderate-gradient mixed control
17	5.91	6.7	227	1.3	Moderate-gradient contained
18	6.22	4.6	225	3.0	Moderate-gradient mixed control
19	6.88	8.0	744	2.7	Moderate-gradient mixed control
20	10.03	7.3	593	2.0	Moderate-gradient mixed control
21	11.36	19.3	495	1.0	Flood plain
22	11.53	9.0	227	1.0	Moderate-gradient mixed control
23	17.54	11.0	156	1.0	Large contained
24	18.50	11.0	1,194	0.7	Flood plain
25	19.50	14.9	898	1.3	Flood plain
26	21.51	11.3	2,417	1.9	Flood plain
27	52.90	22.9	947	1.0	Flood plain
28	78.85	23.8	4,397	1.0	Flood plain

[a] Channel type from Paustian et al. (1992). Containment refers to the degree of bank resistance to erosion. Mixed control refers to bank material that is a mixture of alluvial and colluvial deposits.

Game Creek; however, a 50-year record for Kadashan Creek (located 30 km south of Game Creek) indicates a 50-year flow event occurred in 1953 and several 10-year to 25-year flow events were recorded since that time (U.S. Geological Survey stream gaging data).

The lowlands are predominated by old-growth western hemlock *Tsuga heterophylla* and terraces adjacent to flood plains are often predominated by Sitka spruce *Picea sitchensis*. Sitka alder *Alnus sinuate* and salmonberry *Rubus spectabilis* predominate the steep side slopes, which include first-order streams that are prone to snow and debris avalanches (USFS 1994). Riparian stand density in the lowlands and valley bottoms ranges from 200 to 276 trees/ha (mean 243 trees/ha), and tree height ranges from 6 to 58 m (mean = 20.8 m, median = 19.2 m; Douglas J. Martin, unpublished data). Windthrow can be an important disturbance process as evidenced by the presence of wind generated stands. In Game Creek, 7% of the forests (mostly stands on mountain slopes) blew down about 100 years ago (USFS 1994). At the time of this study approximately 5% of the watershed had commercial timber harvest. In managed areas, riparian buffer zones ranged from 20 to 30 m wide along fish-bearing streams. Game Creek supports productive populations of resident and anadromous salmonids.

Methods

Field data collection.—We defined LWD as logs greater than 10 cm in diameter. In channels less than 5 m wide, pieces 1.5 m or longer were counted, and in wider channels only pieces 3 m longer were measured. The shorter pieces were counted in the smaller streams because they could account for a significant volume of wood, but in the larger streams the volume of short pieces was relatively insignificant. During the summers of 1998 and 1999, channel morphology and LWD data were collected from 28 channel segments composing 9% of network length. Surveys were conducted in a variety of geomorphic channel types (Table 1) that were widely distributed across the channel network. Steep headwater streams ($<$3 m wide and with gradients $>$15%) were not measured because the focus of the study was on fish-bearing channels. Also, because small Sitka alder (maintained by snow avalanches; USFS 1994) commonly borders the headwater streams in Game Creek, the potential recruitment of LWD to larger, fish-bearing channels is limited on this basis. Landslide surveys in the Game Creek basin and in other geomorphically similar watersheds in southeast Alaska have revealed that sediment and associated LWD are rarely transported from small headwater basins into larger streams (Susan Perkins, Seattle, Washington, unpublished data). In southeast Alaska, debris flows typically deposit on broad fans in U-shaped valleys, which limits mass wasting flux of LWD to large channels (Swanston and Marion, 1991; Johnson et al. 2000).

We assigned LWD to one of two location categories: pieces in jams or pieces located between jams. We defined jams as LWD accumulations (two or more pieces) that block at least 20% of the bankfull channel width. Jam length (length of channel cover by a jam), the length of interjam zones, and channel width were measured with a hip chain.

Each LWD piece was assigned to one of three categories: recruited trees (recruits), mobile pieces, and embedded pieces. Recruits are trees that are clearly attached to the adjacent bank (e.g., rooted to bank or trunk extending into riparian forest) or are contained in a landslide deposit. Mobile pieces are those in the bankfull channel that have moved away from the point where they were recruited and generally show signs of fluvial transport (e.g., abrasion, broken limbs, broken ends, located in log jams). Embedded pieces are partially buried either in the bank or streambed and are assumed not to be a recruit. All LWD pieces (including recruits) in jams were defined as either key pieces or not, depending on whether the piece held a jam in place. A jam may have had more than one key piece.

The diameter of each piece (measured in middle of log) was assigned to one of four categories: 10–30 cm, 30–60 cm, 60–90 cm, and $>$ 90 cm. The length of each piece was measured to the nearest 3-m interval, but in narrow channels, smaller LWD was measured to the nearest 1.5 m.

Each recruited tree was assigned to one of three recruitment categories: bank erosion, landslide, or mortality. Bank erosion recruitment was assigned to recruits with root wads that were located near sites with root-throw pits and obvious bank erosion. Landslide recruitment was assigned to trees located near or in landslide deposits. Mortality recruitment included downed trees that were not derived by bank erosion or landslides and originated in the riparian forest. These trees were generally recruited by windthrow or natural mortality (deadfall). In this study mortality refers to chronic inputs of LWD, not to catastrophic inputs (e.g., fire or major storms downing entire stands).

Using a modified version of a snag classification system by Hennon et al. (in press), we assigned all recruits and key pieces to a decay class. Decay class was determined for the portion of a log that was on the bank or was least disturbed by stream flow. Decay categories were classified as I = green leaves or needles present, II = twigs present, III = secondary branches present, IV = only primary branches and nubs present, V = no branches and some nubs present, and VI = log covered with moss and live dependent saplings.

To estimate the age of logs in each decay class, cross sections were taken from dependent saplings growing on the bole or rootwad of recruited trees. Cross sections of the stem were obtained with a pruning saw from the base of the largest sapling; a core was taken with an increment borer from the saplings that were especially large. Only spruce and hemlock saplings with a straight stem, indicating they grew after the recruited tree fell, were selected for aging. Estimates of sapling age were determined by counting the annual rings on tree cross sections following a 60-d drying period. To improve accuracy of the ring counts, one edge of the cross section was sanded smooth with 220-grit sandpaper, and the annual rings were counted under a 10× stereoscope.

Constructing the wood budget.—Construction of a wood budget for Game Creek required solving equation (1). Field measurements of LWD distinguished three recruitment sources: bank erosion, mortality, and landsliding. Catastrophic inputs of LWD (I_f in equation 2) were not included because of lack of field evidence, although windthrow-regenerated stands in the Game Creek basin suggested one or more large windstorms occurred approximately 100 years ago (USFS 1994). Input of LWD from exhumation of the channel bank was observed at several of the larger flood plain segments. This LWD was assumed to originate from buried jams that were abandoned by channel migration in the flood plain portions of Game Creek. In this study, we did not measure LWD exhumation or loss due to channel migration; therefore, we were not able to estimate I_e (equation 2) or O (equation 1). In the absence of other information, we assumed steady-state conditions over the several-decade period were represented by the field measurements; hence, $I_e = O$ and these terms cancel in equation 1. The volumetric loss of LWD by decay (D) was ignored because wood decay over a period of 20–40 years (the age of the majority of recruited pieces) reduces wood density but does not significantly reduce the volume of a log (Hartley 1958). Given these assumptions, equation (1) reduces to

$$\Delta S/\Delta t = [I + (Q_i - Q_O)]\ \Delta x, \qquad (7)$$

To calculate lateral recruitment rates of LWD, the fluvial flux terms (Q_i and Q_O in equation 1) can be ignored because the field measurements distinguished between recruited and mobile (transported) LWD. The flux of LWD increased downstream (as we show later), however the governing terms (I, ϕ, and ξ in equations 5 and 6 changed only slightly from one reach to the next, yielding Q_i approximately equal to Q_O. At this stage with the fluvial terms omitted, equation 7 reduces to

$$\Delta S = I/\Delta T, \qquad (8)$$

where ΔS is the change in recruited LWD storage ($\mathrm{m}^3\ \mathrm{km}^{-1}$) in study segments ($x$) at some time t (i.e., 1998–1999) from each input process, and ΔT is the elapsed time period over which LWD enters and accumulates in the study segments. We determined LWD storage per study segment by summing individual piece volumes. Piece volume was computed from piece length and diameter data using the geometry for a cylinder. In our analysis of recruitment rates using equation (8), $I = \Delta S/\Delta T$, we assumed ΔT to be equal to the weighted mean age of recruited LWD in that segment, as proposed by Murphy and Koski (1989).

The weighted mean age (ΔT) of recruited LWD in each segment was computed by

$$\Delta T = \left(\sum_{i=1}^{6} a_i p_i\right), \qquad (9)$$

where a_i is the mean age of LWD in decay-class i, and p_i is the proportion of LWD in decay-class i in any segment (Murphy and Koski 1989). The mean age of recruited LWD was determined from the age of dependent saplings on recruited LWD for all decay classes except class I (green trees). Recruits in class I were too young to contain dependent saplings and were assumed to be 1 year old. The age data provided an estimate of the minimum resident time for recruits because the lag time between LWD recruitment and the germination of dependent saplings is unknown. We assumed rapid sapling colonization on recruits because of good growing condition in the soil of upturned root wads. We used the mean age of dependent saplings to estimate ΔT instead of the maximum age or another statistic because it was more representative of all recruits in a study segment.

The LWD flux (Q_w) for Game Creek was computed in two steps. First, the average transport distance (ξ) was calculated from equation (6) with the following estimates for each term. Interjam spacing (L_j) was determined from the mean interjam distances in each study segment. The interjam distance is the measured distance between the upstream end of one logjam and the downstream end of the next upstream logjam. The lifetime of pieces (T_p) was estimated from a simple exponential decay model (Harmon et al. 1986) using an average decay rate of 3.0% per year. This rate is based on studies of wood decay of northwestern conifer species on forest floors (2–7% per year; Spies and Franklin 1988) and decay of submerged conifer LWD (2.6–3.8% per year; Bilby et al. 1999). Assuming wood becomes mechanically weak and breaks up in stream environments when it is 95% decayed, T_p was set at 100 years (i.e., decay rate of 3% per year). Jam longevity (T_j) was assumed to correspond to the weighted mean ages of key pieces in the study segments and was computed from equation (9) using the mean ages of recruits in each decay class. An average β was computed from the mean ratio of jam width to channel width for all jams in each study segment.

Finally, calculating the flux of LWD (cubic meters per year; equation 5) required knowing the proportion of wood from recruits that is transportable (ϕ). For significant transport to occur, piece length must be less than a channel width ($L_p/\mathrm{wc} \leq 1$) so that pieces are not caught on channel banks (Lienkaemper and Swanson 1987; Nakamura and Swanson 1993). The proportions of mobile pieces in each segment were estimated from field measurements of piece lengths and channel widths.

Interjam distances and jam longevity were characterized by a range of values that represented spatial and temporal variability in jam formation. Therefore, we also estimated transport distances based on frequency distributions of L_j and T_j. This estimate of ξ is not used in the LWD flux estimate, rather it provided a more realistic picture of LWD lifetime travel distances. Because LWD size and stream channel width are key factors controlling L_j and T_j and these factors are assumed to be un-

TABLE 2.—Channel size categories used to stratify the field data for estimating the probability distribution of large-woody-debris transport distances.

Channel width (m)	Drainage area (km^2)	Gradient (%) and substrate	Number of jams measured
3–5	1–3	4–15 (Cobble–bedrock)	103
5–10	3–20	2–6 (Gravel–small boulder)	82
10–20	12–56	1–3 (Gravel–cobble)	65
20–30	56–93	<1 (Gravel)	22

changed over the decadal time scale of this study, the resulting shape of the frequency distributions for L_j and T_j are assumed to be constant over the same period (although they probably vary over longer periods because of periodic large floods and timber blowdown).

Values of L_j and T_j were stratified by four channel width–morphologic categories to provide a sufficient number of samples for a frequency analysis (Table 2). The distribution of jam ages was determined from the age of dependent saplings on key LWD. The weighted mean age was not used because it could not be calculated for each individual jam and a large number of individual ages were required to estimate the form of the distribution.

The distributions of L_j and T_j were fit with modeled probability distributions based on shape and goodness of fit (Appendix). The interjam spacing data were modeled with 3-parameter lognormal distributions. Jam longevity was modeled with gamma distributions. The parameters of the modeled distributions were estimated separately for each channel width category, but several categories were pooled for both parameters (i.e., 5–20 m for L_j, and 3–10 m and 10–30 m for T_j) because of low sample size and shape similarities. In the calculation of probabilistic ξ, T_p was set at 100 years and β at 0.76 (the mean of all segments).

To estimate a distribution of lifetime travel distances for LWD, the independent values of L_j and T_j were consecutively sampled from each of their respective distributions until the sum of T_j was equaled or exceeded T_p. The series of corresponding L_j were then summed to equal a cumulative transport distance. The Monte Carlo simulations were run for 1,000 iterations for each channel width category.

In the analyses, several variables were related either to drainage area or channel width. This was facilitated by a linear regression equation of channel width (wc) versus drainage area (DA): wc = 0.272 (DA) + 4.754; $r^2 = 0.94$.

Results and Discussion

Characteristics of Large Woody Debris Recruitment

Recruited LWD ranged from 22% to 80% (mean = 58%) of the total volume of LWD in the study segments of Game Creek (Table 3). Recruit storage ranged from 22 m^3/km to 364 m^3/km (for comparison, 2.5 m^3 is the volume of a single tree with an average length of 20 m and a diameter of 0.4 m) and generally increased with drainage area. Bank erosion and mortality were the dominant recruitment mechanisms in all study segments, accounting for 60% and 39% of total volume, respectively. Landslides supplied 1% of the total volume or less than 11% in any segment.

The percentage of recruited LWD in each decay class generally increased with the degree of log decay (Figure 2), indicating that most of the recruited LWD was relatively old. Recruited LWD in decay-classes I to III accounted for less than 24% of the total population. Murphy and Koski (1989) observed a similar distribution of LWD by decay class for old-growth forest streams of southeast Alaska.

The mean age of dependent saplings was related to decay class and ranged from 7.6 years for class II to 31.3 years for class VI (Table 4). The maximum age for decay-class VI ranged up to 126 years. The distribution of sapling ages overlapped among several decay classes (i.e., class II overlapped class III and class V overlapped class VI), indicating high variability in decay-class age. To distinguish ages among the decay classes, the categories were pooled resulting in four decay classes with significantly (F-test, $P < 0.01$) different mean ages (Table 4).

The weighted mean ages of recruited LWD ranged from 1 to 31.1 years and declined with an increase in drainage area (Figure 3). This inverse relationship between age of LWD and drainage area indicates that recruited wood is less stable in larger channels. This is probably due to wider channels and greater total stream power.

Rate of Recruitment

Recruitment rate of LWD from bank erosion (equation 8) showed a systematic increase with drainage area (Figure 4a) ranging from about 1 m^3·km^{-1}·year^{-1} at the smallest drainage areas to about 16 m^3·km^{-1}·year^{-1} at 60–80 km^2 (i.e., 0.4–6.4 trees/year based on an average tree volume of

TABLE 3.—Total large-woody-debris storage by type and recruit storage by input process.

Study segment	Total storage (m^3/km)	Storage type (%)			Recruit storage input process (m^3/km)		
		Embedded	Mobile	Recruit	Bank erosion	Mortality	Landside
1	205	26.3	22.4	51.3	8.8	96.0	0.3
2	157	19.8	28.1	52.1	18.1	63.6	0.0
3	102	28.4	49.7	21.9	1.5	20.7	0.0
4	259	28.7	19.8	51.4	25.0	102.2	6.2
5	279	16.6	7.8	75.7	39.2	162.7	8.5
6	184	17.5	22.5	60.1	32.0	78.4	0.0
7	219	18.4	10.9	70.7	26.7	127.9	0.0
8	348	27.6	3.2	69.2	120.9	120.1	0.0
9	239	18.0	21.4	60.6	40.1	105.0	0.0
10	150	27.1	16.4	56.5	52.4	32.5	0.0
11	235	8.8	11.3	79.9	82.3	105.4	0.0
12	241	24.7	14.3	61.1	17.8	129.0	0.0
13	128	6.0	58.5	35.5	1.0	38.9	5.5
14	263	15.1	13.8	71.0	63.9	103.0	19.8
15	230	25.2	28.7	46.1	34.3	67.2	4.6
16	176	14.1	17.5	68.4	16.0	103.0	1.3
17	278	10.5	20.3	69.2	74.2	117.9	0.0
18	266	11.5	11.8	76.7	97.8	106.6	0.0
19	199	17.6	34.5	47.9	38.2	57.3	0.0
20	176	13.9	10.2	75.9	110.6	22.7	0.0
21	259	22.2	21.8	56.1	94.0	51.4	0.0
22	513	20.4	8.6	71.1	243.4	120.8	0.0
23	442	10.9	28.5	60.6	45.5	219.1	0.0
24	330	17.5	14.7	67.8	75.8	147.7	0.0
25	491	20.4	18.6	61.0	155.9	143.8	0.0
26	296	31.9	18.9	49.2	93.1	42.7	2.3
27	767	14.5	48.6	36.9	277.9	5.1	0.0
28	550	8.8	34.2	57.0	269.3	42.8	1.1

2.5 m^3). Regression analysis with several different models (i.e., linear, lognormal, quadratic) showed a significant relationship between recruitment rate and drainage area ($P < 0.05$) with r^2 ranging from 0.56 to 0.71. A specific model was not selected, however, because we were uncertain about the functional relationship between bank recruitment and drainage area. The statistical fit for the models we tested was strongly influenced by the two data points at the larger drainage areas (53 and 79 km^2, Figure 4a). Analyses without these data showed the regression was still significant ($P < 0.05$), but the strength of the relationships were reduced.

The functional relationship between bank erosion recruitment of LWD and drainage area should

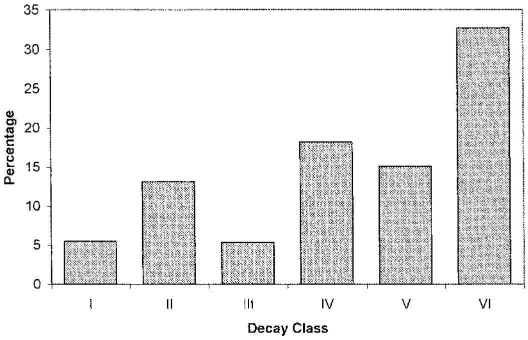


FIGURE 2.—Percentage of recruited LWD by decay class in Game Creek basin in southeast Alaska (N = 2,449).

TABLE 4.—Age statistics for recruited large woody debris by unpooled and pooled decay classes. Age of decay classes determined from dependent saplings.

Decay-class	Mean	Median	SD	Maximum	Number aged
Unpooled					
I	—	—	—	—	0
II	7.6	6.0	3.2	14	14
III	10.1	9.5	5.0	16	8
IV	18.7	17.0	9.4	42	5
V	30.3	29.0	11.9	65	47
VI	31.3	26.0	19.5	126	198
Pooled					
I	1.0[a]	—	—	1[a]	154[b]
II, III	8.5	6.0	4.0	16	22
IV	18.7	17.0	9.4	42	53
V, VI	31.1	27.0	18.2	126	245

[a] Age of decay-class I is assumed to be 1 year.

[b] Number of recruits in decay-class I.

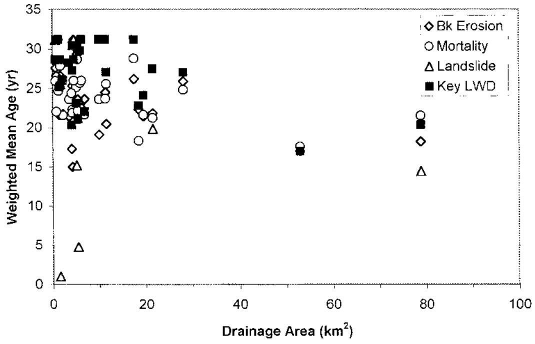
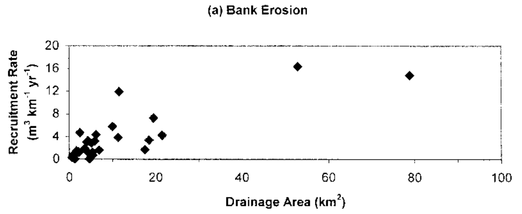
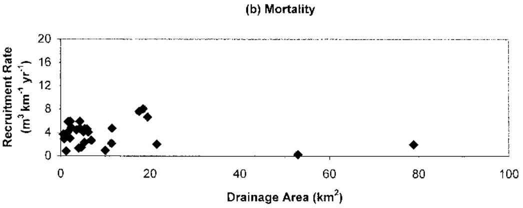


FIGURE 3.—Weighted mean ages of recruited LWD and key LWD in relation to drainage area for Game Creek basin in southeast Alaska.


(a) Bank Erosion


(b) Mortality

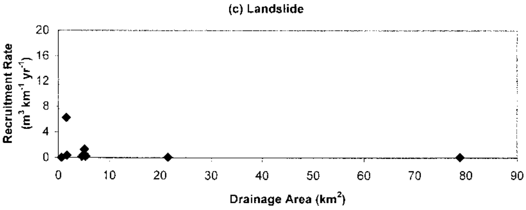

(c) Landslide

FIGURE 4.—Recruitment rate of LWD by bank erosion **(a),** mortality **(b),** and landslide **(c)** in relation to drainage area, Game Creek basin in southeast Alaska.

be largely governed by how bank erosion changes with drainage area. Bank erosion generally increases with increasing drainage area (Hooke 1980). Because bank erosion is a stochastic process linked to floods, the absolute magnitude of recruitment rates partly depends on when the sampling occurred. Data collected over longer periods or over larger areas would be necessary to provide better estimates of this relationship.

Input of LWD from mortality was highly variable among segments and showed no systematic variation with drainage area (Figure 4b). Mortality recruitment rates ranged from 0.3 to 8.0 $m^3 \cdot km^{-1} \cdot year^{-1}$ and averaged 3.8 $m^3 \cdot km^{-1} \cdot year^{-1}$. Variation in mortality recruitment probably represents spatial and temporal variation in forest mortality rates (equation 4), although this was not investigated. Recruitment of LWD from landslides was low in all but one segment and did not appear to be related to drainage area (Figure 4c). Delivery of landslide debris, including trees, to the primary (i.e., fish-bearing) channel network is minor in the Game Creek watershed (Susan Perkins, Seattle, Washington, unpublished ms) due to the U-shaped valley and gentle topography adjacent to streams. A low contribution of LWD to larger streams by mass wasting appears to be typical for the islands of southeast Alaska (Swanston and Marion 1991; Johnson et al. 2000).

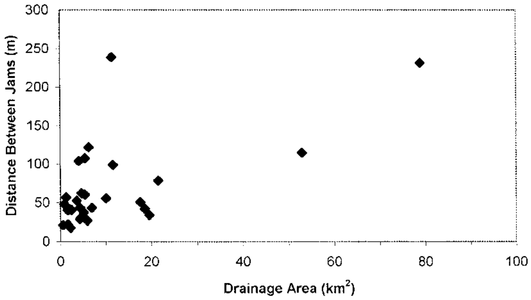
Recruitment of LWD in Game Creek was predominated by mortality in the smallest drainages (<10 km^2), except where landsliding was significant (only one segment), and was predominated by bank erosion in the larger drainages. Because bank erosion increases downstream, the relative contribution from mortality decreases as the proportion of bank erosion recruits increases. Based on this relationship (Figures 4a and 4b), the crossover point in Game Creek where bank erosion recruitment exceeds the maximum mortality recruitment (8.0 $m^3 \cdot km^{-1} \cdot year^{-1}$) was visually estimated to occur in drainage areas larger than about 20 km^2 (about 10-m-wide channel).

Transport Distance

Interjam spacing in Game Creek increased with increasing drainage area and ranged from about 50 m at the smallest drainage areas to greater than 200 m at 80 km^2 (Figure 5a). Jams also increased in size (volume) downstream (Figure 5b). These spatial patterns are consistent with theoretical predictions of wood storage in rivers (Benda, in press). For example, the proportion of trees able to span a channel decreases downstream as a result of increasing channel width (particularly if the distribution of tree heights remains constant throughout the network). As a consequence of increasing interjam spacing, the channel length (between jams) receiving lateral recruitment of LWD also increases downstream, a process that leads to jams of larger debris (Figure 5b).

The mean weighted age of key LWD in jams declined with increasing drainage area similar to the pattern observed for recruited LWD (Figure

(a) Jam Spacing



(b) Jam Size

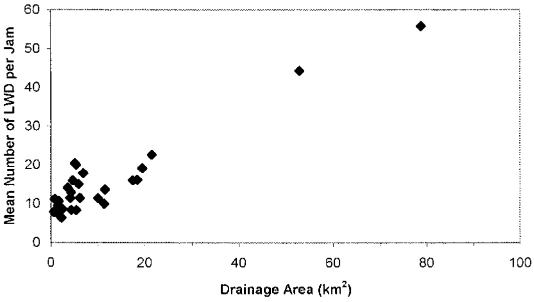


FIGURE 5.—Interjam spacing **(a)** and jam size **(b)** in relation to drainage area, Game Creek basin in southeast Alaska.

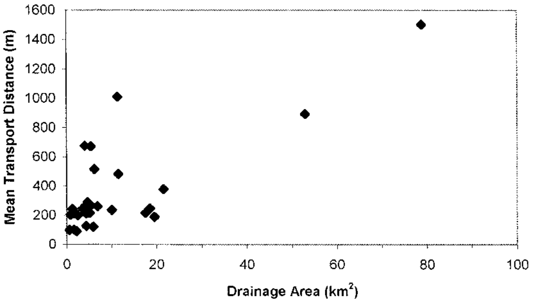


FIGURE 6.—Relationship between LWD transport distance and drainage area, Game Creek basin in southeast Alaska.

3). Values of T_j ranged from 25 to 30 years in small channels and decreased to 15–20 years in larger channels. These age ranges are similar to the majority of LWD ages estimated for a western Washington stream (80% <50 years old; Hyatt and Naiman 2001). Relatively young ages of jams are probably due to a combination of high stream energy in mountain channels and wood decay that weakens key logs. The average β for each study segment did not vary systematically with drainage area and ranged from 0.52 to 0.95 (average 0.76). Regression analysis of β and drainage area was not significant ($F = 1.29$, df = 27, $P = 0.265$). This result may be an artifact of data collection, which excluded jams that block less than 20% of the bankfull channel width.

Fluvial transport of LWD was predicted to increase downstream with increasing drainage area (Figure 6). Using mean values of T_j and L_j for each segment (Figures 3, 5), a β of 0.76, and a T_p of 100 years in equation (6), the average transport distance varied from about 200 m in small channels to greater than 1,500 m in larger channels. Regression analysis of transport distance (log transformed) with drainage area shows the relationship is significant ($F = 16.72$, df = 26, $P < 0.001$). We recognize that the two data points at the larger drainage areas strongly influence the significance of this relationship and that more data are needed to adequately test the transport equations. Because transport distance is sensitive to the lifetime of LWD (calculated to be 100 years in this example, based on a 3% decay rate) and to β, different parameter values would increase or decrease the predicted transport distances in other landscapes.

Monte Carlo simulations that employ the distributions of interjam spacing and jam age provided more realistic estimates of the lifetime travel distances (Figure 7). The probable range of travel distances for LWD increases with increasing channel size. In the smallest channel (3–5 m wide), there was a 90% probability that LWD would be transported at least 50 m and a 10% probability that transport could exceed 300 m. In the largest channel (20–30 m wide), there was a 90% prob-

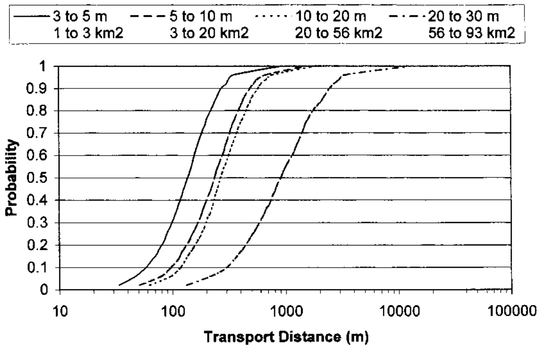


FIGURE 7.—Probability of LWD lifetime travel distances by channel width and drainage area category, Game Creek basin in southeast Alaska. The LWD travel distances were derived from Monte Carlo simulation (see text).

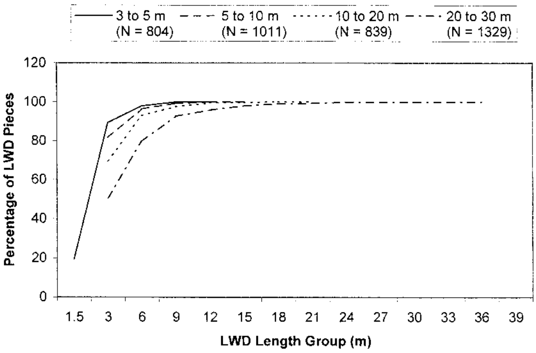


FIGURE 8.—Cumulative percentage of mobile LWD pieces in each length-group by channel-width category, Game Creek basin in southeast Alaska.

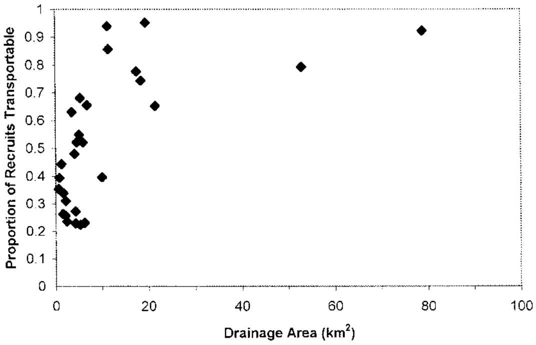


FIGURE 9.—Proportion of recruited LWD that is less than channel width (i.e., transportable) in relation to drainage area, Game Creek basin in southeast Alaska.

ability of LWD traveling at least 300 m and a 10% probability of LWD moving more than 2,500 m. Again, variations in estimated frequency distributions may lead to other predictions in other landscapes. Also, additional data from southeast Alaska would improve our predictions of travel distances.

Large Woody Debris Flux

In Game Creek, the length of nearly all mobile LWD was less than or equaled the channel width (Figure 8). In the 3- to 5-m-wide channel, 90% of the mobile LWD is in the 3-m or smaller size-group (70% is in the 3-m size-group). In the larger channels, more than 95% of the mobile LWD is shorter than the channel width. This finding concurs with others (Lienkaemper and Swanson 1987; Nakamura and Swanson 1993) and supports the assumption in equation (5) that piece length must be less than channel width ($L_p/\mathrm{wc} \leq 1$) for transport to occur. Because channel width increases downstream, an increasing proportion of recruited pieces will be shorter than channel width; therefore, the proportion of recruited LWD that is transportable (ϕ) increases downstream (Figure 9). In Game Creek, the transportable proportion ranged from 20% in the smallest drainages to 90% in the larger drainages and was greater than 80% in drainages larger than 50 km². Theoretically, the proportion transportable becomes 100% where the channel width exceeds the height of the tallest tree. In Game Creek the channel width exceeds the average tree height (20 m) at 50 km².

Flux of LWD (m³/year) was estimated for each study segment from the product of three parameters in equation (5): (1) total lateral recruitment (I), excluding landslide recruitment, because of its minor importance in the drainage network; (2) transport distance (ξ); and (3) the proportion of recruited LWD that is transportable (ϕ). Because each of these parameters is directly influenced by drainage area, LWD flux was predicted to increase with increasing drainage area (Figure 10). The relationship between flux and drainage area, however, is ill-defined because of limited data for drainages greater than 30 km². Significant regressions using either a linear ($P < 0.001$, $r^2 = 0.87$) or log ($P < 0.001$, $r^2 = 0.47$) model could be fit to the flux predictions. In smaller drainages (<50 km²) both models would give similar predictions. However, in the larger drainages (>50 km²) the difference between the model predictions would be significant. Because ϕ is nearly 1 in large drainages, recruitment (I) and transport distance (ξ) are the key parameters controlling flux, according to equation (5). The uncertainty about these variables and their relationship to drainage area translates to a poor understanding for flux in the larger drainages.

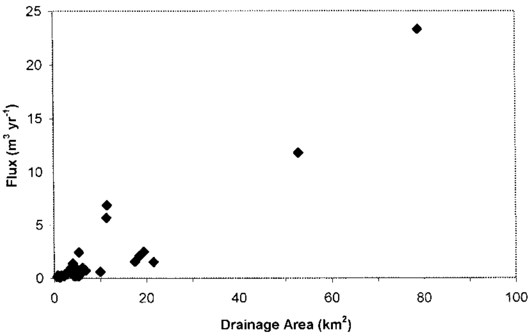


FIGURE 10.—Flux of LWD in relation to drainage area, Game Creek basin in southeast Alaska.

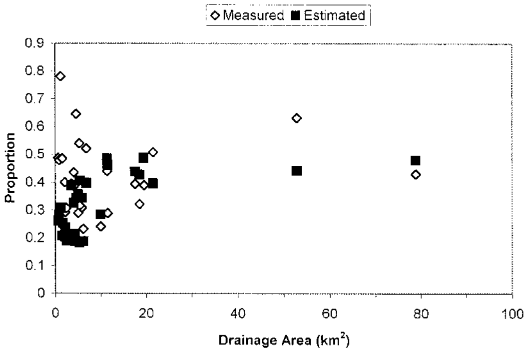


FIGURE 11.—Estimated proportion of LWD in transport (i.e., estimated flux as a proportion of total storage; solid boxes) and measured proportion of total stored LWD that is mobile (open diamonds), Game Creek basin in southeast Alaska.

To examine the significance of LWD transport to the wood budget, flux was compared with lateral recruitment at a length scale equivelent to LWD transport distances (ξ). The fluvial transport of LWD (flux) from an upstream reach was compared with total LWD storage (i.e., transport + lateral recruitment) by the ratio

$$\psi = [(I\phi\xi)\Delta_{x,t}]/[(I\phi\xi)\Delta_{x,t}] + [(I\xi)\Delta_{x+1}], \quad (10)$$

This ratio (Figure 11) shows that the contribution of fluvial transport to total LWD storage rapidly increases from 0.2 in the smallest channels (3 m wide or 1 km^2 drainage area) to about 0.5 (the maximum possible) at 50 km^2 ($\geq$20 m width). The estimated maximum occurs when $[(I\phi\xi)\Delta_{x,t}]/[(I\xi)\Delta_{x+1}] = 1$. Because I and ξ are similar between adjacent reaches, the maximum occurs when ϕ equals 1, which occurs at about 50 km^2 in Game Creek (Figure 9), or when tree height is equal to or less than channel width. The similarity in LWD flux between adjacent stream reaches of length ξ, results in Q_i being approximately equal to Q_O in equation (1); Q_O would be slightly larger because the parameters I, ϕ, and ξ increase downstream. In addition, input would not equal output if there were significant differences in lateral recruitment $f(I)$ from segment to segment, or during periods of punctuated supply of LWD into the network.

Estimates of transport distance (Figure 6) and flux (Figure 11) were tested to evaluate the validity of the predictions. The ideal test would compare the estimates against a long time series (decades to centuries) of wood movement at numerous locations in a drainage network. No such data set exists in Game Creek or elsewhere. The measured proportions of total LWD storage that are mobile (i.e., mobile + embedded) in each of the 28 study segments (Table 3) were used as a proxy to represent transported LWD and to evaluate estimates of flux. These data were not used in developing estimates of recruitment or flux and therefore are an independent data set. The embedded LWD was added to the mobile portion because most embedded LWD was observed within the bed of the active channel and was assumed to be in transport. The potential error from including embedded LWD with mobile LWD is probably greatest in smaller channels where a single embedded tree on the channel edge could represent a large proportion of the total storage.

The comparison of the estimated proportion of LWD in transport to the field-measured mobile LWD showed a similar pattern relative to drainage area (Figure 11). Some of the measured proportions were greater than 0.5 in the smaller drainages, but most fell within the range of the estimated values. This suggests that the general forms of the LWD transport equations (equations 5, 6) and the estimated parameter values in Game Creek produce plausible estimates of wood transport and flux downstream. Other forms of LWD transport data or larger data sets of the type in Game Creek are needed to evaluate the wood transport models used here more fully.

Evaluating Rates of Bank Erosion and Forest Mortality

Forest mortality.—Forest mortality rates can provide insight into forest structure and function that may be useful to plant ecologists and foresters. In addition, mortality rates are necessary for developing LWD simulation models (Beechie et al. 2000). The mortality rate of trees within the riparian zone of Game Creek (not including bank erosion) was estimated for each study segment using equation (3) and our estimates of mortality recruitment for the Game Creek watershed (Figure 4b). Solving for M in equation (3) required estimates of (1) standing live biomass (B_L; i.e., 250 trees/ha or 625 m^3/ha, assuming an average volume of 2.5 m^3/tree, based on data from Douglas J. Martin, Seattle, Washington, unpublished data); (2) P_m, which was estimated to range from 0.08 to 0.21 depending on channel width (L. E. Benda, unpublished data); (3) H of 20 m (from Douglas J. Martin, Seattle, WA, unpublished data); and (4) NB of 2 (both sides of the channel contributing LWD). The mortality estimate, averaged over 24 years, is the mean weighted age of mortality recruits in all study segments.

The calculated mortality rate ranged from 0.1% to 2.6% per year (average 1.2%). We are not aware of other forest mortality rates in southeast Alaska to compare with our estimates. An average forest mortality rate of 0.5% per year has been estimated for mature coniferous forests in western Washington by Franklin (1979). Mortality rate is undoubtedly affected by forest age and stand vulnerability to disturbance. Information on the age of timber stands in Game Creek was not available during this study. Mortality due to disturbances from flooding and windthrow was observed at some locations but was not evaluated.

Bank erosion.—Bank erosion rates can be used to estimate sediment production or to evaluate habitat quality and therefore may be of interest to geomorphologists and fishery biologists. In addition, bank erosion rates can be used to predict input of LWD to streams in simulation models (Benda, in press). Rates of bank erosion were calculated using equation (4) and our estimates of LWD recruitment for the Game Creek watershed (Figure 4a). Solving for *E* in equation (4) required (1) forest biomass (estimated similarly to the solution for mortality); (2) P_b, estimated to range from 0.29 to 0.85 depending on channel width (L. E. Benda, unpublished data); and (3) NB of 1 because bank erosion is assumed to occur only on one side of a channel with sediment accretion occurring on the opposite side (this maintains channel width in long-term steady state, which we believe is not stable in Game Creek, although it probably fluctuates over time around a long-term mean value). This estimate, averaged over 23 years, is the mean weighted age of bank erosion recruits in all study segments.

Average erosion rates in Game Creek varied from about 1 cm/year in the smallest channels to 30 cm/year for channels of drainage areas of 80 km² (Figure 12). These results suggest there is a positive relationship between bank erosion and drainage area, a pattern that is consistent with measured bank erosion worldwide (Hooke 1980). More data are necessary to better define this relationship. Also, additional data may show how variable bank erosion rates may change over time in response to large floods. The construction of LWD budgets may provide another means to estimate bank erosion rates in watersheds, which are an important element of watershed analysis (WDNR 1997).

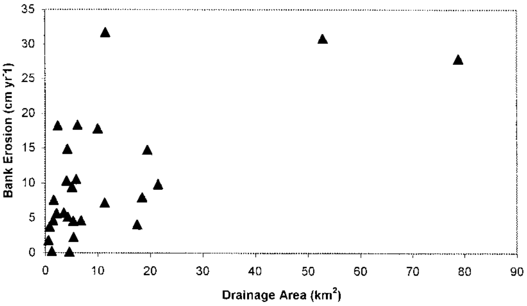


FIGURE 12.—Estimated mean bank erosion rate for the Game Creek watershed.

Based on a visual inspection of the wood recruitment results (Figures 4a and 4b), we estimated that recruitment from bank erosion exceeds the maximum mortality recruitment in Game Creek at drainage areas greater than about 20 km² (about 10-m-wide channel). An inspection of the results in Figure 12 indicates that the bank erosion rates that would correspond to a drainage area of 20 km² range from 5 to 15 cm/year.

Potential Errors and Limitations

There are several sources of errors that can affect our calculated estimates of LWD recruitment, transport distances, and transport flux. Estimates of recruitment rate are affected by potential errors in our estimates of age and the storage volume of recruited LWD. Because there is a lag time between the time of LWD recruitment and establishment of dependent saplings and because dependent saplings are vulnerable to removal by stream flow, the age of dependent saplings probably underestimates the true age of recruited trees. This error would cause an overestimation of LWD recruitment rate that would increase with channel size, because in a larger river, increased flow increases disturbances to dependent saplings. In addition, the increased potential for losing recruited LWD in larger channels reduces the measured storage and could potentially cause an underestimate of recruitment rate. The absolute magnitude of these errors is uncertain given the small data set in Game Creek, although the errors may partially cancel one another. The only viable independent checks would involve comparing the calculated mortality and bank erosion rates associated with the measured recruitment rates in Game Creek to other estimates of these parameters in the literature. The calculated forest mortality rates during this study (0.1–3.2% per year) are of the same order of magnitude compared with the little data available in the Pacific Northwest Ecoregion (Franklin, 1979;

P. Hannon, personal communication). This suggests that our estimates of mortality recruitment are plausible. Calculated bank erosion rates associated with recruitment are also similar to what others have measured in the field and commensurate with long-term soil creep rates (Lehre 1982; Reid 1981). Certainly, more data are needed to develop confidence in our estimates of LWD recruitment for southeast Alaska and to determine the errors in these preliminary estimates. Moreover, additional studies are needed to evaluate how temporal variability in process rates can affect field measurements obtained over relatively short periods.

There are several potential errors involved in predicting wood transport distances and wood flux in Game Creek. These include the form of the transport equations (Equations 5 and 6 from Benda, in press) and the field estimated parameter values for I, T_j, T_p, L_j, β, and ϕ. Only time will tell whether the form of the transport equations is accurate at the scale of watersheds over decades (i.e., the intended use of the equations). The field data for T_j, and L_j show the correct trends and are in agreement with both common experience and theoretical predictions. Estimates of T_j are probably biased low because of the dependent sapling aging problems discussed above. This would cause overestimate transport distance, and the error would increase with drainage area size.

Our estimates of T_p are based on a simple exponential decay model using decay constants in the literature. However, burial of LWD can increase the lifespan of wood in streams that may cause an increase in predicted transport distances and flux rates. The error in (ϕ) is probably relatively small, given the large data set from this study and others. The largest uncertainty is how β affects transport. Our confidence in the estimates of β from field measurements are good ($N = 272$, Table 2), but we are unsure of how the cross-sectional width blocked by a jam relates to wood transport past a jam. The effectiveness of jams in impeding LWD transport probably declines with increasing channel width, although we did not see a trend between the ratio wj/wc and drainage area. This may be due in part to our exclusion of jams that blocked less than 20% of the channel width. The larger channels had many small jams that were not measured, and a few large jams that were measured. If β had changed with channel size, we would have estimated ξ with a probability distribution of β values, similar to the method used for T_j and L_j. We also believe that β probably varies over time with temporal wood flux, but we do not have data to evaluate it. Further studies and larger data sets are undoubtedly needed to build confidence in our understanding of wood transport in mountain rivers. Despite these potential limitations, the close similarity between our predicted proportion of wood in transport and the field measured proportion of mobile LWD provides support for both the general form of the transport equations and our estimated parameter values.

Care should be taken when extrapolating our results to other basins in southeast Alaska or to other regions. We believe the general patterns of recruitment and transport with drainage area will probably be similar in other locations; however, the absolute magnitude of process rates will probably vary in other watersheds across southeast Alaska and other regions. For example, forest mortality may be dependent on forest species, climate, and topography. Bank erosion might vary with topography and lithology. Landsliding may be a more important process in steep landscapes with high connectivity between hillslopes and channels and between headwater streams and larger rivers. In addition, P-values will vary in different landscapes having different tree heights (L. E. Benda, unpublished data). We recommend that the effect of different process rates on the LWD budget in other landscapes be evaluated on a case-by-case basis. Nevertheless, the authors also believe it is feasible to construct regional empirical relationships between climate, topography (lithology), channel geometry, spatial scale, and the recruitment and transport of LWD. Moreover, as more wood budgets are constructed, it should be possible to develop general principles about how LWD supply and storage should vary with changes in climate (wet versus dry), topography (gentle versus steep), and basin size (small versus large).

Potential Applications

A LWD mass budget constructed at the watershed scale can have several important ecological applications. Understanding spatial variation in abundance of LWD across a watershed could yield insights into ecological patterns, including how certain aquatic organisms may be spatially distributed. For example, because LWD influences the storage of particulate organic matter (Naiman and Sedell 1979) and organic storage strongly influences trophic processes and invertebrate distribution (Wallace et al. 1995), LWD storage may affect community structure in systems such as Game Creek. In smaller streams, the higher frequency of debris jams and the longer residence times of jams increases organic storage that favors development of communities dependent on heterotrophic production. Increasing interjam spacing and decreasing jam age with increasing distance downstream should reduce opportunities for particulate organic storage and heterotrophic production. The transition point at which aquatic biota shift from predominately heterotrophic to autotrophic production along the river continuum (Vannote et al. 1980) might be related to patterns of fluvial LWD transport in systems like Game Creek. The relationships between lateral recruitment and wood transport also have ramifications on channel geomorphic processes (e.g., sediment storage and pool formation) that influence habitat complexity and the distribution of lotic fishes (Bisson et al. 1987; Reeves et al. 1998). Combining habitat preferences of fish with knowledge of LWD transport and habitat formation could predict spatial patterns of habitat use or potential use in a watershed. Finally, the ecological importance of wood flux from terrestrial to marine environments (Maser and Sedell 1994) could be estimated from the results of this study.

The wood budget for Game Creek encompassed approximately 25 years; therefore, it does not reflect large stochastic fluctuations of LWD due to windstorms, fires, and landsliding. However, the wood budgeting framework and supporting theory (Benda, in press), could be used to evaluate the importance of stochastic processes in wood recruitment and transport in basins such as Game Creek.

From a forest and fisheries management perspective, information on LWD budgets may be useful for determining how and where to protect LWD sources to streams. Knowing the spatial patterns of LWD recruitment, transport, and storage in Game Creek can provide a watershed context for understanding geomorphic and ecological processes associated with LWD. This may help land managers identify the probable extent of LWD transport, as well as the relative importance of different recruitment processes on LWD storage. This information could be used for identifying and prioritizing those portions of the channel network that are important for supplying LWD to anadromous fish habitat or for other ecological functions. By knowing where LWD is recruited and understanding the variables controlling recruitment, land managers can develop riparian management plans that maintain a long-term supply of LWD, or they can design restoration projects to enhance LWD recruitment and transport at the network scale.

Acknowledgments

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Appendix follows

Appendix: Interjam Spacing and Key Piece Ages by Channel-Width Category

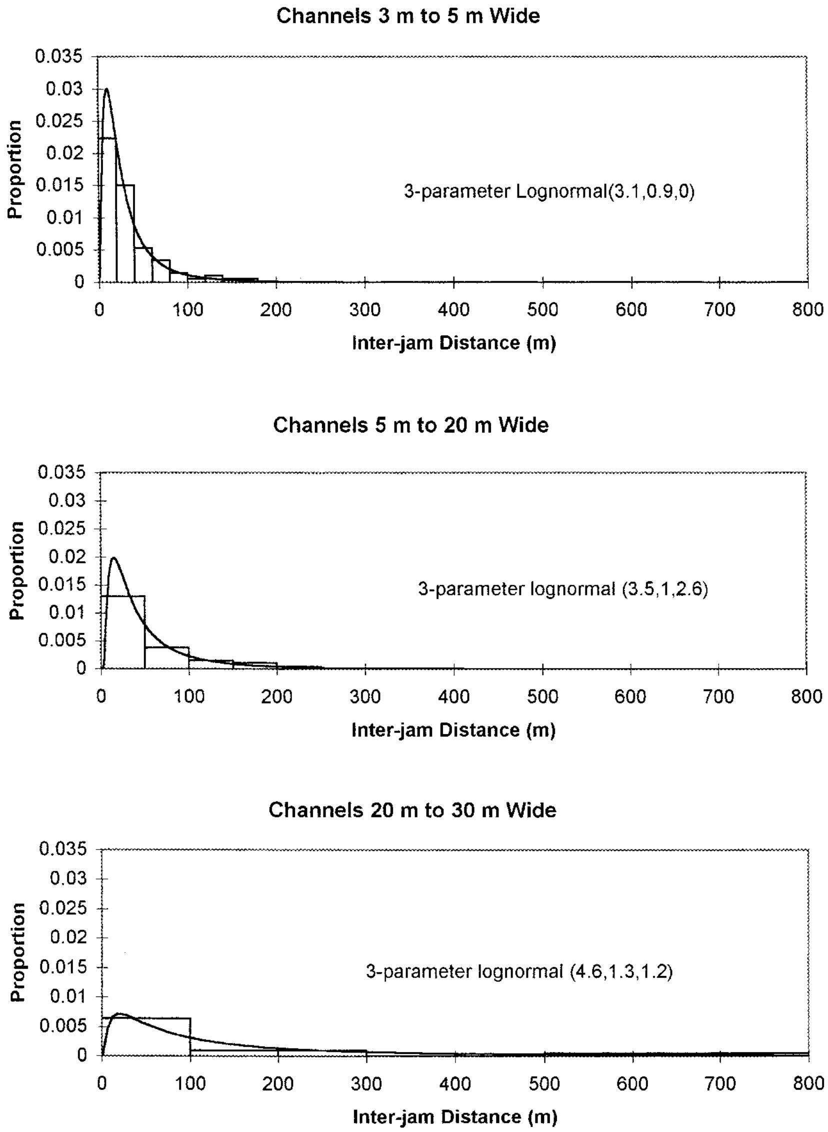

FIGURE A.1.—Lognormal distribution fit to histogram of interjam spacing by channel-width category, Game Creek basin in southeast Alaska.

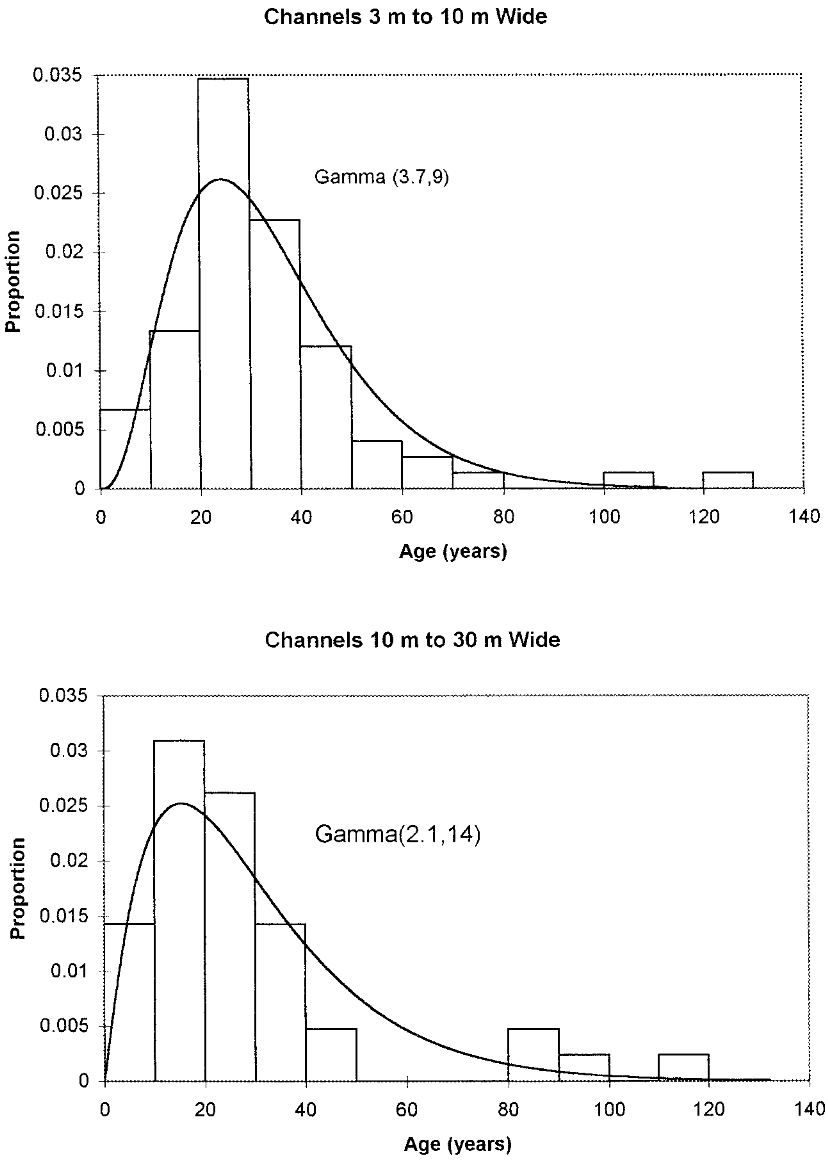

FIGURE A.2.—Gamma distributions fit to histogram of key piece ages by channel-width category, Game Creek basin in southeast Alaska.