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Composition, complexity, and tree mortality in riparian forests in the central Western Cascades of Oregon

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Abstract

Riparian forests contribute to the diversity and function of both terrestrial and aquatic ecosystems. To assess some of these contributions, we compared tree composition, stand complexity, and temporal patterns of tree mortality on permanent plots in seven mature and old-growth stands representing upland forests and forests along low- and mid-order streams in the Western Cascade Range of Oregon. We also assessed recruitment of large wood into stream channels due to tree mortality, both by direct measurement and by estimation from tree mortality and location data. Stands differed in composition due to both stream order and successional stage. Stands on mid-order streams had high abundance of hardwood trees and/or *Thuja plicata*. Stand complexity (variability in tree diameters, tree life-form diversity, and tree species diversity), was high in stands on mid-order streams and in the upland, old-growth stand. Tree mortality was exceptionally high in six of the seven stands in 1996, the year in which the largest flood during the study occurred. However, only in the one stand on an unconstrained reach of a mid-order stream was mortality primarily due to flooding. Estimated recruitment of wood was much higher from the stand on the unconstrained reach than from the other stands on mid-order streams, suggesting that unconstrained reaches may be important for efforts to maintain or restore large wood in streams.

Keywords: Riparian forests; Tree mortality; Large wood in streams; Flood effects; Unconstrained stream reach

1. Introduction

Riparian forests are critical components of the diversity and function of both terrestrial and aquatic ecosystems (Gregory et al., 1991; Naiman et al., 1993). Riparian habitats tend to include a wide variety of substrates, due to the diversity and frequency of geomorphic and other disturbance processes. In many riparian systems, flooding occurs frequently enough to accelerate the changes of vegetation. As a result, riparian forests tend to be very diverse in species composition and physical structure (Gregory et al., 1991). However, diversity of riparian forests and their distinctiveness from upslope forests tend to

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increase with increasing stream size (Naiman et al., 1993).

Riparian forests contribute to the diversity and function of stream systems in a variety of ways. Riparian forests regulate inputs to streams, including solar radiation, dissolved nutrients, foliage and other food resources, and large wood (Gregory et al., 1991). Large wood adds to biological diversity of streams by creating pools and other hydraulic features needed by salmonids and other fishes, and by providing food and habitat for microbes, algae, and invertebrates (Sedell et al., 1988; Gregory et al., 1991; Bragg and Kershner, 1999). Recruitment from the contemporary riparian stand is one of the several mechanisms by which large wood enters streams, along with carry-over from previous stands on the site and transport from upstream or hillslopes (Sedell et al., 1988; Murphy and Koski, 1989; Hedman et al., 1996). To date few studies have assessed rates of tree mortality in riparian forests and subsequent delivery of large wood to streams.

Disturbances of various frequencies and intensities are a general feature of forest dynamics (Runkle, 1985). However, flooding is a disturbance that generally does not affect forests outside of the riparian zone (Oliver and Larson, 1990). Intensity of flood effects on riparian forests tends to diminish with distance from the main channel, contributing to the diversity of riparian forests (Gregory et al., 1991; Stromberg et al., 1993; Piegay and Bravard, 1997; Swanson et al., 1998). Floods can stimulate forest–stream interactions, for example by increasing recruitment of large wood into streams (Sedell et al., 1988).

The purpose of this paper is to compare composition, complexity, and temporal patterns of tree mortality in upland forests and riparian forests along low- and mid-order streams in the Western Cascade Range of Oregon. The sampled forests include both mature and old-growth stands. A primary objective is to determine whether tree species composition changes and compositional and structural complexity increases from upland to low-order streamside to mid-order streamside forests, a sequence of presumed increasing potential for fluvial disturbance.

A second objective is to investigate patterns of tree mortality. Observations of tree mortality are from permanent plot records over an interval of almost two decades that included a large flood. Thus we ask whether the flood increased tree mortality in either low-order streamside or mid-order streamside forests, or both.

In addition to affecting forest composition and structure (Runkle, 1985), tree mortality rates can be used to estimate recruitment of large wood to streams (Van Sickle and Gregory, 1990). At one of the permanent plot locations, large wood was inventoried annually in the adjacent stream reach. Thus we also ask whether the temporal pattern and total amounts of large wood inputs to the stream estimated from tree mortality data can be used to predict the measured recruitment of wood. An additional objective of this paper is to compare estimated wood recruitment from tree mortality for the forests along several mid-order streams.

It must be noted that for the most part, each combination of geomorphic setting (i.e., upland, low-order streamside, mid-order streamside) and successional stage (i.e., mature or old-growth) is represented by a single stand. Thus, we are not able to draw inferences to a larger population of forest stands. However, given the close proximity of the stands and the general lack of direct manipulation, it is likely that differences between stands are influenced by differences in fluvial processes. Furthermore, given the lack of tree mortality data for forests in general (Ryan et al., 1997) and riparian forests in particular, it is important to exploit available data to describe trends and suggest priorities for future research.

2. Methods

2.1. Study area

Riparian and upland stands were measured in and near the H.J. Andrews Experimental Forest in the central Western Cascade Range, Oregon (44°15′N latitude, 122°10′W longitude, Van Cleve and Martin, 1991). The study area is in the Western Cascades geologic province, characterized by volcanic bedrock and steep, dissected topography (Franklin and Dyrness, 1988). Elevations of plot locations ranged from 450 to 1040 m. At the Andrews Forest Headquarters site (elevation 426 m), mean annual temperature is 8.5 °C and mean annual precipitation is 2302 mm (Bierlmaier and McKee, 1989). Dominant tree species in the stands included Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga*

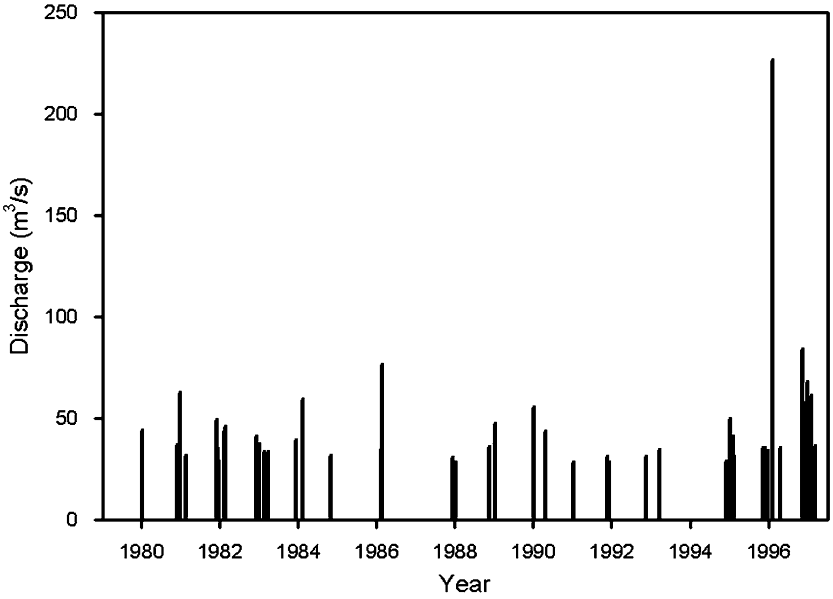

Fig. 1. Extreme peak flows on Lookout Creek, near Blue River, Oregon, from 1980 to 1997. Extreme peak flows for Lookout Creek are defined by the US Geological Survey (USGS) as flows greater than 28 m^3/s. Data obtained from USGS website (http://waterdata.usgs/nwis~w/OR/; the station number for Lookout Creek is 14161500).

heterophylla (Raf.)), western redcedar (*Thuja plicata* Donn.), and red alder (*Alnus rubra* Bong.).

Lookout Creek, the major stream draining the Andrews Forest, has a drainage area 6242 ha. Late fall and winter flooding in this stream is common. Since the establishment of the earliest riparian vegetation plots in 1979, at least one extreme peak flow (defined by the US Geological Survey as greater than 28 m^3/s) has been recorded on Lookout Creek in every year but one (Fig. 1). During this period, the flood of early February 1996 was exceptional. The peak flow of 227 m^3/s was more than 2.5 times larger than the next largest flood during the period of measurement of the vegetation plots. It was also 20% larger than the peak flow of December 1964, the second largest flood in the 40 years of operation of the Lookout Creek gauge. The long-term average discharge of Lookout Creek is 3 m^3/s.

2.2. Vegetation measurements

The study was based on permanent forest plots maintained as part of the Andrews Experimental Forest Long-Term Ecological Research Program (Table 1, Acker et al., 1998). Plot sets exploited for this study include contiguous blocks of about 2 ha within which all trees are mapped (Reference Stands) and 0.1 ha circular plots regularly distributed along transects in two undisturbed watersheds. For the purposes of analysis, the plots on the transects were divided into riparian plots and upland plots. Riparian plots had perennial or intermittent streams running either through or near the plot (up to three plot radii, 54 m, from the center of the plot). While the Reference Stands were delineated to take into account the effects of slope on horizontal-projected area, the circular plots were not. Thus, the horizontal area of some of the circular plots is less than the nominal 0.1 ha. All results are reported on a slope-corrected, horizontal area basis.

The plots include a variety of successional states (mature and old-growth forest), and geomorphic settings (upland, low-order-streamside, mid-order-streamside) (Table 1). Plots were established between 1979 and 1990, at which time live trees ≥5 cm diameter at breast height (1.37 m; DBH) were tagged and measured. Subsequently, trees have been measured at 6-year intervals and checked annually for mortality. At each measurement, any trees growing to 5 cm DBH were added to the dataset. For any trees recorded as new mortality, stem position (standing,

Table 1
Geomorphic setting, successional status, and measurement history of permanent forest plots

Stand label[a]	Geomorphic setting	Successional status	Year of plot establishment	Measurement design	Reach length (m)
UM	Upland	Mature	1982	87, 0.1 ha plots	–
UO	Upland	Old-growth	1982	56, 0.1 ha plots	–
LM	Low-order streamside[b]	Mature	1982	9, 0.1 ha plots	n/a[c]
LO	Low-order streamside[b]	Old-growth	1982	11, 0.1 ha plots	n/a[c]
MM	Mid-order streamside[d]	Mature	1980	2.13 ha Reference Stand	236
MO1	Mid-order streamside[d]	Old-growth	1979	2.0 ha Reference Stand	104
MO2	Mid-order streamside[e]	Old-growth	1990	2.44 ha Reference Stand	175

[a] Labels are composed of geomorphic setting (first character) and successional stage (second character).

[b] 1st- and 2nd-order channels.

[c] Not applicable.

[d] 3rd-order channel.

[e] 5th-order channel.

broken, crushed, or uprooted) was recorded along with other conditions and possible causes of mortality.

In 1996 and 1997 following the flood, the location and relative heights of the various geomorphic surfaces at MO2 were mapped. For purposes of analysis, these surfaces were grouped into the active floodplain zone adjacent to the main channel and less than 2 m above the summer water level; the quiet floodplain zone, including areas adjacent to the main channel but greater than 2 m above the summer water level, and lower surfaces along a secondary channel; and the upland zone which was 3 m or more above the summer water level of the main channel. The pre-flood location of the stream channel at MO2 was determined using notes from the survey of the stand perimeter in 1990, the map of tree locations in 1990, and aerial photographs taken in 1989.

Since 1985, large wood in the stream reach adjacent to and upstream of MO1 has been surveyed annually. Pieces greater than 1 m in length and 10 cm in diameter were identified by labeled tags to track movement and fragmentation, and to allow recognition of newly added wood. Data recorded annually for each piece included diameter, length, location within the study reach, decay class, percent of length within the active channel, and whether the piece was within a log jam. To compare wood recruitment observed in the in-stream wood inventory to potential contributions due to tree mortality in the permanent plot, we considered only newly added wood that was relatively undecayed (i.e., pieces that first appeared in the stream with bark attached) and that did not appear to have floated in from upstream. We restricted analysis of the in-stream wood inventory to the portion of the surveyed reach within the permanent plot.

2.3. Data analysis

Measures of stand complexity included variability in tree diameter, percentage of tree basal area contributed by hardwood species, and species richness and evenness. Increased variability in tree size is associated with increased diversity of microhabitats within forest stands (Spies and Franklin, 1988). Hardwood trees are a significant source of habitat heterogeneity for understory plants, invertebrates, and vertebrates (McComb, 1994; Niemiec et al., 1995). Preservation of biological diversity, including richness and evenness of species, is a major goal of public policy and land management (Westman, 1990).

Given the differences in total area and numbers of individual trees between plot sets, the rarefaction method was used to evaluate species richness (Krebs, 1989). Rarefaction is a quantitative technique to estimate the number of species that would be found in a subsample of a given collection of individuals. Since the mature-forest, low-order streamside plots had both the smallest number of individual trees (147) and the smallest area sampled (0.75 ha), the observed species richness in those plots was compared to rarefaction estimates for the other plot sets. Species evenness was computed using the modified Hill's ratio (Ludwig and Reynolds, 1988).

An additional measure of stand complexity for the mapped Reference Stands was spatial heterogeneity of tree species composition, using cluster analysis of $25 \times 25\ \mathrm{m}^2$ subplots. Although spatial heterogeneity is linked in ecological theory to phenomena such as maintenance of species diversity, in general little is known about patterns of spatial heterogeneity (Legendre and Fortin, 1989). Cluster analysis is a method for defining groups of similar items within a larger set (Van Tongeren, 1995); mapping results of cluster analysis can be particularly helpful for understanding spatial variation in composition (Legendre and Fortin, 1989). We used agglomerative, average-linkage cluster analysis (Van Tongeren, 1995), and the percent dissimilarity index of Bray and Curtis (Ludwig and Reynolds, 1988). Subplots were compared on the basis of relative stem density, the percentage of the stems representing a given tree species in a given subplot. We examined the level in the cluster analysis of each stand which produced four groups of subplots. The average species composition of the resulting groups and the relative dissimilarity among the four groups were compared for the three Reference Stands. Cluster analysis was performed using the program PC-ORD (McCune, 1986).

For the Reference Stands, annual contribution of wood to streams was estimated from tree mortality and stem position data (i.e., standing vs. broken vs. toppled). For MO1, in-stream wood survey data were available for comparison to estimates from tree mortality data. For that stand, four sets of assumptions were employed to generate four sets of estimates of annual wood input:

1) dead trees can add wood to the stream irrespective of position, all trees fall towards the channel;
2) dead trees can add wood to the stream irrespective of tree position, trees fall in random directions;
3) only trees reported as broken or toppled at the time of death can add wood to the stream, toppled trees and pieces of broken trees fall towards the channel;
4) only trees reported as broken or toppled at the time of death can add wood to the stream, toppled trees and pieces of broken trees fall in random directions.

For trees or pieces of trees that were estimated to have deposited wood in the stream channel, the volume of wood deposited was based on the tree's height and distance from the channel, the angle of fall relative to the direction of the main axis of the stream channel, the width of the stream channel, and the taper equation of the form developed by Kozak (Avery and Burkhart, 1994). For conifers, species-specific taper coefficients developed from the Andrews Experimental Forest dendrometer database (S. Garman, pers. comm.) were used (sample sizes from 53 to 351, R^2 values from 0.82 to 0.96). For hardwood species, taper coefficients were derived from Kozak et al. (1969). Tree heights were estimated from DBH using the appropriate species-specific models from Garman et al. (1995).

For all but the first set of assumptions, there was some stochastic element to estimates of wood recruitment (direction of fall, distance moved by broken pieces). In all these cases, averages of 1000 iterations are reported. This approach to estimating wood recruitment from tree mortality is derived from published models (McDade et al., 1990; Robison and Beschta, 1990; Van Sickle and Gregory, 1990).

3. Results

3.1. Tree species composition

The stands differed in composition both as a function of stream order and successional stage. Forests along low-order streams were similar in composition to upland forest in the same watershed. In the mature-forest watershed (UM, LM), Douglas-fir was the dominant species, both in terms of tree density and basal area (Figs. 2 and 3). In the old-growth-forest watershed, in both the upland (UO) and riparian plots (LO) western hemlock was the most numerous species, whereas Douglas-fir accounted for more basal area than any other species. Western redcedar and western yew (*Taxus brevifolia* Nutt.) were also common in both sets of plots. The two sets of plots in the old-growth-forest watershed differed with respect to the most common hardwood species (bigleaf maple (*Acer macrophyllum* Pursh) in the riparian plots, golden chinkapin (*Castanopsis chrysophylla* (Dougl.) DC) in the upland plots). In both the mature- and old-growth-forest watersheds, the streamside forest had lower stem density and tree basal area than the upland forest.

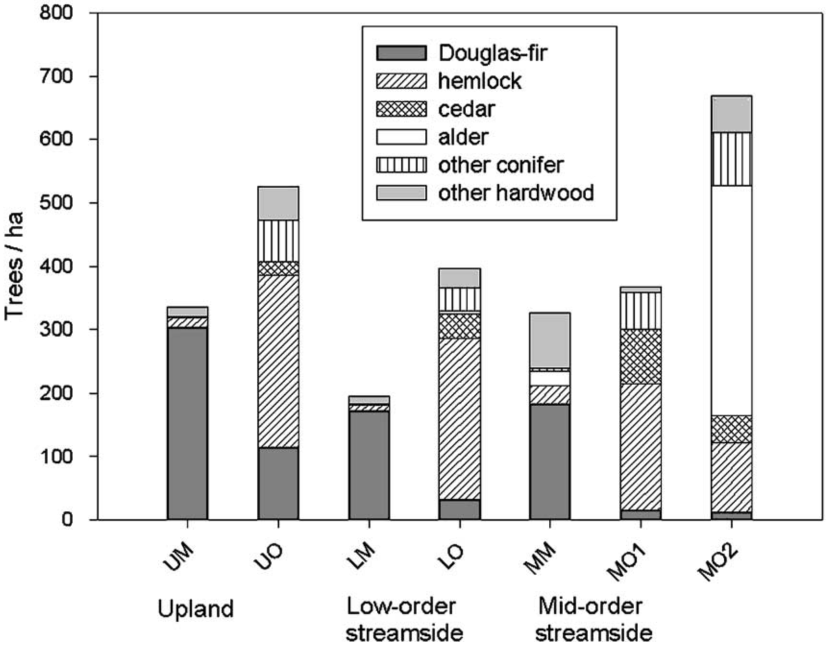

Fig. 2. Density of trees by species in permanent plots representing upland forest (UM and UO), forest along low-order streams (LM and LO), and forests along mid-order streams (MM, MO1, and MO2).

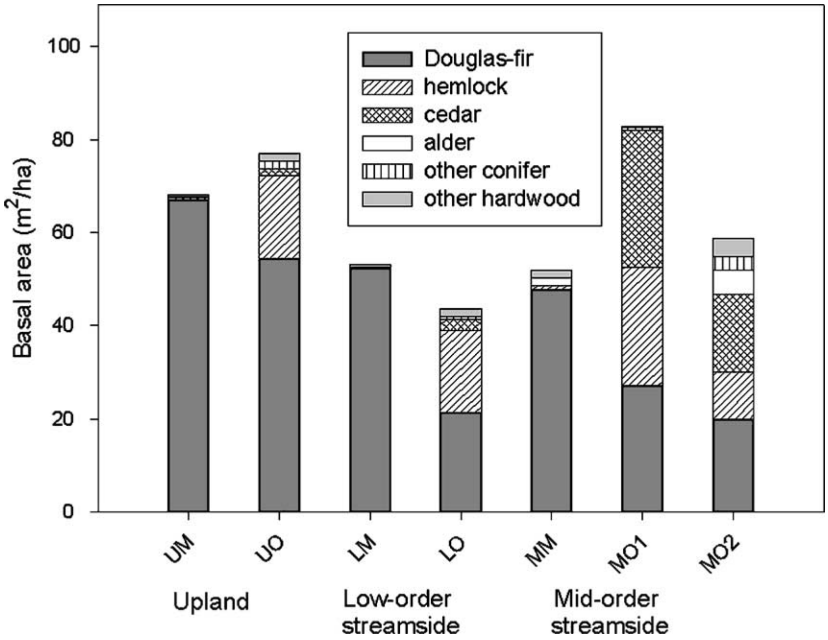

Fig. 3. Basal area of trees by species in permanent plots representing upland forest (UM and UO), forest along low-order streams (LM and LO), and forests along mid-order streams (MM, MO1, and MO2).

With respect to stem densities, the three stands along mid-order streams (MM, MO1, MO2) were distinct from the upland and low-order streamside plots. The distinctive feature of MM was the relatively high density of cascara (*Rhamnus purshiana* DC), bigleaf maple, and Pacific dogwood (*Cornus nuttalli* Aud.) (other hardwood in Fig. 2). MO1 had a higher density of western redcedar than the other stands. MO2 was unique in that red alder was the most abundant tree species. With respect to basal area, MM was quite similar to the upland and low-order streamside forest plots in the nearby mature forest. The high basal area of cedar distinguished MO1, while both cedar and alder accounted for relatively large portions of basal area at MO2.

3.2. *Stand complexity*

At the various levels we examined, structural, life-form, and species, the most complex stand was among those along mid-sized streams. However, there was not a consistent pattern of increasing complexity from upland to low-order streamside forest to mid-order streamside forest. In particular, complexity of the upland old-growth plots was higher than most of the riparian plots for most of the measures of complexity.

Structural complexity, as measured by standard deviation of DBH, was greatest in MO1 (Table 2). The other mid-order streamside stands, and the low-order streamside and upland old-growth plots were intermediate in structural diversity, while the low-order streamside mature (LM) and upland mature (UM) forest plots were the least structurally diverse. Life-form diversity was greatest in MO2 and MM (Table 2). The lowest life-form diversity occurred in mature upland (UM) plots and MO1.

Species evenness was highest in both old-growth, mid-order streamside stands (MO1 and MO2) and lowest in the mature low-order streamside (LM) and upland (UM) plots (Table 2). Species richness estimated from rarefaction was high in MO2, the low-order streamside (LO) and upland (UO) plots in old-growth forest, and MM. Species richness was lowest on the low-order streamside (LM) and upland (UM) plots in mature forest.

The three stands along mid-order streams were quite different with respect to spatial heterogeneity of tree composition, at least from the perspective of cluster analysis within each stand. MO1 was the least heterogeneous. Cluster analysis into four groups of subplots produced three groups in which hemlock was the most abundant species, with varying amounts of western redcedar and yew (Table 3). The fourth group contained a single subplot dominated by cedar, with lesser amounts of hemlock and yew. In the four-group cluster analysis for MM, about two-thirds of the subplots were in a single group in which Douglas-fir was the only consistently abundant species (Table 3). Eight of the nine remaining subplots were in groups in which cascara was either the most abundant or second most abundant species. MO2, in contrast, was split roughly into thirds, with a group in which hemlock and yew were most abundant, a group in which red alder was most abundant, and a group in which all three species were relatively abundant

Table 2
Complexity of upland and riparian plots with respect to stand structure, tree life-form diversity, and tree species evenness and richness

Stand[a]	S.D. of DBH	Relative percent hardwoods		Species evenness		Species richness (S.D.)	
		Stems	Basal area	Stems	Basal area	$E\{S_{147}\}$[b]	$E\{S_{0.75\ \mathrm{ha}}\}$[c]
UM	20.2	4.1	0.8	0.38	0.31	5.6 (1.1)	6.6 (1.0)
UO	31.5	10.1	2.3	0.64	0.61	7.4 (0.7)	8.3 (0.9)
LM	23.1	7.0	1.3	0.47	0.34	4.0 (0.0)	4.0 (0.0)
LO	28.0	8.7	3.8	0.54	0.80	6.9 (0.8)	7.8 (0.4)
MM	26.7	33.3	5.4	0.58	0.38	7.2 (0.5)	7.3 (0.5)
MO1	41.7	2.5	0.2	0.70	0.99	6.3 (0.7)	6.8 (0.4)
MO2	26.2	62.8	15.2	0.60	0.86	7.9 (0.8)	9.2 (0.7)

[a] See Table 1 for definitions of stand labels.

[b] Expected species richness in a sample of 147 individuals.

[c] Expected species richness in a sample of 0.75 ha.

Table 3
Results of average-linkage agglomerative cluster analysis with the Bray–Curtis dissimilarity measure of $25 \times 25\ m^2$ subplots within riparian Reference Stands

Stand[a]	Subplot group	N	Species (average relative density in percent)
MO1	1	18	Hemlock (47), cedar (23), yew (22)
	2	3	Hemlock (47), cedar (36)
	3	10	Hemlock (76), cedar (17), yew (3)
	4	1	Cedar (65), hemlock (18), yew (12)
MM	1	25	Douglas-fir (64), hemlock (11), maple (10), cascara (4)
	2	6	Douglas-fir (36), cascara (26), maple (11), hemlock (8)
	3	1	Hemlock (29), maple (24), Douglas-fir (24), cascara (6)
	4	2	Cascara (68), Douglas-fir (13), maple (9), hemlock (6)
MO2	1	15	Hemlock (41), yew (24), alder (5)
	2	1	Yew (67), hemlock (11)
	3	11	Alder (36), hemlock (20), yew (10)
	4	12	Alder (81), yew (8), hemlock (2)

[a] See Table 1 for definitions of stand labels.

(Table 3). The alder-dominated subplots in particular were aggregated in space, and were adjacent to stream channels (Fig. 4). The values of dissimilarity between the four groups in each Reference Stand confirms that spatial heterogeneity was greatest at MO2, followed by MM. The cluster formation that yielded four groups occurred at a dissimilarity value of 0.96 for MO2, 0.76 for MM, and 0.25 for MO1.

3.3. Tree mortality

For the most part, tree mortality averaged between 1 and 2% of stems annually, and did not vary much between upland and riparian study areas (Table 4). The most notable exception was MO2, where annual mortality averaged 4%. At the opposite end of the spectrum was MO1, where over the entire 18 years of observation annual mortality averaged 0.4% and there were 5 years with no recorded tree mortality.

For six of the seven study areas, annual mortality was higher in 1996 than for any other year, and for all study areas mortality in 1996 was at least 50% greater than the average (Table 4). Thus, tree mortality was elevated for both upland and riparian study areas in 1996. The highest mortality in 1996 was observed at MO2, where 11.9% of trees died. For most of the study areas, tree mortality in 1997 was lower than in 1996, and in fact was below the long-term average for the upland study areas (Table 4). However, considerable tree mortality occurred in MO2 in 1997, with 10.2% of trees succumbing.

For the upland and low-order stream-side plots, at least two-thirds of the trees that died in 1996 were either broken or uprooted (Fig. 5). In contrast, two-thirds of the trees dying in MM died standing, and mortality in MO1 was fairly evenly distributed between standing, broken, uprooted, and crushed trees. In MO2, over 70% of the trees killed in 1996 were removed by the flood. The flooding contributed to the death of more than half of the dying trees that

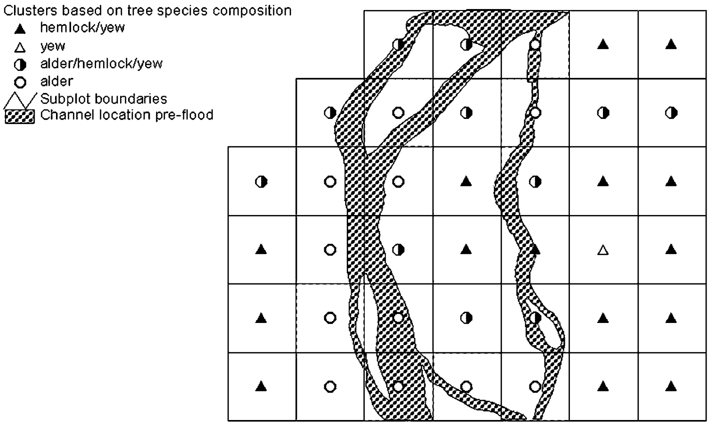

Fig. 4. Spatial distribution of $25 \times 25\ m^2$ subplots in MO2 as classified into four groups on relative density of trees by average-linkage agglomerative cluster analysis. The location of the stream channel in 1990 is indicated.

Table 4
Average annual mortality and annual mortality for 1996 and 1997 (in percent of number of stems)

Stand[a]	Average annual mortality, 1991–1997 (S.D.)	Total length of record (years)	Average annual mortality for entire record (S.D.)	1996 mortality (rank among years for stand)	1997 mortality (rank among years for stand)
UM	1.3 (0.8)	15	1.6 (0.7)	3.0 (1)	1.0 (17)
UO	1.6 (0.9)	15	1.3 (0.7)	3.1 (1)	1.1 (8)
LM	1.9 (1.5)	15	1.5 (1.2)	4.8 (1)	2.2 (3)
LO	1.1 (0.6)	15	1.0 (0.7)	1.7 (1)	1.7 (1)
MM	1.3 (0.6)	17	1.2 (0.8)	1.8 (5)	1.8 (5)
MO1	0.9 (0.8)	18	0.4 (0.6)	2.2 (1)	0.8 (4)
MO2	4.4 (4.6)	7	4.4 (4.6)	11.9 (1)	10.2 (2)

[a] See Table 1 for definitions of stand labels.

were not removed from the stand (e.g. by excavating streambanks and causing toppling, or by battering trees with flood-borne debris). The majority of tree deaths in this stand in 1997 was also due to effects of high water, though in 1997 death by uprooting due to flood waters was more common than removal by flood waters (data not shown). It is important to note that at least one-quarter of trees dying in the stand in 1997

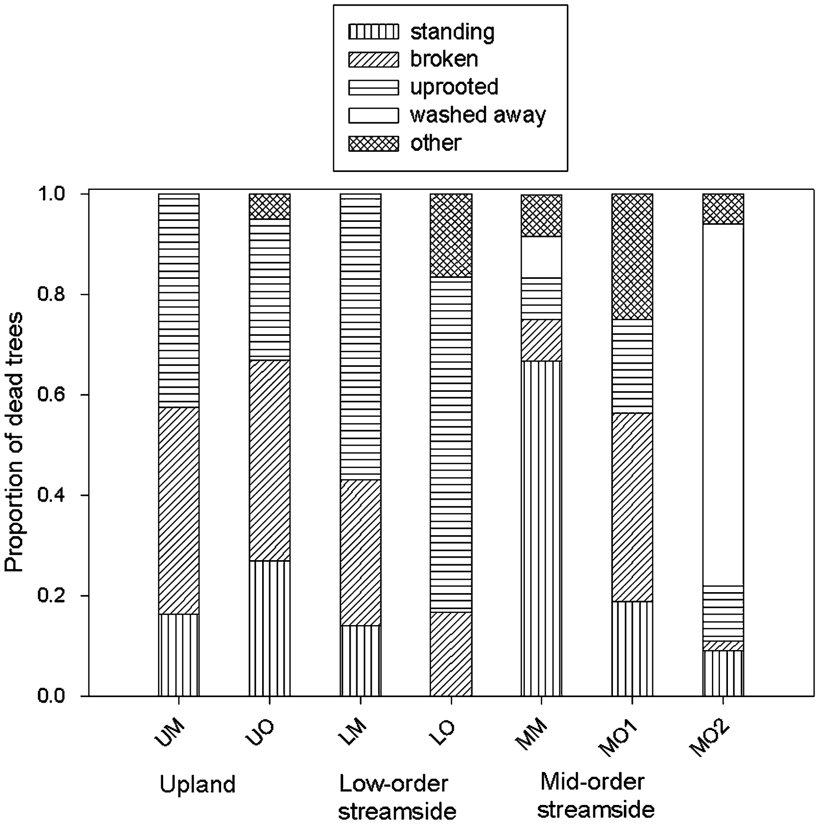

Fig. 5. The fate of trees reported dead in 1996 in permanent plots representing upland forest (UM and UO), forest along low-order streams (LM and LO), and forest along mid-order streams (MM, MO1, and MO2). Other mortality was mostly related to flooding in MO2, and mostly related to wind in other plots.

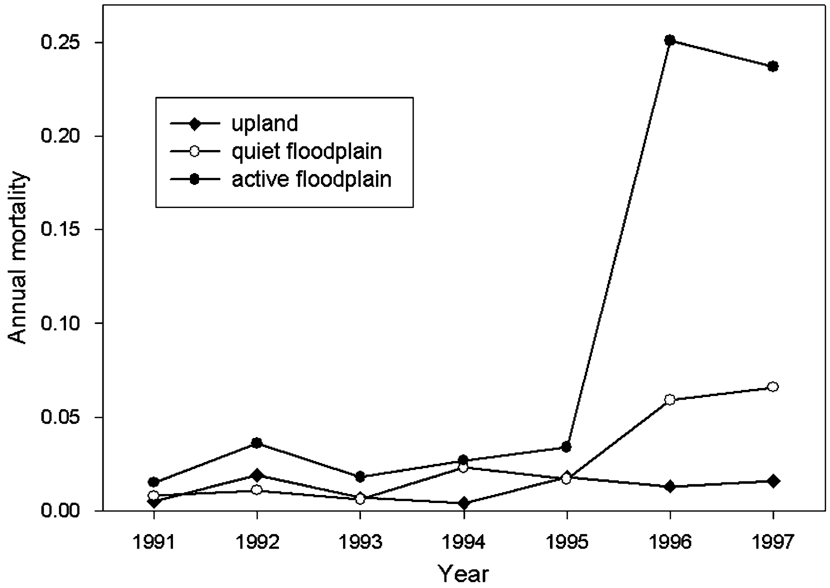

Fig. 6. Annual tree mortality (decimal proportion of population dying) in MO2 by geomorphic zone. Active floodplain refers to areas adjacent to the main channel and less than 2 m above the summer water level. Quiet floodplain includes areas adjacent to the main channel and more than 2 m above the summer water level, and lower surfaces along a secondary channel. Upland refers to areas at least 3 m above the summer water level.

apparently succumbed to delayed effects of the flood of 1996 (e.g. trees that were uprooted and buried in 1996, but still had live foliage), with little or no obvious additional damage inflicted by high water in 1997.

The three geomorphic zones in MO2 displayed distinct patterns of tree mortality both prior to the high flows of 1996 and 1997, and during that period (Fig. 6). During each of the years with relatively low peak flows, mortality was greatest in the active floodplain zone. During the years with high peak flows, mortality was quite high in the active floodplain zone (i.e., loss of nearly one-quarter of stems each year). Mortality was also notably elevated during the high-flow years in the quiet floodplain zone. For this zone only, the highest annual mortality for the entire period occurred during the second of the high-flow years. In the upland zone, mortality during the high-flow years was only slightly higher than the average over the entire period.

Within the active floodplain zone, flood-related mortality was aggregated in space, creating distinct disturbance patches (Fig. 7). Most trees removed by the floods were in patches where lateral movement or enlargement of the stream channel left no trees in place. Trees toppled by the floods also tended to be clustered, but were inter-mixed with surviving trees, creating a heterogenous structure.

3.4. Inputs of large wood into streams

Comparison of wood input estimated from tree mortality data for MO1 to annual inventories of wood in the adjacent stream reach demonstrates that mortality data can be used to approximate wood inputs. The temporal pattern of wood recruitment as estimated from trees that were broken or uprooted on dying matches the information from the in-stream inventories (Table 5). However, when all dying trees close enough (and tall enough) to reach the channel are included, there are years with large estimated inputs of wood that do not correspond to actual recruitment of wood in the inventories (i.e., 1992, 1994). The four sets of assumptions also differed in the total amount of wood recruited (Table 6). As would be expected, assuming all dead trees contribute wood to the channel and that all dying trees fall toward the channel resulted in the largest estimated recruitment of wood. For the

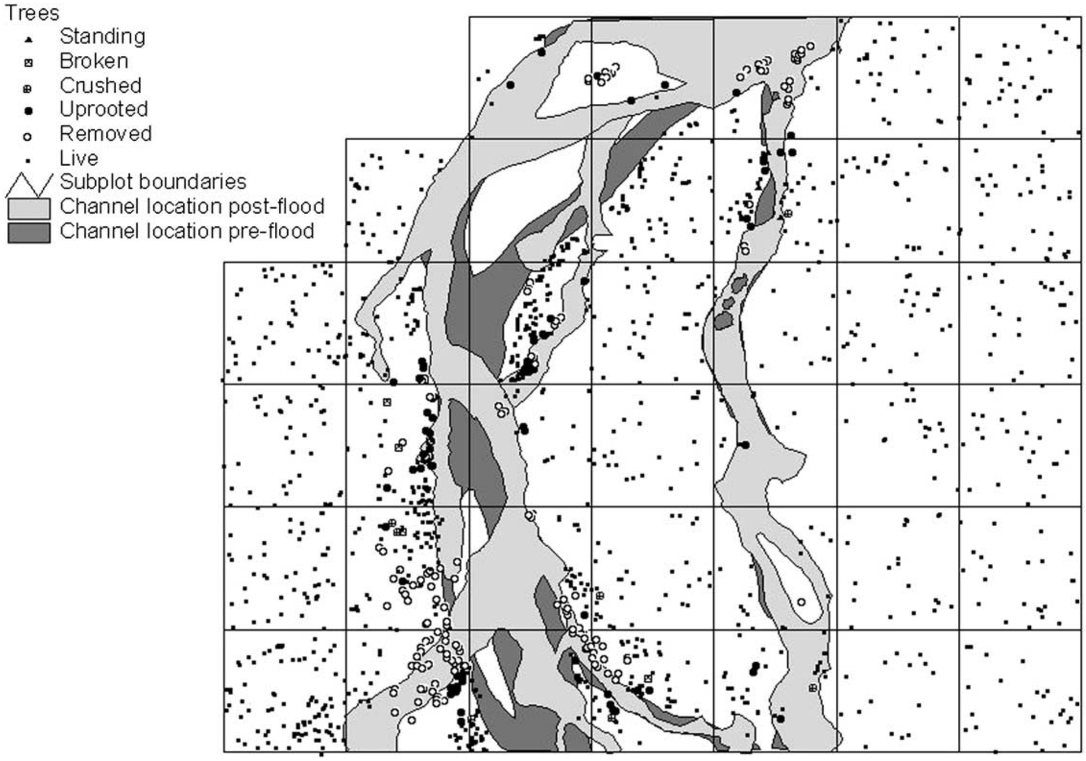

Fig. 7. Spatial distribution of trees killed by flooding in 1996 and 1997 at MO2 by mode of mortality. The locations of the channel both before and after the flood of 1996 are indicated.

Table 5
Annual amounts of large wood recruited (m^3) into adjacent stream reach from 1986 to 1997 due to tree mortality in stand MO1, estimated from mortality data using alternative sets of assumptions and measured by annual, in-stream inventory

Data source	Tree mortality data				In-stream inventory
	All dead trees		Broken and uprooted only		
	Towards channel	Random	Towards channel	Random	
1986	0.00	0.00	0.00	0.00	0.00
1987	0.00	0.00	0.00	0.00	0.00
1988	0.00	0.00	0.00	0.00	0.00
1989	0.00	0.00	0.00	0.00	0.00
1990	0.00	0.00	0.00	0.00	0.00
1991	0.00	0.00	0.00	0.00	0.00
1992	4.87	1.11	0.00	0.00	0.06
1993	0.00	0.00	0.00	0.00	0.00
1994	14.61	5.84	0.00	0.00	0.03
1995	0.00	0.00	0.00	0.00	0.00
1996	13.25	5.17	13.25	5.28	19.01
1997	0.80	0.22	0.76	0.23	0.00

Table 6
Total amounts of large wood recruited into adjacent stream reach from 1986 to 1997 due to tree mortality in MO1, estimated from mortality data using alternative sets of assumptions and measured by annual, in-stream inventory

Data source	Tree mortality data				In-stream inventory
	All dead trees		Broken and uprooted only		
	Towards channel	Random	Towards channel	Random	
Total large wood (m^3) (CV[a])	33.7[b]	12.4 (0.77)	14.1 (0.005)	5.5 (1.14)	19.1

[a] Coefficient of variation for total CWD recruited, 1980–1997.

[b] No variation due to deterministic set of assumptions.

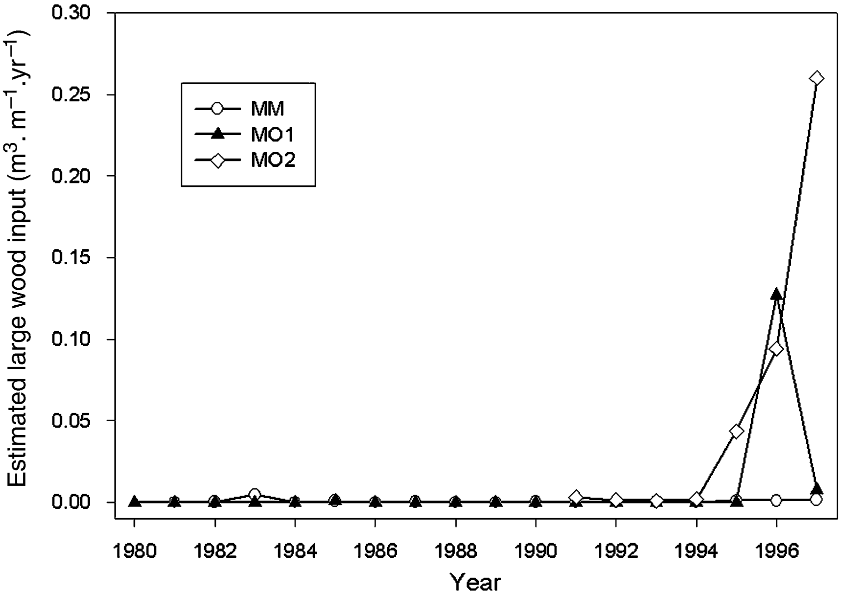

Fig. 8. Time trend of estimated inputs of large wood to stream channels (m^3 of wood per m of stream channel per year) within permanent plots along mid-order streams. Estimates were generated from tree mortality assuming only broken or toppled trees contribute wood to the channels, and that stems or pieces of stems fall toward the channel.

11 years with in-stream inventories, wood recruitment estimated assuming that only toppled or broken trees add wood and that trees and pieces fall toward the channel came closest to matching observed recruitment of wood (Table 6).

Recruitment of wood from the live tree stand at MO1 is clearly episodic over the time scale of this study, whether estimated from tree mortality or measured in the stream. From the in-stream inventories, the average standing crop of wood in the stream reach flowing through the Reference Stand is about 300 m^3. In recent decades, the live stand appears to be adding about 1–2 m^3 per year of wood to the stream (Table 6, Fig. 8). Thus, with no other inputs and no losses, the current levels of wood would take several centuries to attain.

The three Reference Stands have different temporal patterns and magnitudes of wood inputs as estimated assuming that only uprooted and broken trees add wood to streams and that boles and pieces of boles fall directly toward the channel (Fig. 8). As mentioned above, inputs at MO1 were very episodic, with 94% of the input estimated over the 18 years of record occurring in 1 year. In the in-stream inventories, the bole of one tree accounted for 90% of the wood input in that year. Average input over the entire period

7.5×10^{-3} m^3/(m per year). Input has been much less episodic at MM, with the largest single year input accounting for less than 50% of the entire input over 17 years. Average input was 5.6×10^{-4} m^3/(m per year). Although it was estimated that wood was added to the stream every year at MO2, inputs varied between years by more than two orders of magnitude, with small annual totals from 1991 to 1994 and large annual totals from 1995 to 1997. The largest single annual input accounted for 64% of the total estimated input. Average annual input was 5.8×10^{-2} m^3/(m per year).

4. Discussion

4.1. Composition and complexity

Tree species composition of stands along 3rd- and 5th-order streams was distinct from the composition of upland stands or stands along smaller streams of similar seral stage. For the old-growth stands (UO, LO, MO1, and MO2), this difference was manifested in both basal area and stem density. For the stands in mature forest, the difference was apparent only from the perspective of stem density. Basal area was predominantly Douglas-fir for upland, low-order streamside, and mid-order streamside forests. In addition to riparian setting, seral stage (mature vs. old-growth) had a pronounced effect on tree species composition. The similarity of tree species composition between upland and low-order streamside riparian plots supports the statement by Naiman et al. (1993) that the riparian corridor is often small in headwater streams that are almost completely embedded in the forest (see also Swanson et al., 1982; Pabst and Spies, 1999). Similarly, Hupp and Osterkamp (1985) found that there is evidence that some bottomland species become limited in their headward distribution as stream size decreases. Complexity of stands also varied with both riparian setting and seral stage. Spatial heterogeneity of tree species composition was greatest in the stand along the 5th-order stream. This stand occupies an unconstrained stream reach (Gregory et al., 1991; Grant and Swanson, 1995), unlike the other stands along mid-order streams which are located on reaches where bedrock and other geological features constrain the lateral mobility of the channel. Gregory et al. (1991) considered a high degree of complexity of riparian vegetation to be characteristic of unconstrained stream reaches, where fluvial disturbance can create vegetation patches of various ages representing past flood events. Scott et al. (1996) also found greater complexity of vegetation (i.e., diversity of age-classes of cottonwood trees) on an unconstrained reach than on a constrained reach of the Missouri River.

With respect to structural complexity (represented by standard deviation of DBH), the stands sorted into two groups based on a combination of riparian setting and seral stage. Greater structural complexity occurred in stands along mid-order streams, and old-growth stands irrespective of riparian setting. Lower structural complexity occurred in the plots in mature upland (UM) and mature low-order streamside (LM) stands. The highest and the lowest diversity of tree life-forms (hardwood vs. conifer) occurred in old-growth stands along mid-order streams (MO2 and MO1, respectively). Species evenness and richness had patterns similar to structural complexity: high values for stands along mid-order streams, and old-growth stands, and low values for mature upland and low-order streamside forest. The high compositional and structural complexity of old-growth forests relative to other seral stages in the Pacific Northwest is well documented (Franklin et al., 1981; Franklin and Spies, 1991), and must be taken into account in comparisons between upland and riparian forests.

4.2. Tree mortality

In stands along low-order and mid-order streams, as well as upland stands, 1996 was an extreme year for tree mortality based on records of 7–18 years duration. In addition, the largest flood in 40 years of record for Lookout Creek occurred in 1996. However, only in MO2, the stand along the largest of the mid-order streams, was tree mortality in 1996 primarily due to the flood. Elevated mortality in the other stands appears to have resulted from unusually high breakage and toppling due to snow-loading in an event unrelated to the flood. MO2 occupies an unconstrained reach, where the effects of floods would be expected to extend over a broader area than in constrained reaches (Gregory et al., 1991; Grant and Swanson, 1995). Floods typically cause lateral migration of channels and deposition of new surfaces in unconstrained reaches. This is consistent with observations from MO2, where nearly three-quarters of the trees that died in 1996 were washed away. Tree mortality was also elevated in 1997 in MO2, due to another, smaller flood, delayed effects of flood damage in 1996 (e.g. uprooted trees that still had some living branches when observed in the summer of 1996), and possibly continued adjustment of channel position and stream banks to changes in channel gradient and position of obstructions to flow caused by the 1996 flood (cf. Gottesfeld and Gottesfeld, 1990).

4.3. Synthesis of tree mortality and stand composition and complexity

The aftermath of the flood of 1996 provides some insight into the effects of flooding on the structure of mature and old-growth riparian forests. In the mid-order, old-growth streamside stand along an unconstrained reach, flooding apparently promotes complexity at the life-form, species diversity, and stand structural levels. Tree mortality was concentrated closest to the stream channel, an area dominated prior to the flood by small stems of red alder. Freshly exposed, moist mineral soil and full sunlight are optimal conditions for establishment of red alder (Harrington, 1990), so the surfaces exposed or newly created by the flood of 1996 should provide suitable conditions for alder recruitment. These results are consistent with observations on rivers and streams in many other locations. Lateral channel movement and other flood effects create the substrates needed for recruitment of pioneer woody species for riparian forests in both humid and arid environments (Stromberg et al., 1993; Shankman, 1993; Friedman et al., 1996; see also Hupp and Osterkamp, 1985; Harris, 1987). Floods can also increase structural complexity directly by toppling trees and emplacing large wood in riparian forests (Piegay and Bravard, 1997).

In the other two stands along mid-order streams, the flood of 1996 did not have much effect on stand structure, apparently due to smaller size of the streams and constraint on the lateral mobility of the channels. In the old-growth stand (MO1), it appears that any significant hardwood component of the stand that may have been present following the last stand-replacing disturbance (i.e., fire) has died out due to competition from the conifers. The relatively high abundance of hardwoods in the mid-order, mature streamside stand may be a legacy of the wildfire that initiated the stand. This interpretation does not explain the relatively high stem density of bigleaf maple in the low-order streamside plots in the old-growth watershed. The high degree of complexity of old-growth stands not subject to fluvial disturbance may also be due to tree mortality, but at a finer scale than flood-induced mortality, allowing only recruitment of shade-tolerant conifers (Spies and Franklin, 1988).

4.4. Recruitment of large wood

Across all three stands along mid-order streams, average wood inputs estimated from tree mortality varied by two orders of magnitude (from 6×10^{-4} to 6×10^{-2} m^3/(m per year)). There was also considerable year-to-year variation within stands in estimated wood inputs. Due to this spatial and temporal variability, it is difficult to predict how much wood recruitment to expect from mature and old-growth riparian forests. However, these are important questions for management and policy.

The largest average annual input was from the old-growth stand along an unconstrained reach of a 5th-order stream. This was also the stand with the highest tree mortality, and the only stand where elevated tree mortality in 1996 was related to the flood. Temporal variability in this stand corresponded to the stream discharge record, with high wood inputs in high-flow years.

Studies of wood inputs from riparian forests in other regions have reached generally similar conclusions. Flooding, bank erosion, and channel migration have been cited as important processes for converting live trees to in-stream large wood in coastal Alaska and British Columbia (Murphy and Koski, 1989; Gottesfeld and Gottesfeld, 1990) and the southeastern US coastal plain (Palik et al., 1998). The importance of the spatial pattern of trees for estimating large wood inputs has been demonstrated from both field and simulation studies (Murphy and Koski, 1989; Malanson and Kupfer, 1993). Our mature forest stand along a mid-order stream (stand age 140 years, Klopsch, 1985) had the lowest estimated rate of wood input. Relatively low wood inputs from forests in middle stages of succession have also been observed in coastal Alaska and the southern Appalachians (Murphy and Koski, 1989; Hedman et al., 1996). Contrary to our results, Palik et al. (1998) found greater tree mortality and recruitment of wood following a flood in constrained rather than in unconstrained reaches of a southeastern US coastal plain stream, apparently due to greater current velocities in constrained reaches. Thus the significance of channel constraint for severity of flood disturbance may be different in mountainous versus relatively flat terrain.

Given the input rates estimated for the three Reference Stands, chronic input of wood from the live stands adjacent to the channel would take several decades to several thousand years to accumulate the standing amounts of in-stream wood observed in the inventoried stream reach (cf. Murphy and Koski, 1989; Hedman et al., 1996). Thus, understanding the dynamics of large wood in forest streams in the Pacific Northwest will require other information in addition to estimates of recruitment due to tree mortality in mature and old-growth forests. In particular, more must be learned about the effects of stand-replacing disturbance, the fate of snags throughout succession, delivery of wood from hillslopes due to mass soil movements, and the roles of in-stream transport and decomposition of large wood. However, it does appear that land managers in the region should pay particular attention to forests along unconstrained reaches as likely sources of large wood for streams.

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