Recruitment of wood to streams in old-growth and second-growth redwood forests, northern California, U.S.A.

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Abstract: From an ecological perspective, one aim of forest management is to supply wood to streams to protect and enhance aquatic habitats. An analysis was made of the mass balance of in-stream wood along 9 km of channels in old-growth and 50-year-old second-growth redwood (*Sequoia sempervirens* (D. Don) Endl.) forests in northern California, U.S.A. High volumes of wood storage in streams in old-growth forests were due primarily to streamside landsliding and bank erosion. Logging-related debris and high forest mortality rates in conifer and deciduous forests contributed to high wood storage in second-growth forests. Volumes of in-stream wood in second-growth forests were similar to volumes in one old-growth system and less than another. Diameters of wood were significantly greater in older forests. Wood recruitment from forest mortality in old-growth forests was low compared with second-growth sites, driven by differences in conifer mortality rates of approximately 0.04 and 0.9%·year^{-1}, respectively. Contrasting old-growth redwood mortality with values reported for unmanaged Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in Washington State (0.5%·year^{-1}) and unmanaged Sitka spruce (*Picea stichensis* (Bong.) Carrière) forests in southeastern Alaska (1.2%·year^{-1}) point to a strong latitudinal gradient of forest mortality reflected in tree size. The mass balance analysis of in-stream wood also allowed an estimation of bank erosion along large channels and soil creep along small, steep streams.

Résumé : D'un point de vue écologique, un des buts de l'aménagement forestier est d'approvisionner les cours d'eau en bois pour protéger et améliorer les habitats aquatiques. Un bilan de masse du bois présent dans les cours d'eau a été réalisé sur 9 km le long de cours d'eau dans des forêts anciennes et des forêts de seconde venue de séquoia (*Sequoia sempervirens* (D. Don) Endl.) âgées de 50 ans et situées dans le Nord de la Californie, aux États-Unis. L'accumulation de volumes élevés de bois dans les cours d'eau situés dans les forêts anciennes est surtout due aux glissements de terrain et à l'érosion des berges sur le bord des cours d'eau. Les débris de coupe et les taux élevés de mortalité dans les forêts de conifères et de feuillus contribuent à la forte accumulation de bois dans les forêts de seconde venue. Dans les forêts de seconde venue, les volumes de bois dans les cours d'eau sont semblables à ceux observés dans une forêt ancienne et inférieurs à ceux observés dans une autre. Le diamètre des bois était significativement plus grand dans les forêts anciennes. Dans les forêts anciennes, la mortalité est une source de bois moins importante que dans les forêts de seconde venue à cause de la différence dans le taux de mortalité des conifères, soit respectivement 0,04 et 0,9 %·an^{-1}. La différence entre le taux de mortalité observé dans les forêts anciennes de séquoia et les valeurs rapportées de 0,5 %·an^{-1} dans les forêts non aménagées de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) dans l'État de Washington et de 1,2 %·an^{-1} dans les forêts non aménagées d'épinette de Sitka (*Picea stichensis* (Bong.) Carrière) dans le Sud-Est de l'Alaska suggère l'existence d'un fort gradient latitudinal de mortalité des arbres qui se reflète dans la dimension des arbres. L'analyse du bilan de masse du bois dans les cours d'eau permet également d'estimer l'érosion des berges le long de larges cours d'eau et la cryptosolifluxion le long des petits ruisseaux escarpés.

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Introduction

There is increasing interest in protecting the sources of in-stream wood in managed forests because of the important role wood plays in the geomorphology and ecology of streams and rivers (Bilby 1981; Bisson et al. 1987). This often involves defining the ideal amount of wood in streams

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and the forest management prescriptions to support that target. Most management and regulatory approaches do not consider spatial and temporal variability in wood supply and its consequences for in-stream wood abundance. In addition, most regulatory efforts typically focus on forest mortality and ignore the potential wood supply to streams by other processes, including bank erosion and mass wasting.

Several key questions should underpin an analysis of wood recruitment to streams and rivers. At what rate does wood from conifer and deciduous forests enter channels of various sizes? How do recruitment rates of wood vary between second-growth and old-growth forests, and hence, how do tree mortality and wood recruitment vary with forest age? How important are other processes in wood recruitment, particularly bank erosion and mass wasting? How do

recruitment processes govern the source distances of wood to streams?

To answer these questions, we apply a new technology referred to as "wood budgeting", a quantitative framework for evaluating the mass balance of in-stream wood (Benda and Sias 2002; Benda et al. 2002). A wood budget was constructed for small to moderate-size streams in old-growth and 50-year-old second-growth redwood (*Sequoia sempervirens* (D. Don) Endl.) forests in northern California, U.S.A. A principal objective of the study was to examine how different processes, namely mortality, bank erosion, and landsliding, govern the volumetric rates of wood recruitment and the distances to sources of wood in old-growth and second-growth redwood forests. A further objective was to estimate rates of forest mortality in both conifer and deciduous forests and rates of bank erosion using data on wood recruitment.

Study areas

Field sites were selected to identify the range of processes and rates of wood recruitment in old-growth and second-growth redwood forests in northern California. Continuous field surveys were conducted along 4.4 km of channels located in Redwood National Park (unmanaged old-growth forests) and along 4.7 km of channels located in relatively uniform 50-year-old second-growth forests in the Van Duzen River watershed (Fig. 1, Table 1). In Redwood National Park (Prairie and Little Lost Man Creeks), surveys took place in 14–17 m wide channels that had morphologies that ranged from steep and boulder bedded (6%) to lower gradient and meandering (1%). In second-growth forests, surveys occurred within 2–10 m wide channels that ranged from steep (20%) to low gradient and meandering (1%) (Table 1). Although our sample size is small relative to the entire channel networks of Redwood Creek and Van Duzen River basins, the selected sites were used to make a preliminary census of the range of recruitment processes and their rates in small to intermediate size channels.

The Mediterranean-style climate of northern California is characterized by high annual precipitation (150–200 cm) that falls primarily between October and April, and it includes a summer drought with persistent coastal fog (Harden 1995). Coastal redwood is the dominant tree species throughout the lower elevations of the study area, and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies grandis* (Dougl.) Lindl.), and tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) are mixed with redwoods at higher elevations (Keller et al. 1995). In both forest types, alder (*Alnus* sp.) and big leaf maple (*Acer macrophyllum* Pursh) dominate the deciduous tree species in riparian areas. Most of the old-growth forest in the Van Duzen watershed was harvested by 1954 (California Department of Water Resources 1975). Mechanical removal of in-stream wood (i.e., stream cleaning) could only be documented in one of 16 second-growth study sites. There was no documented stream cleaning in the five old-growth study sites in Redwood National Park.

The geology of the northern California region is characterized by mélanges of the Franciscan complex, a mixture of highly deformed and weakly metamorphic sedimentary rocks that are mixed with some marine volcaniclastic sediments (Cashman et al. 1995). Mechanically weak rock in combination with heavy rainfall and earthquake activity has created a steepland landscape highly prone to mass wasting and produces some of the highest erosion rates in the continental United States (Nolan and Janda 1995).

Materials and methods

Wood budgeting

In-stream large wood can be evaluated in the context of a mass budget (Benda and Sias 2002; Benda et al. 2002). The volumetric mass balance of wood is governed by differences among input, output, and decay, a relationship that can be expressed as

$$[1] \qquad \Delta S = [I\Delta x - L\Delta x + (Q_i - Q_o) - D]\Delta t$$

where ΔS is a change in storage within a reach of length Δx over time interval Δt. Change in wood storage is a consequence of wood recruitment (I), loss of wood due to overbank deposition in flood events and abandonment of jams (L), fluvial transport of wood into (Q_i) and out of (Q_o) the segment, and in situ decay (D). The terms I and L 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 the terms are also functions of location (position in a network).

Wood is delivered to channels from a variety of sources. Total input can be summarized as

$$[2] \qquad I = I_m + I_f + I_{be} + I_l + I_e + I_a$$

Inputs include tree mortality by suppression, disease, or sporadic blowdown (I_m); toppling of trees following stand-replacing fires and windstorms (I_f); punctuated inputs from bank erosion (I_{be}); wood delivered by landslides, debris flows, and snow avalanches (I_l); exhumation of wood buried in the bed or bank or the recapture of wood previously deposited on the banks (I_e); and wood introduced by anthropogenic processes (I_a), such as logging or restoration activities.

In the solution of eq. 1, the loss of volume due to decay was omitted because our estimates of recruitment over approximately two decades would be insignificant, because decay occurs primarily as a loss of mass due to decreasing wood density (Hartley 1958). In addition, we did not observe significant inputs from exhumation of buried wood, and so, we set I_e to zero. Furthermore, in the small- to moderate-sized channels in the study area (2–17 m wide), we did not observe wood being deposited onto off-channel areas, such as terraces, and hence, we set L in eq. 1 to zero. Given these conditions in our short-term budget, eq. 1 reduces to

$$[3] \qquad \frac{\Delta S}{\Delta t} = [I + (Q_i - Q_o)]\Delta x$$

The primary objective for constructing the partial wood budget in northern California was to estimate the relative importance of three recruitment processes, specifically mortality, bank erosion, and landsliding. Hence, we did not assess

Fig. 1. Location map showing study sites in the old-growth reaches of Redwood National and State Parks and in the second-growth forests of the Van Duzen watershed, northern California.
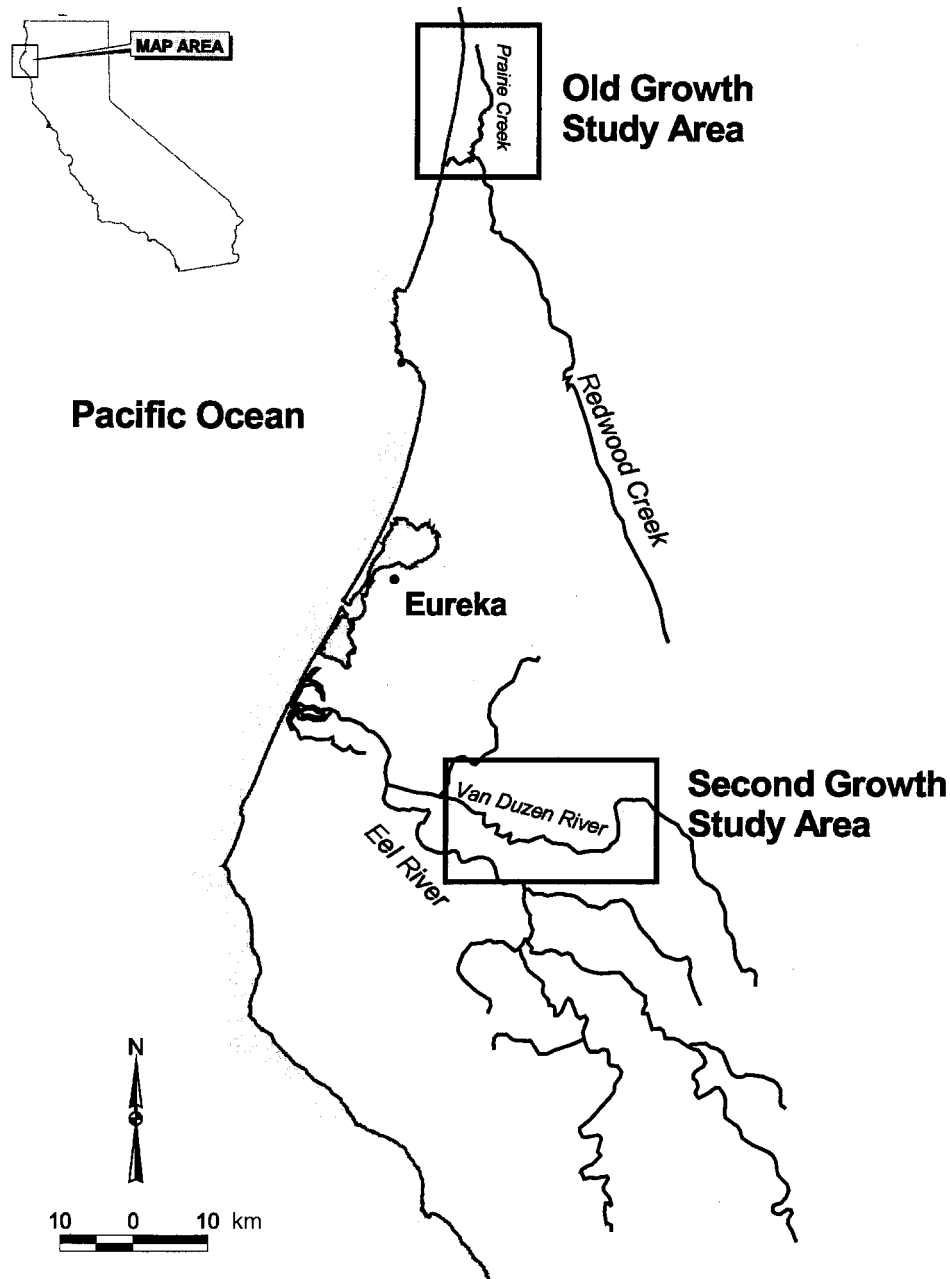
fluvial transport of wood and the fluvial flux terms (Q_i and Q_o in eq. 1) were omitted. Equation 3 then becomes

[4] $$\Delta S = \frac{I_m + I_{be} + I_1}{\Delta T}$$

where ΔS is the change in recruited wood storage (m^3·km^{-1}) in study segments over some elapsed time period ΔT. Wood storage in terms of piece volume was computed from piece length and average diameter using the geometry for a cylinder. The term ΔT was assumed to be equal to the weighted mean age of recruited wood in that segment (Murphy and Koski 1989; Martin and Benda 2001), computed by

[5] $$\Delta T = \left\{ \sum_{i=1}^{n} a_i p_i \right\}$$

where a_i is the mean age of wood in decay classes i and p_i is the proportion of wood in decay class i in any segment (decay classes described below). Over short time periods, ΔT is sensitive to the sequence of recruited trees of various sizes (i.e., ΔT would be significantly different if a large tree fell in year 10 versus year 1 during a 10-year period). Hence, the proportion of wood in each decay class was based on number of trees, rather than on volume, to reduce the variability in ΔT that can arise because of variations in the temporal sequence of recruitment. In addition, eq. 5 gives more weight

Table 1. Characteristics of the 21 field study sites.

Site No.	Creek name	Reach length (m)	Drainage area (km²)	Geologic unit*	Mean slope (%)	Mean stream width (m)	Dominant substrate	Channel type
1	Upper Little Lost Man	700	7.4	QTpc	5.9	14	Cobble	Step pool
2	Lower Little Lost Man	670	8.2	QTpc	4.0	14	Cobble	Pool–riffle
3	Lower Prairie	1200	24.0	KJfl	1.0	17	Gravel	Pool–riffle
4	Middle Prairie	700	22.3	KJfl	1.0	17	Gravel	Pool–riffle
5	Upper Prairie	1200	22.0	KJfl	1.0	17	Gravel	Pool–riffle
6	Lower Cummings	274	12.1	Qal	1.0	9.0	Gravel	Pool–riffle
7	Lower Root	305	15.8	Qal	1.0	10	Gravel–sand	Pool–riffle
8	Lower Hely	305	9.4	Qal	1.0	9.2	Gravel	Pool–riffle – plane bed
9	Upper Root	305	12.2	QTw	1.5	10	Gravel–sand	Plane bed – forced pool
10	Corbett Ranch Tributary	305	4.4	QTw	2.8	6.9	Gravel	Forced pool–riffle
11	Middle Cummings	335	11.6	QTw	1.8	10	Cobble	Pool–riffle
12	Middle Hely	274	9.1	QTw	2.4	8.4	Gravel–sand	Plane bed – forced pool
13	Middle Root	305	13.2	QTw	2.1	8.0	Cobble	Variable
14	Lower Grizzly	305	43	TKy	1.2	14	Cobble	Plane bed
15	Middle Grizzly	609	27	TKy	4.0	12	Cobble	Plane bed – forced pool
16	Stevens Creek	305	14	TKy	2.8	10	Cobble–gravel	Plane bed – forced pool
17	Cummings Tributary No. 1	305	1.9	QTw–Qls	10	4.8	Gravel–cobble	Step pool
18	SD Tributary	274	2.3	QTw	9	6.1	Sand	Plane bed – forced pool
19	BD Tributary	183	0.2	TKy	41	2.2	Boulder–cobble–gravel	Cascade
20	Cummings Tributary No. 2	305	0.2	QTw	26	2.7	Sand	Step pool
21	Keller Ranch Tributary	274	0.3	QTw	20	2.9	Sand	Step pool

Note: The first five sites are located in old-growth redwood forests in Redwood National and State Parks, and the remaining 16 sites are located in second-growth forests in the Van Duzen watershed.

*Qal, alluvium–terrace; Qls, Landslide; Qtpc, Prairie Creek Formation; QTw, Wildcat–Carlotta Formation; TKy, Yager Formation; KJfl, Franciscan–Lacks Creek.

to trees that have been recruited longer ago to account for the assumed increasing loss of trees (and hence their undercount) with increasing time since recruitment (Murphy and Koski 1989).

The flux of wood to streams by chronic forest mortality can be expressed as

$$[6] \quad I_m = (B_L \times M_c \times H \times P_m) \times N$$

where I_m is annual flux of wood (m³·m⁻¹·year⁻¹); B_L is the volume of standing live biomass per unit area (m³·m⁻²); M_c is the rate of mortality (year⁻¹) (fraction of live biomass per unit time); H is average forest height (m); P_m is the stand-average proportion of standing trees that becomes in-channel wood when trees fall within a stream-adjacent forest; and N is 1 or 2, depending on whether one or both sides of the channel are forested (Benda and Sias 2002). Several of the parameters in eq. 6 are functions of time, namely B_L, M_c, and H. However, time dependence is excluded in eq. 6 since recruitment rates, and hence, mortality rates in this study, are analyzed over only a couple of decades.

To estimate P_m, a random geometric tree fall model (Van Sickle and Gregory 1990) was applied to a hypothetical uniform stand of trees within a distance H normal to the bank. The term P_m is simply the stand-average ratio of the total surface area covered by the stem length from all trees that intersect a stream channel to the total surface area covered by the random, 360° fall of all trees. Our calculation of P_m

assumes that trees are cylinders, because we were unsure of how taper of the bole varies with species, height, and tree age across all study sites. The parameter P_m is dependent on channel width and tree height (Benda et al. 2002). For instance, P_m is approximately 12% for a 15 m wide channel and a mean 40-m tree height. Predicted P_m values for all study sites are presented later.

The flux of wood to streams by bank erosion can be expressed as

$$[7] \quad I_{be} = (B_L \times E \times P_{be}) \times N$$

where I_{be} is the annual wood recruitment and E is the mean bank erosion rate (m·year⁻¹) (Benda and Sias 2002). The term P_{be} is analogous to P_m, although its value is different because trees tend to fall toward the channel when undercut. The calculation of P_{be} assumes a 100% fall probability towards the channel (based on our field observations and on Murphy and Koski 1989). Over long periods, bank erosion should occur only along one side of a channel (i.e., $N = 1$) to maintain the stream geometry in long-term steady state. Over yearly to decadal time periods, however, bank erosion could occur along both sides of a channel during large floods.

Field data collection and data analysis

Along the continuously surveyed segments (Table 1), we inventoried all pieces of wood within the bankfull width that

were greater than 8 cm in diameter (as measured in the middle of the log) and 1.8 m in length, corresponding, in general, to definitions of "large wood" (Sedell and Triska 1977). Each qualifying piece was grouped into bins by diameter (8–30, 31–61, 62–91, 92–183, and over 183 cm) and length (1.8–3.1, 3.2–6.1, 6.2–9.1, 9.2–15.0, and over 15 m). The volume for each piece of wood was calculated as a cylinder using the mean diameter and length of each bin. Segments of pieces that extended outside of the bankfull width were inventoried when possible to calculate total tree volumes, data that are necessary to estimate B_L in eqs. 6 and 7. The distance of each recruited piece of wood from the edge of the bankfull channel to its source (location of root) was measured with a tape.

To estimate recruitment rates of in-stream wood, the origin of pieces had to be identified and this could only be accomplished for a small proportion of the total number of pieces. Trees, or pieces of unknown origin (i.e., mobile pieces), had no obvious connection to the adjacent riparian stand and generally showed signs of fluvial transport (abrasion, broken limbs, broken ends, located in log jams). Each tree with an identified source was assigned to one of four source categories: bank erosion, landslide, mortality, or anthropogenic (i.e., logging related). Wood recruited by bank erosion had roots connected to the stream bank. Wood recruited by landslides was located within landslide deposits. Wood recruited by forest mortality originated from within the riparian forest. Logging-related pieces had cut ends (i.e., saw marks).

For wood with identified origins, pieces were assigned a decay class using a modified version of a snag classification system by Hennon et al. (2002). Because of the longevity of redwood trees in streams (Keller and Tally 1979), we only tallied those decay classes that encompasses a period of several decades when branches were still present on fallen trees. The Hennon decay categories that were used included (*i*) leaves or needles, (*ii*) twigs (no needles), (*iii*) full branches, (*iv*) primary branches, and (*v*) partial primary branches (nubs). To assign an age to the youngest decay categories for the pieces of identified origins, perennial vegetation growing near or on the trees or overturned stumps were dated by counting branch nodes. For the older decay classes, larger saplings growing on logs were dated using an increment borer or primary stem was cut with a saw and tree rings were counted.

Using the data on distance to wood recruitment sources, we calculated the relative proportion of wood that entered streams from varying distance away from channel banks. The cumulative distributions that were constructed are referred to as source distance curves (McDade et al. 1990; Robison and Beschta 1990). We also made theoretical predictions of source distance curves to compare with field data. To estimate the changing proportion of trees that can intersect a channel from increasing distance away from stream edge, we applied a random 360° fall trajectory for each tree (using a uniform stand density) within a maximum distance of a mean tree height normal to the bank (based on the model of Van Sickle and Gregory (1990)). The theoretical source distance curves assume that trees are cylinders; adding taper would proportionally reduce the amount of wood originating further away from the channel.

Data on mortality recruitment were used to specify I_m in eq. 6; values are summarized in Table 2. Standing forest biomass (B_L) for both coniferous and deciduous trees was calculated at each site by estimating the mean tree volume and multiplying that by the mean stand density (Table 3). A mean tree volume for each study segment was estimated by adding the volume of pieces in the channel to the volume of any pieces attached to them that were located outside of the channel banks. In many cases, recruited pieces of wood were attached to trees that extended onto the forest floor. In some cases, broken trees precluded identifying the length of the entire tree. Hence, B_L is underestimated, and this would tend to increase our calculated mortality and bank erosion rates. The largest error may occur in the old-growth sites where our estimates of stand density in second-growth forests would not apply well. To counter this limitation, we also calculated forest mortality in old-growth forests using biomass values for old-growth forests cited in the literature.

We estimated bank erosion rates at all 21 study sites using eq. 7 to illustrate another application of wood budgeting. Standing forest biomass is estimated as described previously. Theoretical P_{be} values were estimated for all study sites. Large floods that occurred in northern California during the last decade (U.S. EPA 1999) may have caused increased bank erosion and hence we report bank erosion values for one and both sides of the channel.

In small streams that are bounded by hillslopes, bank erosion rates can be equivalent to soil creep rates (Reid and Dunne 1996), and soil creep represents another important parameter in sediment budgets and environmental assessments (WDNR 1997). We calculated soil creep along an additional 1.7 km of headwater channels (first- and second-order streams) bounded by colluvium-mantled hillslopes in the Van Duzen watershed. The parameters used in eq. 7 for each study segment were estimated similarly to those in our analysis of bank erosion in larger channels.

Results

Characteristics of wood recruitment in old-growth and second-growth forest

The volume of wood with sources that could be identified (i.e., recruited versus total) was low (mean 27%) in both old-growth study segments (Fig. 2), a finding consistent with other studies (Murphy and Koski 1989; Martin and Benda 2001). On average, coniferous trees accounted for 76% of recruited wood volume in old-growth with deciduous trees making up the remainder. The species composition of the old-growth forest is unknown, but it is dominated by redwood. The diameter of wood recruited from old-growth sites, on average, was up to twice that in second-growth sites (Table 3).

The volume of total in-stream wood in the old-growth study segments exhibited a high degree of spatial variability. In Prairie Creek, wood volumes ranged from a high of 200 m³/100 m along a distance of 800 m to a low of less than 50 m³/100 m along a 1000-m reach (Fig. 2, Table 2). Field measurements indicated that the reach containing the high volume (100–200 m³/100 m) located in the middle of the segment was characterized by bank erosion recruitment (Fig. 3). In the low wood volume reaches in Prairie Creek,

Table 2. Summary of large wood (LW) volumes and weighted mean ages.

Site No.	Total LW (m³/100 m)	Logging LW (m³/100 m)	LW recruit volume (m³/100 m)				Weighted mean age (years)				
			Erosion	Mortality	Slide	Total	Erosion	Mortality	Deciduous mortality	Conifer mortality	Slide
1	124–411	0	0–33	0–21	0–157	19–169	8.6	9.3	0.0	9.3	22.1
2	35–381	0	0–6	0–5	0–6	0–7	8.9	0.0	0.0	0.0	0.0
3	17–108	0	0–9	0–35	0	3–35	12.8	14.0	14.9	11.6	0.0
4	48–255	0	2–83	3–31	0	8–112	10.2	6.2	2.0	10.3	0.0
5	8–139	0	0–75	0–12	0	0–87	10.4	12.6	13.0	12.4	0.0
6	1–25	1–3	0	1–4	0	1–4	14.0	13.5	13.0	24.0	0.0
7	16–46	1–5	1–4	1–3	0	2–6	11.4	16.7	16.8	16.5	0.0
8	28–143	1–32	1–3	4–6	0	5–9	9.8	9.1	9.1	0.0	0.0
9	92–314	0–73	5–10	5–40	0–16	10–66	13.4	13.4	13.9	4.4	19.0
10	95–298	5–44	0–15	1–25	0–10	2–51	8.0	14.4	14.8	13.5	14.7
11	48–104	0–20	0–8	0–3	0	3–8	7.2	10.0	14.0	4.0	0.0
12	88–110	4–7	0–1	3–9	1–47	6–51	13.3	13.9	13.9	0.0	21.3
13	9–75	0–21	2–8	0–0.1	0	2–8	9.4	19.0	19.0	0.0	0.0
14	2–31	0–13	1–7	0–1	0	1–7	10.4	11.2	9.1	10.0	4.0
15	1–68	0–45	0–1	0–3	1–15	0–15	19.0	3.0	0.0	3.0	22.1
16	41–55	1–15	0–4	0–1	0–18	2–23	4.0	12.9	12.9	0.0	4.2
17	107–144	0–22	0–14	4–29	2–11	11–44	5.6	12.9	0.0	12.9	16.2
18	131–165	20–49	1–19	5–42	5–43	29–65	11.0	15.0	13.8	21.5	9.5
19	54–129	17–68	1–20	2–10	0	11–22	7.4	8.7	0.0	8.7	0.0
20	65–279	40–169	0–27	4–10	0–22	4–59	14.0	9.1	0.0	9.1	5.0
21	233–286	10–56	3–25	4–77	0–21	29–80	3.7	9.8	1.0	10.9	0.0

Table 3. Large wood (LW) recruitment rates, *P* values, estimated biomass density, mean recruitment diameters, and percentage of conifer and deciduous recruited wood by volume.

Site No.	LW recruitment rates (m³·km⁻¹·year⁻¹)					P value		Biomass density (m³/ha)	Mean recruit diameter (m)	Percentage of recruits by volume	
	Erosion	Deciduous mortality	Conifer mortality	Slide	Total	Erosion	Mortality			Conifer	Deciduous
1	5.9	0.0	2.1	3.8	11.7	0.37	0.08	2159	0.80	99	1
2	1.9	0.0	0.0	0.0	1.9	0.37	0.08	2159	0.70	84	16
3	1.1	1.0	1.2	0.0	3.3	0.43	0.09	5129	0.74	58	42
4	2.7	3.2	4.2	0.0	10.1	0.43	0.09	5129	1.21	91	9
5	5.0	0.1	0.9	0.0	5.9	0.43	0.09	5129	0.81	51	49
6	0.05	0.6	0.5	0.0	1.1	0.54	0.10	79	0.27	60	40
7	2.0	0.6	0.1	0.0	2.8	0.58	0.11	145	0.24	7	93
8	1.8	5.5	0.0	0.0	7.3	0.55	0.10	213	0.30	0	100
9	5.0	13.8	11.7	0.06	30.6	0.56	0.11	417	0.42	25	75
10	7.8	1.7	5.1	1.9	16.5	0.45	0.09	844	0.52	81	19
11	6.0	0.3	1.8	0.0	8.1	0.58	0.11	319	0.55	19	81
12	0.4	3.2	0.0	2.6	6.2	0.51	0.10	126	0.32	53	47
13	4.0	0.02	0.0	0.0	4.0	0.5	0.10	414	0.46	33	67
14	3.1	0.5	0.6	0.0	4.2	0.69	0.13	307	0.34	6	94
15	0.004	0.0	1.9	0.7	2.6	0.65	0.10	2300	0.96	90	10
16	5.2	0.3	0.0	0.4	5.9	0.35	0.11	120	0.42	2	98
17	3.1	0.0	0.4	3.9	7.5	0.35	0.06	992	0.60	98	2
18	7.2	3.7	0.3	6.0	17.3	0.41	0.08	406	0.51	34	66
19	1.4	0.0	1.0	0.0	2.3	0.19	0.03	212	0.59	92	8
20	2.4	0.0	2.7	12.2	17.3	0.22	0.04	416	0.55	100	0
21	1.2	1.4	6.7	0.0	9.2	0.24	0.04	849	0.82	98	2

Fig. 2. Storage of total wood and wood with identified recruitment processes located in the old-growth sites of Little Lost Man and Prairie Creeks. Distance increases downstream.

Little Lost Man Creek, Old Growth
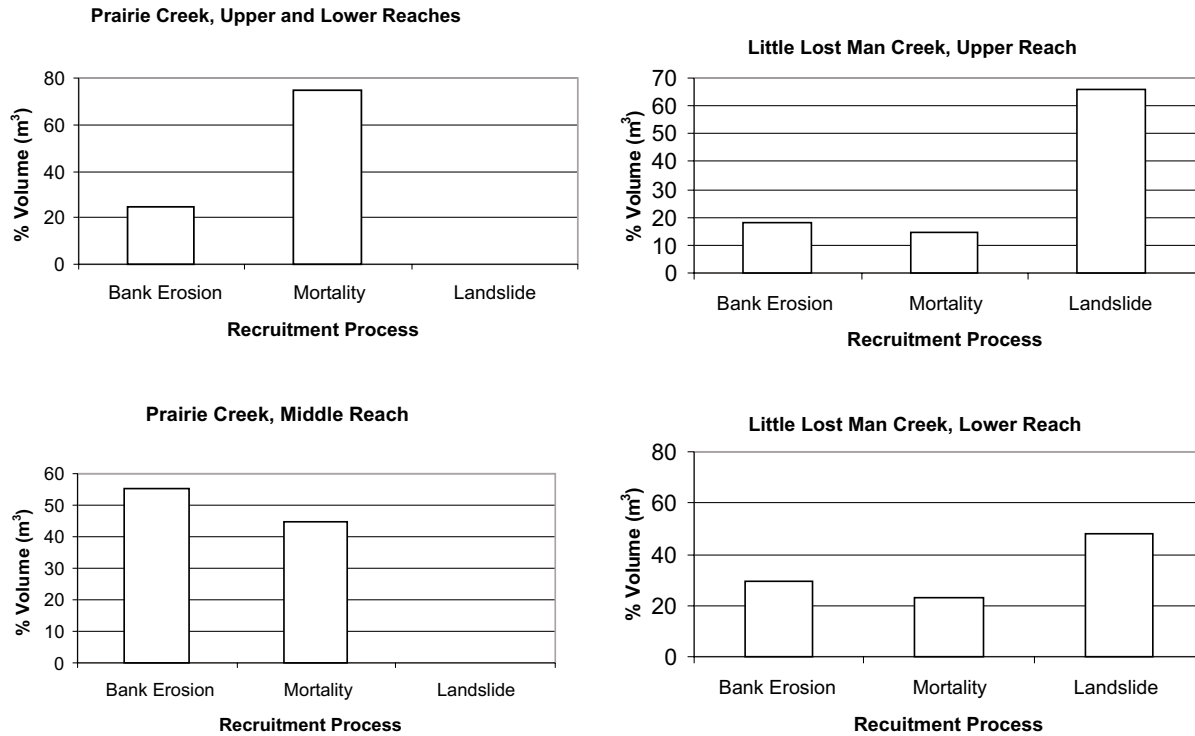

Prairie Creek, Old Growth
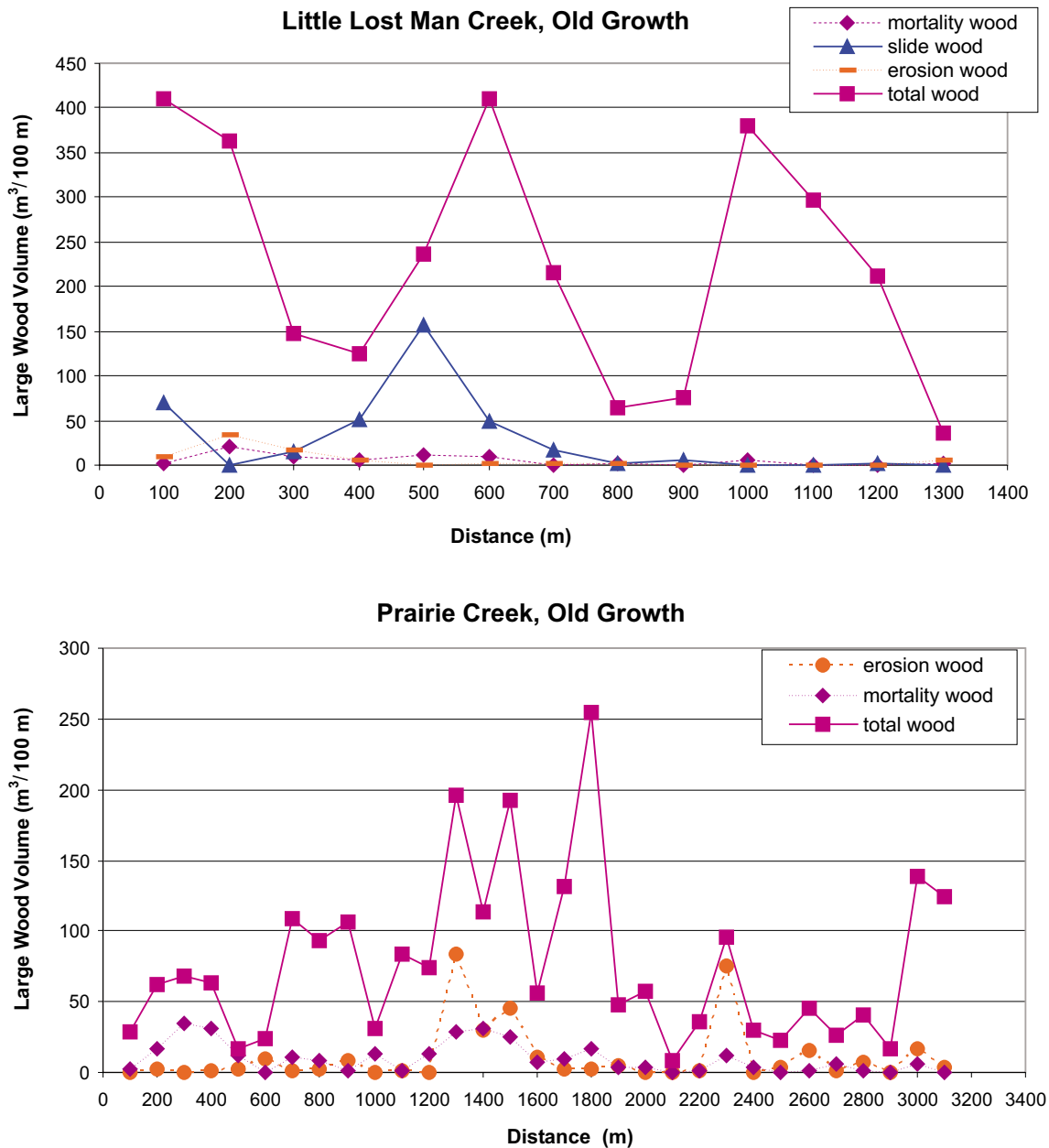
little bank erosion was observed (i.e., few trees recruited by bank erosion). Similarly, in Little Lost Man Creek, wood storage was spatially variable, ranging from highs of 400 m³/100 m to a low of 50 m³/100 m. The very high wood storage in upper Little Lost Man Creek (0–800 m, Fig. 2) was driven by streamside landsliding (Fig. 3). The average proportion of tree volume recruited by mortality, bank erosion, and landsliding in Prairie Creek averaged 60, 40, and 0%, respectively, and in Little Lost Man Creek averaged 20, 22, and 58%, respectively.

Wood storage was also highly variable throughout the streams in second-growth forests of the Van Duzen basin. For example, in Lower Root Creek (site 7; Table 2) total wood storage varied from less than 10 m³/100 m to a high of 70 m³/100 m. Similar to the old-growth study sites, volumes of wood with known origins were small compared with total

wood storage (mean 32%). The recruitment processes for the second-growth sites included logging debris from timber harvest activities that spanned the early to middle 20th century. Logging debris included large pieces of old-growth timber and root wads that were identified by saw marks. The mean proportion of tree volume recruited in the second-growth sites by the four processes of mortality, bank erosion, landsliding, and logging averaged 21, 18, 13, and 50%, respectively, (Table 2, Fig. 4). On average, conifer trees accounted for approximately 50% of recruited wood by volume in second-growth forests. The proportion of deciduous trees along riparian zones in the Van Duzen watershed averaged approximately 35% (Pacific Lumber Co. 2001).

Volumes of wood in streams located in second-growth forests at the scale of reaches (i.e., hundreds of metres) often exceeded the volume of wood in the old-growth forest of

Fig. 3. Relative proportion of wood recruitment processes in the five study reaches in old-growth forests.

Prairie Creek, Upper and Lower Reaches

Little Lost Man Creek, Upper Reach

Prairie Creek, Middle Reach



Little Lost Man Creek, Lower Reach

Prairie Creek (Fig. 5). This appears to be due to large amounts of logging-related wood (Fig. 4) and high forest mortality rates in the second-growth forest study sites compared with low rates of forest mortality and bank erosion in Prairie Creek (see calculated mortality and bank erosion rates below). However, volume of wood in second-growth streams were much lower compared with Little Lost Man Creek (Fig. 5), a channel in old-growth forests prone to bank erosion and landsliding. The wood volumes in our second-growth sites were, in general, greater than the wood storage reported for old-growth sites in Redwood National Park by Harmon et al. (1986) (Fig. 5). Moreover, the wood volumes in the Van Duzen study sites were higher compared with measurements of wood in other second-growth forests (Knopp 1993). This may be the result of relatively large quantities of logging-derived wood contained in the Van Duzen tributaries we surveyed and the occurrence of recent large floods that may have increased wood recruitment during the last decade (U.S. EPA. 1999) (Table 2, Fig. 4).

Although wood loss may increase with increasing channel width (Bilby and Ward 1989), our data in both old-growth and second-growth streams did not reveal this relationship (Fig. 5). Regressions between wood storage (m³/100 m) and channel width produced r^2 of 0.05 (Van Duzen channels), 0.05 (Prairie Creek), and 0.007 (Little Lost Man Creek).

Distance to sources of wood

Because of the diversity of recruitment processes in both old-growth and second-growth sites (Figs. 3 and 4), the distances from wood sources to channel banks were highly variable. Source distance curves for all 16 second-growth and 5 old-growth study segments are plotted in Fig. 6 along with the theoretical source distance curves for mortality recruitment alone. The wood source data in Prairie Creek

Fig. 4. The distribution of recruitment processes averaged across the 16 sites located in the second-growth forests in the Van Duzen basin. Bars are means, and error bars are ranges.
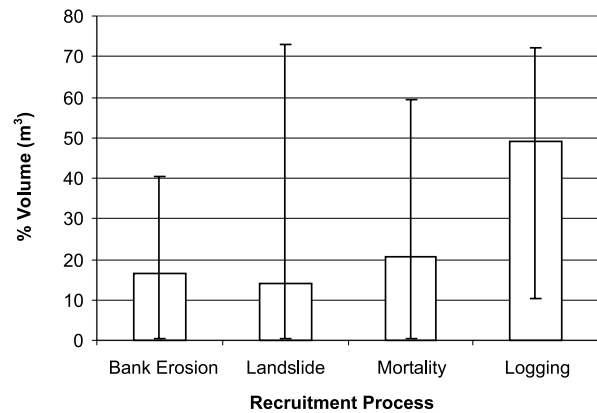

show that over 90% of the wood enters the channel from within 30 m (slope distance) of the stream edge, and the source distances are shorter compared with the theoretical prediction from mortality alone (Fig. 6). This is because bank erosion is responsible for greater than 50% of the wood volume (in the middle, high wood loading reach) in Prairie Creek (Fig. 3). Even though mortality accounted for over 70% in the low wood storage sites along Prairie Creek, the proximity to the channel of tree fall suggests that mortality is higher nearer to the stream for reasons that are not certain but may be due to wetter soils and susceptibility to windthrow from channel canopy opening.

The empirical source distance curve for Little Lost Man is extended beyond the theoretical prediction for mortality alone (Fig. 6). This is because streamside landsliding is the dominant wood-recruitment process in the uppermost 600 m

Fig. 5. (Top) Cumulative distributions of wood volume are plotted for the two old-growth basins, 16 sites in the second-growth Van Duzen watershed, Redwood National Park old growth (Harmon et al. 1986), and other second-growth sites (Knopp 1993). (Bottom) Wood storage in this study is stratified according to channel width.
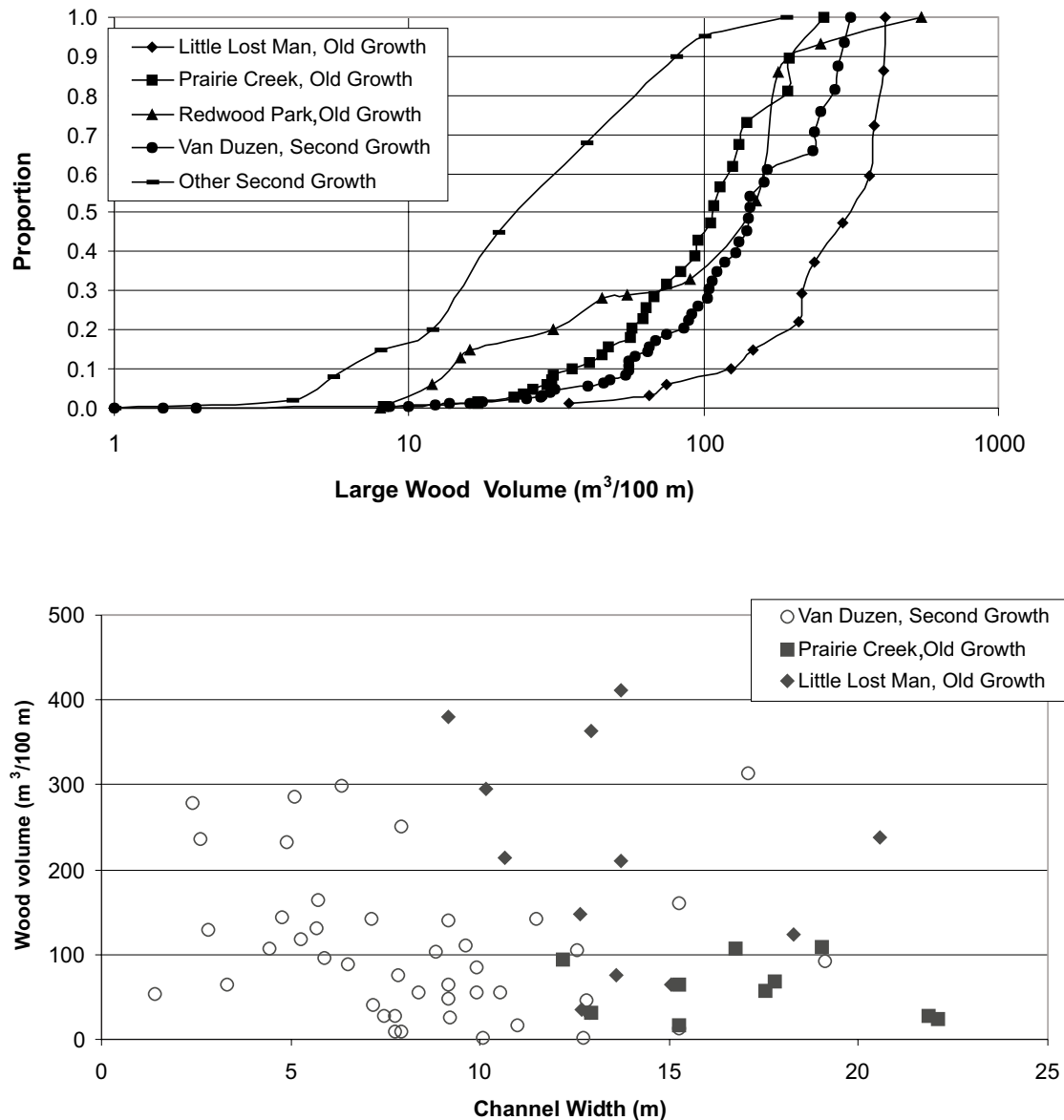
of that study segment (i.e., approximately 70% of volume linked to landsliding) (Figs. 2 and 3). The empirical source distance curve indicates that 75% of wood enters the channel from a distance of about 45 m compared with 86% for the same distance based on the theoretical predictions.

The source distance data for the majority of second-growth sites in the Van Duzen basin indicate that the distance of wood from their sources is controlled by recruitment processes. The majority of sites have significant recruitment from bank erosion, and this reduces the source distances of wood to less than the theoretical prediction from mortality alone (Fig. 7). In those cases, approximately 90% of wood originates from within 10 m of the bank. For those sites where the source distance curves exceed the theoretical prediction (i.e., wood coming from distances further away), the majority of them have significant recruitment

from streamside landsliding (Fig. 7, Table 2). Finally, because deciduous trees are likely to grow closer to stream edges and lean towards the channel because of phototropism, the source distance curve for deciduous is shifted to the left when contrasted with conifer source distance curves (Fig. 7).

In-stream wood recruitment rates

We estimated rates of wood recruitment (i.e., I_m ($m^3 \cdot m^{-1} \cdot year^{-1}$)) for chronic mortality, bank erosion, and landsliding based on the volumes of recruited wood and the weighted mean age of recruited wood in each category (eq. 5). To calculate age – decay class relationships, we aged 41 in-stream pieces out of a total of 941 pieces with known origins (4%). We included age – decay class data from an additional 32 trees collected from a similar second growth

Fig. 6. (Top) The source distance curve for Prairie Creek plots to the left of the theoretical source distance curve (i.e., mortality recruitment only using random 360° fall trajectories) because bank erosion is a significant recruitment mechanism (e.g., Fig. 3). The source distance curve for Little Lost Man Creek plots to the right of the theoretical curve because streamside landsliding is the dominated wood recruitment agent. (Bottom) The sites located in second growth forests plot both to the left and right of the theoretical curve.
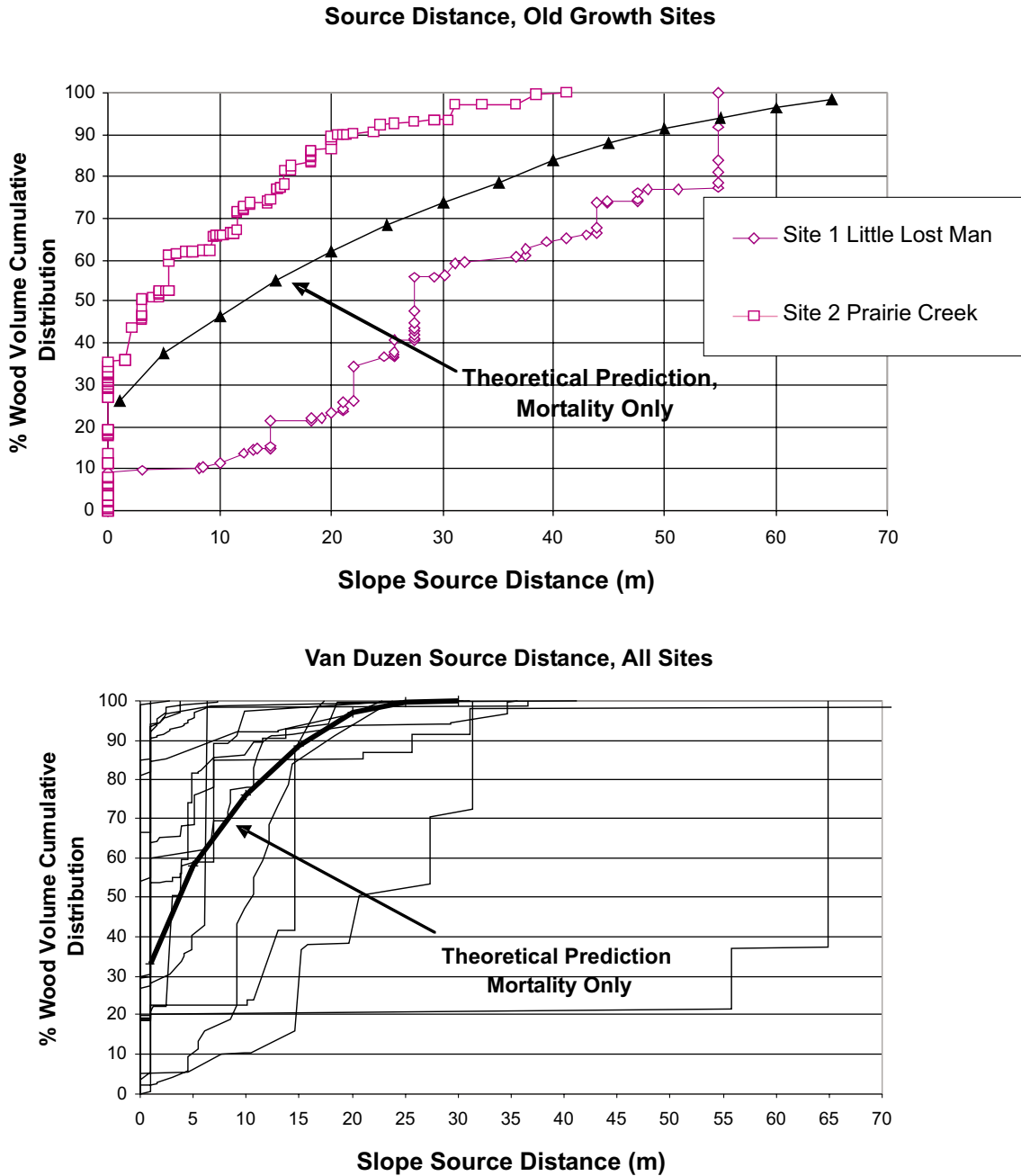
redwood forest in northern California to enhance the data set (74 pieces total). The mean ages were calculated for five decay classes of conifer and deciduous trees individually and ranged from 1 year for deciduous trees with leaves to 24 years for conifers with partial branches (Table 4). As a result of variable decay rates, several age decay classes overlapped. Overlapping decay classes were pooled to create four decay classes that had significantly different mean ages (*t* test, $P < 0.2$) (Table 4). This age – decay class relationship was used to assign ages to all recruited trees in our sur-

veys. The weighted mean age using eq. 5 for each of the 21 study sites are shown in Table 2.

Streams in second-growth forests (sites 6–21) had wood recruitment rates (conifer and deciduous combined) that ranged from 1.1 to 30.6 $m^3 \cdot km^{-1} \cdot year^{-1}$ (mean 4.0) for mortality, from 0 to 7.2 $m^3 \cdot km^{-1} \cdot year^{-1}$ for bank erosion (mean 3.2), and from 0 to 12 $m^3 \cdot km^{-1} \cdot year^{-1}$ for landsliding (mean 1.7) (Table 3, Fig. 8). Streams in old-growth forests (sites 1–5) had wood recruitment rates (conifer and deciduous combined) that ranged from 0 to 7.4 $m^3 \cdot km^{-1} \cdot year^{-1}$ (mean 2.5)

Fig. 7. Variation in source distance curves across all second growth sites is governed to a large degree by recruitment process and the proportion of wood originating from deciduous forests. (Top) Study sites with significant recruitment by bank erosion generally plot to the left of the theoretical source distance curve (i.e., mortality recruitment only using random 360° fall trajectories). (Middle) In study sites that have little recruitment by bank erosion and some recruitment by landsliding, source distance curves generally plot to the right of the theoretical curve. (Bottom) Source distance curves for deciduous trees plot to the left of the theoretical curve because of the preferential location of deciduous trees near channel margins and because deciduous trees often lean towards the channel.
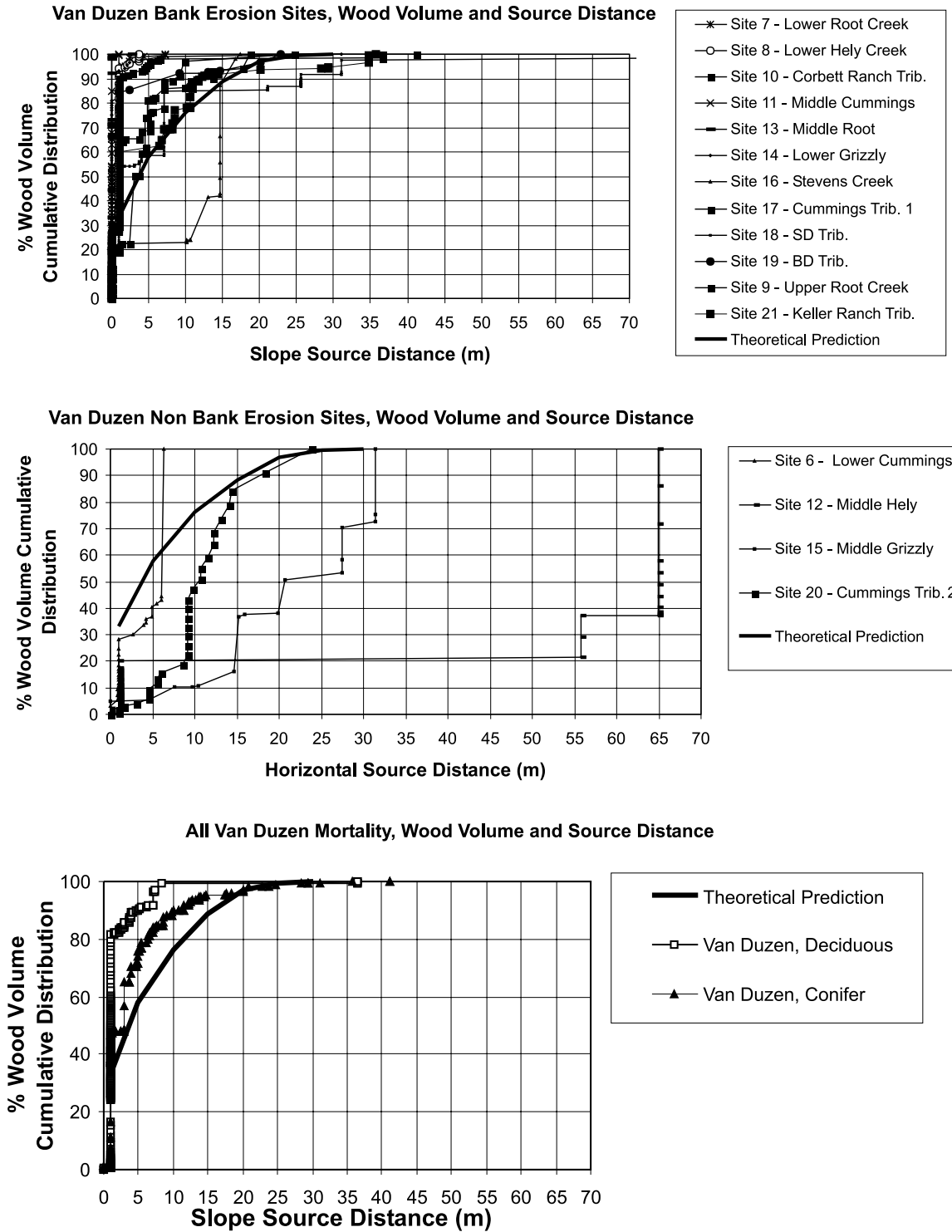
for mortality, from 1.0 to 5.8 $m^3 \cdot km^{-1} \cdot year^{-1}$ for bank erosion (mean 3.3), and from 0 to 3.8 $m^3 \cdot km^{-1} \cdot year^{-1}$ for landsliding (mean 0.8) (Table 3, Fig. 8).

Forest mortality rates

The data on mortality recruitment were used to estimate forest mortality rates for coniferous and deciduous trees us-

Table 4. Age statistics for pooled and unpooled decay classes of recruited large wood.

Unpooled							Pooled						
Class	Mean	Median	SD	Maximum	N	P^a	Class	Mean	Median	SD	Maximum	N	P
Conifers													
Needle	2.7	2	2.0	5	6	0.16	Needle	2.7	2	2.0	5	6	0.06
Twig	4.1	5	1.5	5	8	0.22^b	Twig, branch	4.6	5	1.5	8	18	0.02
Branch	5.0	5	1.4	8	10	0.03	Primary	14.3	12	11.3	40	10	0.07
Primary	14.3	12	11.3	40	10	0.07	Nub	24.3	23	15.1	55	15	
Nub	24.3	23	15.1	55	15								
Deciduous													
Leaf	1.0	1	0.0	1	3	0.005	Leaf	1.0	1	0.0	1	3	0.0001
Twig^c	4.1	5	1.5	5	8	0.55^b	Twig, branch	4.4	5	1.6	8	14	0.01
Branch	4.7	4	1.8	8	6	0.01	Primary	8.8	10	1.9	10	4	0.19
Primary	8.8	10	1.9	10	4	0.19	Nub	19.3	22	5.4	27	3	
Nub	19.3	22	5.4	27	3								

Note: Decay-class ages in years were determined from dependent saplings and other field evidence of recruitment age.
[a]P values result from two tailed t tests assuming unknown and unequal variances between adjacent decay classes.
[b]Populations considered similar ($P > 0.2$).
[c]Twig decay class data were not available for deciduous trees; consequently, conifer data were used as a surrogate.

ing eq. 6. Stand density in mature, Pacific coastal forests commonly ranges between 200 and 400 trees/ha (McArdle et al. 1961), and we chose an average stand density of 320 trees/ha to represent all trees over 10 cm in diameter, the minimum piece size inventoried in streams (Pacific Lumber Co. 2001). Using our field estimates of tree volume, our calculated biomass volumes ranged from 2150 to 5130 $m^3 \cdot ha^{-1}$ in redwood old-growth forests (mean 3800 $m^3 \cdot ha^{-1}$) and from 80 to 2300 $m^3 \cdot ha^{-1}$ (mean 500 $m^3 \cdot ha^{-1}$) in second-growth forests (Table 3). To allocate the estimated standing biomass to conifer and deciduous components at each site, the total standing biomass was multiplied by the volumetric proportion of in-stream wood associated within each species group (Table 3). Mean tree height was estimated to be 80 m in old-growth redwood and 30 m for 50-year-old second-growth forests (McArdle et al. 1961).

In the 50-year-old second-growth forests, total conifer mortality ranged from 0 to 6.2%·year^{-1} and averaged 0.9%·year^{-1} over a period of approximately two decades (Fig. 9). Mortality in deciduous second-growth forests ranged from 0 to 2.5%·year^{-1} and averaged 0.6%·year^{-1}. Conifer mortality rates in old-growth redwood forests were much lower and ranged from 0 to 0.08%·year^{-1} and averaged 0.04%·year^{-1} (Fig. 9). Deciduous mortality in old-growth forests ranged from 0 to 0.09%·year^{-1} and averaged 0.02%·year^{-1}.

The method that we used to estimate mean tree volume based on in-stream wood volumes may have underestimated forest biomass, particularly in old-growth forests. In addition, stand density of large old trees may be less than our estimate of 320 trees/ha. Higher forest biomass values of approximately 10 000 $m^3 \cdot ha^{-1}$ have been reported for old-growth redwood forests in northern California (Westman and Whittaker 1975). Using the higher mean forest biomass yielded an old-growth conifer mortality rate of 0.012%·year^{-1} using eq. 6.

Estimating bank erosion rates

Using eq. 7 and our estimates of wood recruitment by bank erosion (Fig. 8), we calculated bank erosion rates in

old growth of 0.014 m·year^{-1} for both banks and 0.027 m·year^{-1} for one bank (Fig. 10); we report both values, because bank erosion may have occurred along one or both sides of a channel. In the second-growth sites, bank erosion averaged 0.22 m·year^{-1} (one bank) to 0.11 m·year^{-1} (both banks). Calculated mean soil creep rates ranged between 17.9 and 1.7 cm·year^{-1} (Table 5). In general, soil creep rates decreased with increasing weighted mean ages of recruited wood.

Discussion

Characteristics of wood recruitment in old-growth and second-growth forests

A diversity of wood recruitment processes was responsible for a high degree of spatial variability in wood storage that varied up to almost an order of magnitude for 100- to 1000-m scales (Fig. 2). In old-growth forests in particular, low recruitment from mortality led bank erosion and landsliding to dominate wood loading in certain areas (i.e., 100–700 m in Little Lost Man Creek; Fig. 2). In addition, in old-growth forests, little bank erosion, in combination with very low mortality rates, contributed to low rates of wood recruitment in certain segments (50–1000 m and 2100–2800 m in Prairie Creek; Fig. 2). On average in second-growth forests, recruitment of wood from mortality was approximately equivalent to the recruitment attributable to bank erosion or landsliding (Fig. 3), but wood storage was dominated (50%) by logging-related debris. In sum, volumes of in-stream wood in second-growth forests were similar to volumes in Prairie Creek, a site having limited bank erosion and mortality, and less than in Little Lost Man Creek, a segment that had recruitment by bank erosion and streamside landsliding. Diameters of in-stream wood in old-growth sites were greater than second-growth areas (Table 3). Unfortunately, our largest bin size for tallying tree diameters was only 183 cm, and hence, we are unable to better quantity the difference between the diameters of old-growth versus second-growth trees.

Fig. 8. Calculated recruitment rates for mortality, bank erosion, and landsliding across all 21 study sites. Sites 1–5 are located in old-growth forests, and sites 6–21 are located in second-growth forests. Data are arrayed by channel width. Study site numbers also shown in parentheses.
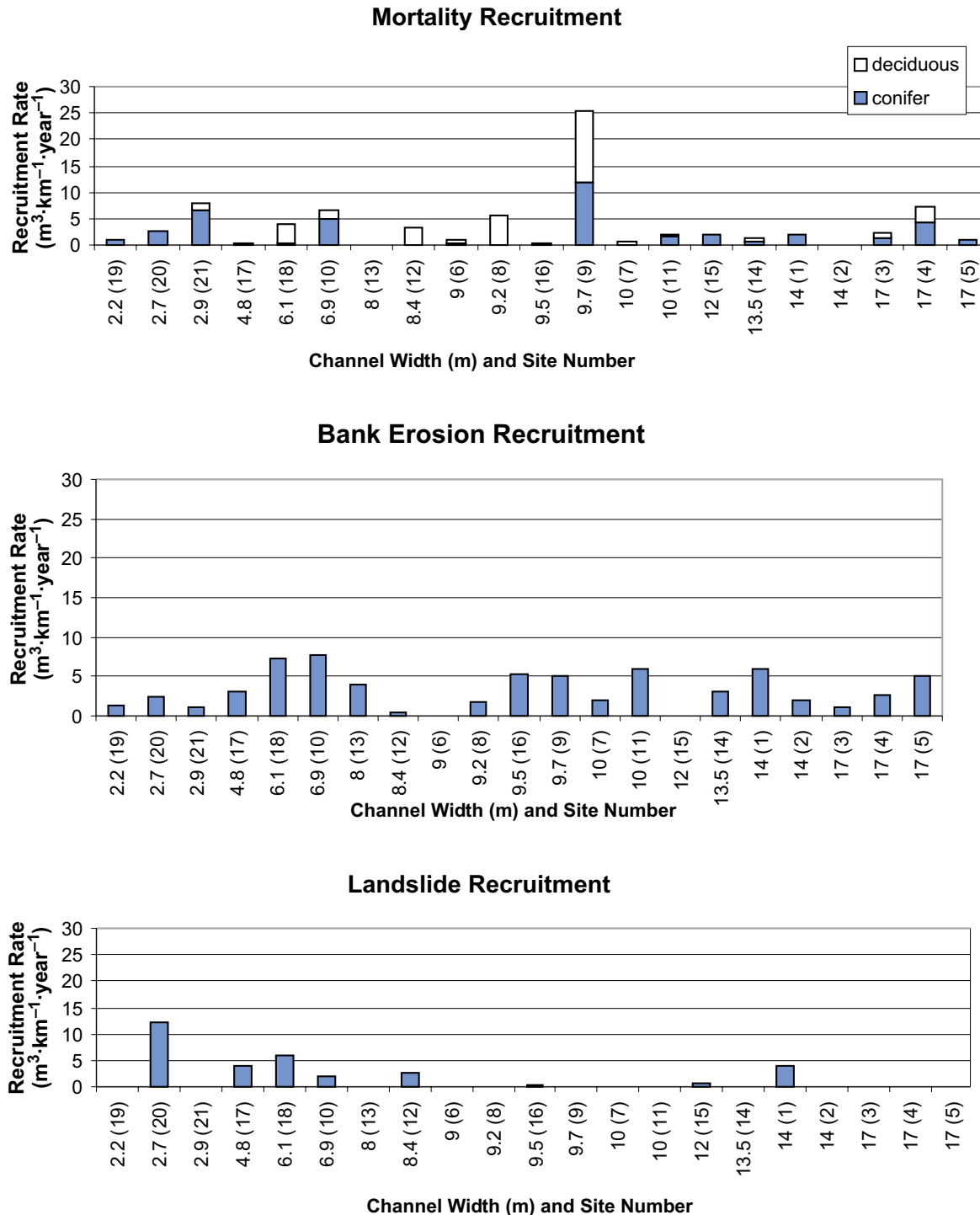

Wood recruitment rates in old-growth and second-growth forests (conifer and deciduous combined) averaged 2.5 m³·km⁻¹·year⁻¹ and 4.0 m³·km⁻¹·year⁻¹, respectively. The larger rates in second-growth forests may reflect a heightened mortality rate because of suppression and other factors associated with tightly stocked young stands. There are no other values of wood recruitment rates in northern California from which to compare our estimates. In southeastern

Alaska, Martin and Benda (2001), using eq. 6, estimated a mean recruitment rate of 3.8 m³·km⁻¹·year⁻¹; this is the only other recruitment rate of which we are aware. Most of the disparity between the mortality recruitment rates in old-growth and second-growth forests occurred in the deciduous stands, where mortality recruitment varied between 0.8 and 1.9 m³·km⁻¹·year⁻¹, respectively. Conifer mortality between old-growth and second-growth forests varied between 1.7

Fig. 9. Rates of conifer forest mortality show large difference between old-growth (mean $0.04\%\cdot year^{-1}$) compared with second-growth sites (mean $0.9\%\cdot year^{-1}$). Deciduous mortality accounted for approximately 30% of the total mortality rates in both forest types.
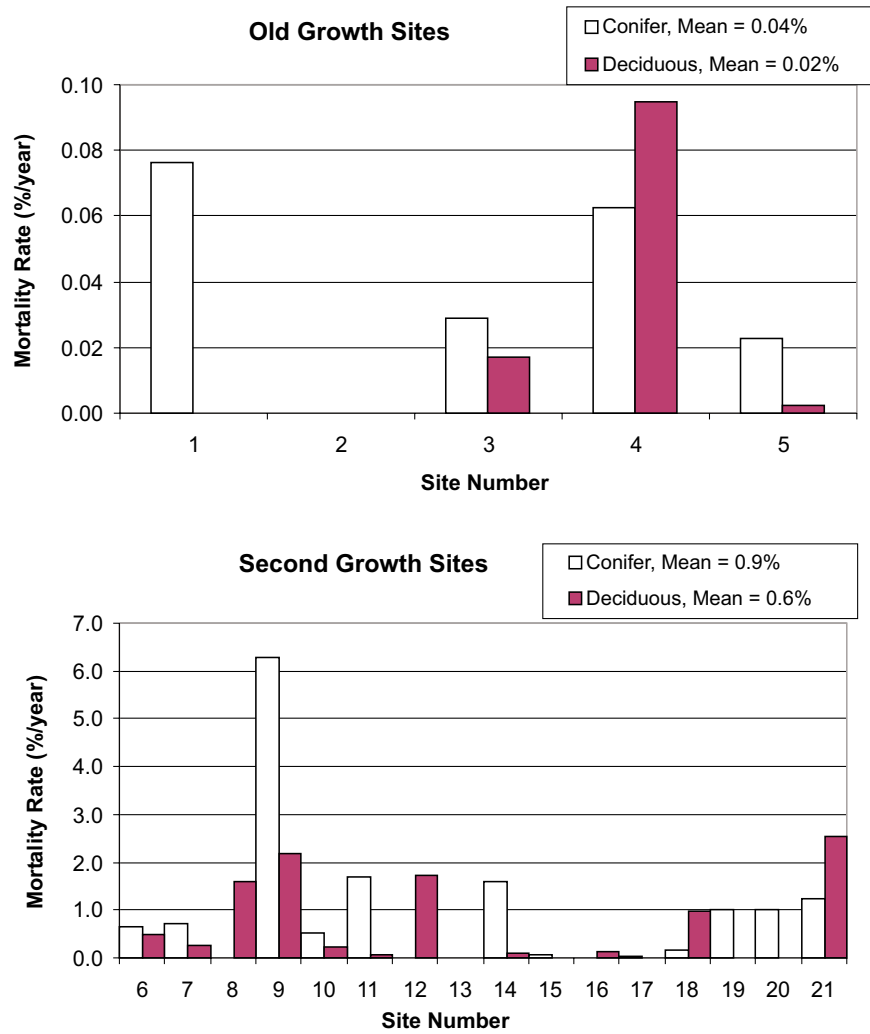
Fig. 10. Calculated bank erosion rates across all study sites are stratified by channel width. Study site numbers are shown in parentheses.
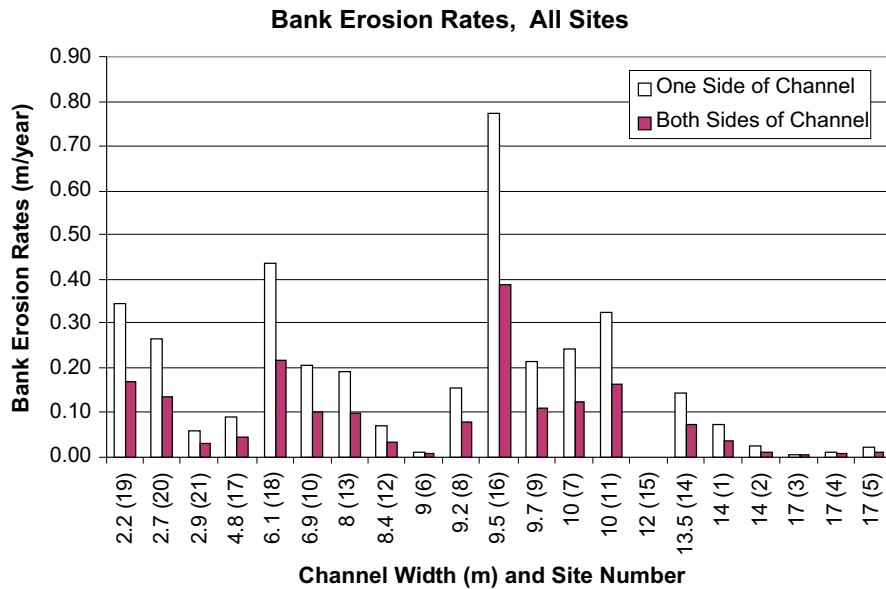
and 2.0 m³·km⁻¹·year⁻¹, respectively. Even though conifer wood supply rates are similar between forest types, the difference in the diameter of trees between the two sites (Table 3) indicates that there are fewer but larger logs in old-growth streams. In addition, because of the much higher standing forest biomass in older forests, the parity in wood supply rates reflects large differences in mortality rates between the two forest types (i.e., higher forest mortality in younger forests).

In the absence of landsliding, wood recruitment in both old-growth and second-growth study sites originated from within 20–40 m of the stream (Figs. 6 and 7). Bank erosion caused wood to enter from within approximately 5 m of the channel. It is possible that trees that we identified as recruited by bank erosion (root wad in the channel) may have been blown down (i.e., mortality) because of their proximity to the channel canopy opening and wetter soils. This might be more apt to occur in deciduous trees but the extent of this process, if it occurs, is not known. Landsliding caused recruitment distances to extend to over 60 m. Even in old-growth forests, most wood was recruited from close to the channel margins. This may be due to greater exposure to wind and possibly wetter soils in the riparian zone. Undoubtedly, field surveys over longer distances and over longer time spans would record some wood entering from further away (i.e., theoretical curves in Fig. 6).

Across all study sites, the proportion of wood originating from bank erosion (compared with mortality) ranged from 0 to 100% and averaged 67% (Fig. 8). Although an increasing proportion of wood recruitment with increasing drainage area is anticipated because bank erosion rates typically increase downstream (Hooke 1980; Martin and Benda 2001), no such relationship was apparent in the data from our study (Fig. 8). Additional data over a larger geographic area may be needed to define the relationship between channel size and bank erosion. In addition, the rates of recruitment for mortality also do not show any apparent relationship to location in the basin (Fig. 8). However, landsliding recruitment is the highest in the smallest channels, indicating that landslide-prone inner gorges may preferentially be located in the steepest and narrowest channels (Fig. 8).

Knowledge of forest mortality rates is important to foresters and vegetation ecologists, and it is necessary for predicting wood recruitment using mathematical models (Beechie et al. 2000; Benda et al. 2002). We calculated large differences in mortality rates between the older and younger forest types. Conifer mortality in old-growth and second-growth forests averaged 0.04 and 0.9%·year⁻¹, respectively, a difference factor of 22. A similar disparity exists in deciduous forests where the average mortality between older and younger forests was 0.02 and 0.6%·year⁻¹, respectively, a difference factor of 30. If we compare the mortality estimate using the higher biomass volumes in old-growth forests in the literature (yielding a mortality rate of 0.012%·year⁻¹), the total difference in the total mortality rate between forest types is between one and two orders of magnitude.

There is little data available on forest mortality rates in either second-growth or old-growth forests in northern California from which to compare our estimated values. Viers (1975) reported a replacement rate for coastal redwoods of 2 or 3 trees/ha every 50 years. If we assume that a replacement

Table 5. Physical characteristics of soil creep sites.

Site	Geologic unit	Landslide unit	Drainage area (km²)	Channel Slope (%)	Channel width (m)	Substrate	Channel type	Colluvium texture	Right bank hillslope (%)	Left bank hillslope (%)	Weighted mean age (years)	Soil creep rate (cm·year⁻¹)
22	Wildcat		0.74	18	4.0	Boulder–gravel–fines	Step pool	Soil–coarse	48	28	7.1	17.9
23	Yager	Inactive	0.37	35	1.8	Fines and gravel	Step pool	Soil	37	37	8.3	14.9
24	Yager	Relict	0.47	10	2.7	Fines	Step pool	Soil	33	27	21.0	11.2
25	Yager		0.57	15	3.0	Cobble	Step pool	Coarse	64	49	16.0	4.3
26	Wildcat	Relict	0.79	14	3.7	Boulder–cobble–sand	Step pool	Coarse	64	26	21.6	2.4
27	Wildcat	Inactive	0.29	15	1.5	Gravel–sand	Step pool	Soil–coarse	18	33	26.4	1.7

rate is equivalent to a mortality rate, and if we assume 320 trees/ha, this would yield a mortality rate of 0.013 to 0.019%·year^{-1}. Using another estimate of 180 redwood trees/ha (Hallin 1934), the mortality rate would be 0.02 to 0.03%·year^{-1}. These values are similar to our estimate of 0.04%·year^{-1} using eq. 6 and even closer to our estimates using the higher forest biomass values in the literature (i.e., a mortality rate of 0.012%·year^{-1}).

There may be several reasons for a disparity in forest mortality between old-growth and second-growth forests. First, redwood trees are resistant to disease and insects and are remarkably long lived; redwood trees of 500–1000 years old are not uncommon (Noss 1999). Fires are the most significant stand-replacing disturbance, but the thick bark of redwoods in conjunction with generally cool and moist macro- and micro-climates, limit redwood tree death by fire (Abbott 1987). Under these conditions, it would be anticipated that forest mortality rates would be less than in northern coniferous forests, such as in Washington, where mortality in mature Douglas-fir forests is approximately 0.5%·year^{-1} (Franklin 1979). Second, mortality rates may be high in second-growth forests because of density-dependent mortality (i.e., senescence of closely spaced and younger trees). Death of deciduous trees also accounted for approximately 40% of the total forest mortality rate in second-growth sites. In contrast, deciduous mortality was very low in the old-growth forests. Tightly stocked second-growth conifer forests may also be more prone to insects, disease, and blowdown. Low mortality rates in older redwood forests would cause other recruitment processes, such as bank erosion and streamside landsliding, to become proportionally more important compared with forests with higher mortality rates in more northern portions of the coastal ecoregion.

Mortality rates estimated in other parts of the Pacific coastal ecoregion range from 0.5%·year^{-1} in Oregon and Washington Douglas fir forests (Franklin 1979) to 1.2%·year^{-1} (range 0.1–2.6%·year^{-1}) in mature forests in southeastern Alaska (Martin and Benda 2001); the latter rate was estimated using eq. 6. From the sparse data, there appears to be a latitudinal control on forest death rates that correspond to tree size. Mortality is highest in areas of the smallest trees in southeastern Alaska. Mortality is intermediate in the midsize Douglas-fir forests in Washington and Oregon, and it is the least in the largest trees in the northern California redwoods. The range of variation spans three orders of magnitude.

Bank erosion is an important process, and it is a key component of wood and sediment budgets. Bank erosion, however, is often a difficult parameter to quantity because of the paucity of long-term field measurements, particularly in small streams. We have used the wood budgeting technology to estimate this form of erosion. The calculated bank erosion rates (over an average 10-year period; Fig. 10) were relatively high in the study segments that were located in second-growth forests in the Van Duzen watershed (mean 0.22 and 0.11 m·year^{-1}, respectively, for one and both sides of the channel). The apparent high rates of bank erosion appear to be the result of channel meandering and migration against erosion-prone colluvium and alluvium that borders the channels and the occurrence of large floods. Three of the 10 largest floods on record in the Van Duzen watershed oc-

curred between 1993 and 1998, with the 1995 flood being the second largest on record (U.S. EPA 1999). The Van Duzen watershed also contains areas of significant active and dormant deep-seated landslides and earthflows (Kelsey 1980), landforms that may contribute to high bank erosion rates. An additional factor may be the large volumes of logging-related debris in second-growth channels that could result in increased flow divergence during floods and consequently heightened bank erosion, although the magnitude of the effect, if it occurs, is unknown.

Estimated bank erosion rates in the old-growth sites were much lower and averaged 0.027 and 0.014 m·year^{-1}, respectively, for one and both sides of the channel. The lower rates of bank erosion in the old-growth sites appear to be related to the composition of the banks that were predominantly bedrock that should be resistant to high rates of bank erosion. Moreover, the larger rooting systems of old-growth trees may be more resistant to undercutting compared with smaller deciduous and coniferous trees.

The soil creep rates we estimated using eq. 7 in small, headwater streams varied over the time interval in which wood entered the channel by bank erosion (Table 5). The highest rates of soil creep were associated, in general, with the shortest weighted mean ages. Presumably, over short time periods, the stochastic nature of floods will yield soil creep rates that are much higher than the long-term mean. High rates of bank erosion may have occurred during the last decade, a period that contained 3 of the 10 largest storms on record in northern California (U.S. EPA 1999). Hence, soil creep rates associated with the longest weighted mean ages likely represent our best estimate of the long-term average value, namely 2.4 to 1.7 cm·year^{-1}, reflecting weighted mean ages of 22 and 26 years, respectively. Relatively high soil creep rates appear to be consistent with reported high erosion rates in northwestern California (Kelsey 1980; Nolan and Janda 1995). Our measured rates may also reflect the legacy of channel disturbances associated with historical logging.

Potential errors and limitations

There are several potential sources of errors that can affect our estimates of wood recruitment and mortality and bank erosion rates. Recruitment rate is governed by our estimates of mean weighted ages and the storage volume of recruited wood. Because there is a lag time between the time of wood recruitment and establishment of saplings and because near stream vegetation is vulnerable to removal by stream flow, the age of saplings may underestimate the true age of recruited trees. This error would cause an overestimation of wood recruitment rate, an error that may increase with increasing channel size because of the increased potential of flow disturbances in larger channels. This error could also lead to overestimates of forest mortality and bank erosion. The absolute magnitude of these errors is uncertain given our small data set. Independent checks would involve comparing our calculated mortality and bank erosion rates to other estimates of these parameters in the literature. The method of calculating mean age of recruited wood (eq. 5), however, will tend to compensate for this potential error, since it provides greater weight to older trees.

Potential errors associated with calculating mortality rates include defining standing biomass and detailed stand surveys may be required. In addition, mortality rates should be sensitive to forest age and other stochastic factors, including insects, disease, and windstorms. Contrasting mortality rates between forest types or ages within or across regions should consider these factors. Undoubtedly, additional field data are needed to develop confidence in our estimates of wood recruitment in northern California. Moreover, additional studies are needed to evaluate how temporal variability in process rates can affect field measurements obtained over relatively short time periods.

Care should be taken when extrapolating our results to other basins in northern California or to other regions. Rates of forest mortality are dependent on stages of stand development, stocking, climate, and topography and should have strong controls on wood recruitment over decades to centuries (Benda et al. 2002). In addition, bank erosion and soil creep vary with climate, topography, lithology, and channel size. In other watersheds, landsliding may be more, or less, important than what we found depending on topography and the connectivity between hillslopes and channels. In addition, the stand-mean fraction that becomes in-channel woody (i.e., the parameter P in eqs. 3 and 4) may vary in streams that are bounded by steep hillslopes. Preliminary field data from the Sierra Mountains in northern California suggest that the theoretical values of P are similar to field conditions in conifer forests but that they underestimate the field values obtained in deciduous forests (P. Bigelow, Earth Systems Institute, unpublished data).

Acknowledgements

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