Riparian tree fall directionality and modeling large wood recruitment to streams

Daniel J. Sobota, Stanley V. Gregory, and John Van Sickle

Abstract: Directionality of tree fall in riparian forests can strongly influence predictions of large wood recruitment to streams, yet accuracy of this model parameter has rarely been assessed with field data. We measured fall directions of 1202 riparian trees distributed among 21 stream sites across the Pacific Northwest, USA. Fall directions were oriented towards the stream at 16 sites, upstream at four sites, and not distinguishable from random at one site. Average tree fall direction across sites was correlated with valley constraint (Spearman \( r = -0.53; p = 0.02 \)), but variability of fall directions was not correlated with this variable. When grouped by species (six conifers and one deciduous), individual trees exhibited stronger tendency to have fallen towards the channel on steep hillslopes (>40%) than on moderately sloped landforms (<40%). Integration of field data into an established recruitment model indicated that 1.5 to 2.4 times more large wood (by number of tree boles) would be recruited to stream reaches with steep hillslopes than to reaches with moderate side slopes or flat banks, if riparian forest conditions are assumed to be constant. We conclude that stream valley topography should be considered in models that use tree fall directions in predictions of large wood recruitment to streams.

Résumé : L’orientation de la chute des arbres dans les forêts ripariennes peut grandement influencer les prédictions concernant le recrutement des grosses pièces de bois dans les cours d’eau. Cependant, l’exactitude de ce paramètre a rarement été évaluée avec des données prises sur le terrain. Nous avons mesuré l’orientation de la chute de 1202 arbres ripariens distribués parmi 21 stations situées près de cours d’eau dans la région nord-ouest du Pacifique, aux États-Unis. Des arbres étaient tombés vers le cours d’eau dans 16 stations, vers l’amont du cours d’eau dans quatre stations et au hasard dans une station. En moyenne dans l’ensemble des stations, l’orientation de la chute des arbres était corrélée avec les contraintes de la vallée (Spearman \( r = -0.53; p = 0.02 \)) mais les variations dans l’orientation de la chute n’étaient pas corrélées avec cette variable. Regroupés par espèce (six conifères et un feuille), les arbres avaient plus tendance à tomber vers le chenal sur les pentes abruptes (>40 %) que sur les formes de relief avec des pentes modérées (<40 %). L’intégration des données de terrain dans un modèle reconnu de recrutement indiquait que 1,5 à 2,4 fois plus de grosses pièces de bois (par le nombre de troncs d’arbre) seraient recrutées dans les tonçons de cours d’eau bordés par des pentes abruptes que dans les tonçons bordés par des pentes modérées ou des berges plates, en assumant que les conditions des forêts ripariennes demeurent constantes. Nous concluons que la topographie des vallées où coule un cours d’eau devrait être considérée dans les modèles qui utilisent l’orientation de la chute des arbres pour prédire le recrutement des grosses pièces de bois dans les cours d’eau.

[Traduit par la Rédaction]

Introduction

Exchange of materials between riparian zones and adjacent stream ecosystems often produces complex physical, chemical, and biological properties in each system (Gregory et al. 1991; Naiman et al. 2000). Input of terrestrial vegetation litter to streams has been recognized as a particularly important exchange process that influences the distribution and timing of ecological processes in both aquatic and terrestrial ecosystems (Vannote et al. 1980; Webster et al. 1999; Johnson et al. 2000). Wood is a conspicuous component of allochthonous organic matter input to streams in forested landscapes, often accounting for over 50% of organic matter in these systems (Anderson et al. 1978; Allan 1995). A 30-year literature record of field surveys, field and laboratory experiments, and modeling studies has demonstrated that input of wood to streams, especially recruitment of large pieces in the form of tree boles, limbs, and rootwads, strongly influences physical complexity of streams and riparian zones (e.g., Bisson et al. 1987), channel retention of organic matter and nutrients (e.g., Bilby and Likens 1980), and succession dynamics of riparian forests (e.g., Johnson et al. 2000).
Recruitment of large pieces of wood to streams is a dynamic process consisting of episodic disturbances, chronic riparian forest mortality, and stream erosion processes (Lienkaemper and Swanson 1987; Benda et al. 2003). The importance of these processes to overall large wood recruitment dynamics varies according to a myriad of factors, including stream size, riparian forest structure and productivity, and landscape disturbance regime (Robison and Beschta 1990; Welty et al. 2002; Benda et al. 2003). Recruitment in some systems may be strongly influenced by catastrophic disturbances (Bragg 2000; Benda et al. 2003). Recruitment rate to a stream in the Intermountain West of North America was simulated to be four (spruce beetle outbreak) and five (catastrophic fire) times greater for a 30-year period following disturbance than loading from chronic mortality processes over the same period (Bragg 2000). On the other hand, large wood recruitment in some systems generally reflects chronic mortality associated with frequent small-scale disturbances, riparian forest succession, and stream channel erosion (Murphy and Koski 1989; Meleason et al. 2003). In old-growth forests of southeast Alaska, an average of 69% of large wood in streams could be attributed to bank erosion, windthrow, or forest mortality (Murphy and Koski 1989). Only 4% was attributed to landslides; the origin of the remaining 27% was not identified.

Empirical models are powerful tools for quantitative analysis of patterns, processes, and mechanisms of large wood recruitment to streams. These models allow assessments and virtual experiments that otherwise would not be possible given the large spatial and temporal scales of recruitment dynamics (Meleason 2001). Gregory et al. (2003) presented a synopsis of 14 models that have been developed for large wood recruitment to streams. Most of these models (13 of 14) are mechanistic and describe explicit relationships among riparian forest productivity, tree mortality, and channel entry mechanisms. As with any model of a real system, comparisons with empirical data are needed to validate accuracy of individual wood models and provide estimates of uncertainty associated with modeled processes (Gregory et al. 2003). It usually is not feasible to collect long-term and large-scale data on processes and mechanisms of large wood recruitment. Instead, validations typically are performed from field surveys of patterns associated with riparian forest production and structure, size structure of large wood pieces, and spatial distribution of large wood in channels and riparian zones (Van Sickle and Gregory 1990; Bragg et al. 2000; Welty et al. 2002). However, few field data comparisons have been made for several important parameters common to many recruitment models (Gregory et al. 2003).

Direction of tree fall is an important parameter of many large wood recruitment models that lacks substantial validation with field data. Of models surveyed by Gregory et al. (2003), only one (Murphy and Koski 1989) does not consider tree fall direction in simulation of recruitment. Yet only two make direct comparisons with published field data on tree fall directions (Van Sickle and Gregory 1990; Bragg et al. 2000). Van Sickle and Gregory (1990) concluded that the position of unmoved large wood pieces in an old-growth forested stream in the central Oregon Cascades was not distinguishable from random fall directions around a circle. In contrast, Bragg et al. (2000) surveyed fallen trees along 13 streams in northwestern Wyoming and found that fall directions exhibited a trimodal distribution, with trees tending to fall upstream, downstream, or directly towards the stream to a greater degree than would be expected from random fall. While these field data provide important information needed to accurately assess recruitment in these particular systems, they are limited in scope because only one stream or small geographic area was surveyed. Others have speculated that riparian trees in general may have a strong tendency to fall directly toward streams (Lienkamper and Swanson 1987; Robison and Beschta 1990; Hairston-Strang and Adams 1998; Welty et al. 2002) or reflect pathways of dominant storm winds (Steinblums et al. 1984; Andrus and Froelich 1992; Ott 1997). If trees are modeled to fall directly towards the stream with little or no variation, three times more large wood pieces (number of intact tree boles) are expected to enter the stream channel as compared with random tree fall directions (Van Sickle and Gregory 1990). Thus, comparisons with field data are critical tests on accuracy and uncertainty of using directional riparian tree fall in large wood recruitment modeling.

In this study, we collected field data on riparian tree fall directions along streams from a diverse array of forest types and topographic conditions in the Pacific Northwest, USA. Our objectives were to evaluate patterns of riparian tree fall directions in diverse environmental conditions and evaluate correlations with tree characteristics, forest structural variables, and topographic features. We were specifically interested in correlations between fall directionality and tree species type, tree size, riparian forest structure, and valley topography (side slope). To conduct these analyses, we employ statistical techniques developed for circular data, which are appropriate for this type of field data but had not been used in previous studies. We conclude by incorporating field data into an established model of large wood recruitment (Van Sickle and Gregory 1990) and discuss implications for future modeling studies.

Site descriptions

Twenty-one field sites in the Pacific Northwest of North America were surveyed during September–November 2000 (five sites), July–August 2001 (15 sites), and June 2002 (one site). Streams were located west of the Cascades Mountains crest (11 sites; Coast Range and west slopes of the Cascades) and in the interior Columbia Basin (10 sites; east slopes of the Cascades, Blue Mountains, and Northern Rockies) of Oregon, Washington, Idaho, and Montana, USA. (Fig. 1). Specific streams were chosen nonrandomly but without bias from lands managed by private timber companies and the US Forest Service. Streams were second- to fourth-order channels (Strahler 1957) and had riparian forests that were approximately 40 to >200 years old. Locations of specific study reaches (200–300 m stream length) on each stream were selected randomly.

Estimated riparian forest ages were identified from discussions with land managers and stand age maps for the sites. Exact stand ages were not known because tree cores were not collected. Sites in western Oregon and Washington were in the western hemlock (Tsuga heterophylla (Raf.) Sarg.) forest zone (Franklin and Dyrness 1973) and dominated in
basal area by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Douglas-fir, ponderosa pine (*Pinus ponderosa* Doug. ex P. & C. Laws.), and white alder (*Alnus rhombifolia* Nutt.) were the major canopy species at two sites on the east slopes of the Cascade Mountains in Washington. Lodgepole pine (*Pinus contorta* Dougl. ex Loud.), western larch (*Larix occidentalis* Nutt.), and grand fir (*Abies grandis* (Dougl.) Lindl.) constituted riparian forests at study sites in northeastern Oregon, central Idaho, and northwestern Montana. The presence of old logging slash at sites with 40- to 60-year-old forests indicated that these stands initiated or were planted following historical timber harvest (except Piper Creek, Montana, which regenerated following fire), while older stands regenerated after stand-clearing fires. All streams had similar riparian forest conditions on both stream banks, except Bloom Creek, Idaho, and Stillman Creek, Washington, where only one bank was completely forested.

**Methods**

Stand density (trees·ha⁻¹), basal area (m²·ha⁻¹), and dominant tree species by basal area at each site were characterized with the point-center quarter method (Cottam and Curtis 1956). Two to four 50 m transects (perpendicular to the active channel) were randomly selected per site. Each transect was divided into 10 m segments for a total of five estimates of tree density and basal area per transect. The minimum tree size measured in these transects was 0.1 m diameter at breast height (DBH; 1.37 m tall on the uphill side of the tree).

Active channel width and valley floor width were measured at every 20 m stream length interval within each site. The active channel was defined as the area of the stream channel with exposed rock substrates and annual vegetation (Gregory et al. 1991). Total valley floor width was considered to be the perpendicular distance between slope breaks on both sides of the channel where the hillslope or nonfluvial landform began (i.e., glacial terraces for several sites in Montana). Valley constraint was defined as average valley floor width divided by average active channel width (Gregory et al. 1991).

Minimum size criteria for a fallen tree in this study were DBH of 0.1 m and height of 5 m. The minimum DBH followed a definition for diameter of large wood in a long-term data set in our research group (S.V. Gregory, unpublished data, H.J. Andrews Experimental Forest). The 5 m length represented approximately half the width of the active channel at most sites. We measured all fallen trees that met these criteria at each study site up to 50 m slope distance away from the stream channel until the entire site was surveyed or we had measured 100 fallen trees. We sampled approximately equal numbers of trees from both sides of the channel, except at the two sites where only one bank was forested.

For each fallen tree, we measured azimuth of tree fall direction, species, DBH, and valley side slope (%; 100% slope = 45°; refers to bank slope perpendicular to the channel) at the base of the tree. Species type was determined by bark morphology and branch structure (Harlow and Harrar 1968); for trees in which branches and bark were not present, we recorded the species as unknown. For comparison among sites, we standardized all measurements of tree fall to the stream valley axis and by streamside location (upstream = 0° and 360°; toward stream = 90°; downstream = 180°; away from stream = -90° and 270°; upstream and away from stream definitions contained two equivalent values for fall direction for data display purposes and this did not influence statistical analyses).

Average direction of tree fall, standard deviation (SD) of tree fall directions, and a 95% confidence interval (CI) for mean fall direction were calculated for each study site with statistical methods for angular data (Fisher 1993). Approxima-
mate 95% CIs for the mean tree fall direction for each site were estimated at locations where >25 trees were recorded (Fisher 1993). At sites where <25 trees were found, 95% CIs for the mean fall direction at each site were constructed using bootstrap techniques (Fisher 1993). For all sites, the 95% CI for mean fall direction at a site was referred to as “undefined” if the 95% confidence width was >360° (full range of possible tree fall directions).

Stream valley physical characteristics and riparian forest characteristics were compared with site-level statistics of tree fall directions using Spearman rank correlation coefficients. Average direction and SD of tree fall directions by site were each correlated with valley constraint, mean valley side slope, mean active channel width, mean tree density, and mean basal area of the riparian forest (21 sites). Significant correlations were indicated by $P < 0.05$. Analyses were performed in Sigma Stat version 2.03.

Following site-level analyses, trees were pooled among sites and classified by tree species for further analyses of species, tree size, and valley side slope effects. We excluded individual trees from this analysis if the species was not identified or a tree was a species that represented <5% of the overall number of fallen trees in the entire study. Average fall direction and SD of fall directions were calculated for trees (regardless of species) grouped in 10%-interval valley side slope classes beginning with a 0%–10% class and ending with a >90% class. Within each species, we looked for differences in tree size according to side slope by determining whether the 95% CIs of DBH (natural log transformed to reduce positive skew) for each side slope category overlapped with one another (nonoverlapping 95% CIs indicated a significant difference at the $P = 0.05$ level). We also assessed the number of sites represented within each species and side slope category to assess possible site-based effects in results.

Large wood recruitment model

Choosing an appropriate representation of the channel entry process is a critical aspect of modeling large wood recruitment to streams (Van Sickle and Gregory 1990; Meleason 2001). Based on our field data, we used a probabilistic model of tree fall (Van Sickle and Gregory 1990) to investigate effects of fall directionality on predictions of large wood recruitment to streams from chronic mortality in riparian forests.

The probability that a falling tree will contact a stream ($P_s$) is a function of tree height ($h$), distance to the channel ($z$), and a probability density function for fall angle $a$ ($f(a)$), expressed in degrees (Van Sickle and Gregory 1990). For random fall directions, $f(a)$ has a uniform distribution (McCcad et al. 1990), and the $P_s$ of a tree of a given height ($h$) and distance to the channel ($z$) is

$$P_s = (\cos^{-1} z/h)180$$

For our model simulations, we approximated a normal probability density function to represent field data as probability of tree fall into a stream. Tree fall directions cannot be exactly rescaled to a standard normal curve because data are angular (Fisher 1993). However, a reasonable approximation of $P_s$ can be obtained with the following equation (modified from Fisher 1993):

$$P_s = P\left(\frac{a_s - \bar{a}}{\sigma} < X < \frac{(180 - a_s) - \bar{a}}{\sigma}\right)$$

where $\bar{a}$ and $\sigma$ are the sample mean and SD of fall direction, respectively, $X$ is a random variable from the standard normal distribution, and $a_s$ to $180 - a_s$ is the circular arc in which a tree has the capacity to directly fall into a stream ($a_s = \sin^{-1}(z/h)$) (Van Sickle and Gregory 1990).

Given $P_s$ for a slope distance $y$, the expected number and variance of falling trees intersecting the channel ($N$) per unit stream length over a specified time period that originated within the bounds of 0 to $z$ distance upslope follow the binomial distribution:

$$E[N(z)] = DL P_{T} \int_{0}^{z} P_s(y)dy$$

where $D$ is the riparian stand density for one tree height class (e.g., trees·ha$^{-1}$), $L$ is stream reach length (m), and $P_T$ is the probability of tree fall (Van Sickle and Gregory 1990). If the independence of variables is assumed, eq. 3 applies for any distance $y$ between $z = 0$ and $z = h$.

Using eq. 3, we compared influence of $P_s$ on large wood recruitment among different tree fall directionality scenarios. As end members, we chose random tree fall directionality to represent the minimum capacity of a riparian forest to contribute large wood to the stream and direct tree fall towards the channel to represent the maximum capacity. We also evaluated specific cases of tree fall directionality observed in our field data. For simplicity, we assumed that tree height, forest density, stream reach length, probability of tree fall, and time scale were similar for all cases. For random fall directions, eq. 1 was used to calculate $P_s$ in eq. 3. For tree fall completely towards the channel, $P_s$ was set to 1.0 for all distances upslope to reflect a 100% likelihood that some piece of a tree would fall into the stream between $z = 0$ and $z = h$. In scenarios based on field data, empirical observations were used to represent $\bar{a}$ and $\sigma$ in eq. 3. Because tree, forest, and scaling variables were held constant in all scenarios, differences in area under $P_s$ curves over the distance range of 0 to $h$ are equivalent to relative differences, by numbers of tree boles, in large wood recruitment among different scenarios (Van Sickle and Gregory 1990).

We also calculated cumulative percentage of large wood recruitment between the stream bank and a slope with a distance equal to tree height as a proportion of the maximum capacity for wood recruitment from the adjacent riparian forest. We assumed that the maximum capacity for large wood recruitment was equivalent to the scenario in which trees completely fall towards the channel ($P_s = 1.0$). We divided cumulative recruitment for each scenario (random fall, two scenarios based on field data, and fall completely towards the channel) by the maximum capacity at intervals of $h/1000$, beginning at 0 and ending at $h$. These curves reflect cumulative wood inputs relative to the maximum wood recruitment capacity for the riparian forest over the slope distance 0 to $h$. Because these curves have been transformed to the same scale, differences in area among curves for a given
slope distance reflect the proportional difference in large wood recruitment between the stream bank and the slope distance.

Results

Topographic and forest characteristics at study sites encompassed a wide range of conditions (Table 1). Active channels ranged from 3.3 to 13.0 m wide (average) and valley constraint ranged from 1.2 to 25.7 (Table 1). Forests at 19 of 21 sites were dominated in basal area by conifer tree species; two sites west of the Cascades crest were dominated by red alder (Alnus rubra Bong.) (Table 1). The dominant species at the other nine sites west of the Cascades crest was Douglas-fir. East of the Cascades crest, Douglas-fir (two sites), western redcedar (four sites), lodgepole pine (two sites), western hemlock (one site), and grand fir (one site) dominated basal area at study sites (Table 1). Forest density ranged from 185 to 1751 stems-ha$^{-1}$, and basal area ranged from 20 to 155 m$^2$-ha$^{-1}$ (Table 2).

A total of 1202 fallen trees were surveyed at the 21 sites in this study. Between 30 and 100 fallen trees were measured at 19 of the sites; only 10 and 16 trees were found at two sites in northeast Oregon (Table 2). Average fall direction at each site ranged from 7° to 128°, with SD ranging from 36° to 80° (Table 2). Sixteen sites had a 95% CI for mean tree fall direction that included or was within 8° of directly towards the stream, four had a 95% CI that included 0° (directly upstream), and one site had a 95% CI that was “undefined”, which is consistent with random fall directions (Table 2).

Average direction of tree fall by site was significantly correlated with valley constraint (Spearman $r = -0.53; P = 0.02$) (Fig. 3A). This indicated that trees in the most-constrained stream reaches had a central tendency to fall towards the channel, whereas mean tree fall direction in more unconstrained reaches was not consistently oriented towards the channel and also tended to be oriented more upstream (Fig. 2A). Average direction of tree fall by site was weakly correlated with active channel width, tree stem density, and basal area ($P > 0.05$), with Spearman $r$ coefficients of 0.22, –0.21, and 0.39, respectively. The standard deviation of tree fall directions at individual sites was not strongly correlated with valley constraint (Fig. 2B), active channel width, tree density, or forest basal area (for all variables, Spearman $r < 0.21; P > 0.35$).

For analysis of tree fall directions pooled among sites, 139 trees were removed from the total number of fallen trees surveyed (adjusted $N = 1063$). The seven species included in this analysis were Douglas-fir, western redcedar, red alder, Engelmann spruce (Picea engelmannii Parry ex Engelm.), western hemlock, lodgepole pine, and western larch (Table 3). We further distinguished Douglas-fir by whether a tree occurred west (coastal form) or east (interior form) of the Cascades crest because growth forms and physiology differ between these subspecies (Harlow and Harrar 1968).

In the initial analysis, statistics describing tree fall directionality were calculated for 10%-interval side slope classes. However, we observed that SDs of fall directions for trees located on valley side slopes in the 0%–10%, 10%–20%, 20%–30%, and 30%–40% classes ($n = 4$ classes) were 25° to 43° larger (95% CI) than that of trees in side slope classes >40% ($n = 6$ classes) (Fig. 3). Because the original analysis of fall directionality by species according to 10% side slope classes would have resulted in small sample sizes (<10 trees) for many of the species when grouped by side slope classes, we modified our method by grouping trees by species within two side slope categories, slopes <40% or slopes >40%, to increase our confidence of fall directionality estimates. For each species – side slope class, mean fall direction, SD of fall directions, and a 95% CI for mean fall direction were calculated.

Within each species, fall directions differed between trees on valley side slopes <40% and trees on slopes >40% (Table 3). Trees on valley side slopes >40% for each species had a 95% CI that only included falls directly towards the stream channel (Table 3); trees on side slopes <40% had a 95% CI for mean fall direction that included directly upstream, downstream, away from the stream, towards the stream, or all four directions simultaneously (consistent with random fall directions), depending on species (Table 3). Within each species, SD of tree fall directions was 1.4 to 1.9 times larger (95% CI) on side slopes >40% than on side slopes >40%. Among the eight species groups, SD of fall directions averaged 68° ± 3° (standard error) for side slopes >40%, while SD averaged 42° ± 2° on side slopes <40%.

The 95% CIs of tree DBH overlapped between the two different side slope categories (<40% or >40%) for six of the eight species (Table 3), indicating that tree size was not significantly different between side slope categories for these species at the $P = 0.05$ level. The exceptions were the coastal form of Douglas-fir and red alder (Table 3). For coastal Douglas-fir, trees on side slopes >40% had a median DBH 1.2 to 1.9 times greater (95% CI) than that of trees on side slopes <40% (Table 3). For red alder, trees on side slopes >40% had a median DBH 1.1 to 1.6 times greater (95% CI) than that of trees on side slopes <40% (Table 3). Seven of the nine species (subspecies) used in this analysis were found at five or more sites (numbers per site not presented); only western larch and lodgepole pine were found at three or fewer sites (Table 3).

Model results

In addition to random fall and directional fall, relative differences in large wood recruitment based on tree fall directionality observed at two resolutions were estimated. The first resolution was based on site-level differences in valley constraint. Of the 21 sites, 10 sites were located in valleys with constraint <2.5. We thus chose to evaluate relative differences in large wood recruitment based on observed tree fall directionality between two constraint categories: <2.5 and ≥2.5. Sites in each constraint category were almost evenly split among geographic regions (6 of the 10 sites with constraints <2.5 and 6 of the 11 sites with constraint ≥2.5 were west of the Cascades). For each valley constraint category, values for $\mu$ and $\sigma$ in eq. 3 were set according to observations. Average fall direction ($\bar{\mu}$) for valley constraints <2.5 was 95° (95% CI = 74°–115°), while $\bar{\mu}$ = 69° (95% CI = 46°–92°) for constraints ≥2.5. Standard deviations of fall directions were similar among the two categories, with SD ($\bar{\sigma}$) = 54° (95% CI = 48°–60°) for sites with
Table 1. Physical and forest characteristics of study sites in the Pacific Northwest, USA.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Site code*</th>
<th>Active channel width (m)</th>
<th>Valley constraint†</th>
<th>Estimated forest age (years)</th>
<th>Density (trees·ha(^{-1}))</th>
<th>Basal area (m(^2)·ha(^{-1}))‡</th>
<th>Hardwood basal area (%)</th>
<th>Basal area dominant species</th>
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<tr>
<td><strong>Interior Columbia Basin</strong></td>
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<td></td>
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<td>N.F. Cabin Creek, Ore.</td>
<td>ICB1</td>
<td>4.1</td>
<td>25.7</td>
<td>40</td>
<td>624</td>
<td>89</td>
<td>16</td>
<td>Grand fir</td>
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<td>ICB2</td>
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<td>15.1</td>
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<td>450</td>
<td>48</td>
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<td>ICB3</td>
<td>9.3</td>
<td>2.5</td>
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<td>960</td>
<td>97</td>
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<td>11.3</td>
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<td>623</td>
<td>47</td>
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<td>13.0</td>
<td>2.0</td>
<td>150</td>
<td>444</td>
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<td>6</td>
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<td>2.1</td>
<td>150</td>
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<td>125</td>
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<td>2.2</td>
<td>200</td>
<td>1313</td>
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<td>&gt;200</td>
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<td>1162</td>
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<td><strong>West of Cascades Crest</strong></td>
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<td>Sturdy Creek, Ore.</td>
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<td>11.8</td>
<td>2.3</td>
<td>40</td>
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<td>Forks Creek, Wash.</td>
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<td>51</td>
<td>Red alder</td>
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<td>11.4</td>
<td>1.9</td>
<td>50</td>
<td>346</td>
<td>20</td>
<td>15</td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>Green Canyon Creek, Wash.</td>
<td>WCC4</td>
<td>8.7</td>
<td>3.4</td>
<td>60</td>
<td>919</td>
<td>41</td>
<td>10</td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>Stillman Creek, Wash.</td>
<td>WCC5</td>
<td>4.4</td>
<td>3.5</td>
<td>60</td>
<td>498</td>
<td>155</td>
<td>29</td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>Crim Creek, Wash.</td>
<td>WCC6</td>
<td>10.5</td>
<td>1.2</td>
<td>80</td>
<td>193</td>
<td>78</td>
<td>74</td>
<td>Red alder</td>
</tr>
<tr>
<td>Hagan Creek, Ore.</td>
<td>WCC7</td>
<td>11.3</td>
<td>3.3</td>
<td>110</td>
<td>202</td>
<td>75</td>
<td>11</td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>McCain Creek, Wash.</td>
<td>WCC8</td>
<td>10.6</td>
<td>6.9</td>
<td>120</td>
<td>447</td>
<td>42</td>
<td>29</td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>Flynn Creek, Ore.</td>
<td>WCC9</td>
<td>11.9</td>
<td>2.4</td>
<td>170</td>
<td>185</td>
<td>35</td>
<td>37</td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>Cedar Creek, Ore.</td>
<td>WCC10</td>
<td>11.6</td>
<td>1.3</td>
<td>500</td>
<td>570</td>
<td>38</td>
<td>3</td>
<td>Douglas-fir</td>
</tr>
<tr>
<td>Mack Creek, Ore.</td>
<td>WCC11</td>
<td>9.2</td>
<td>2.5</td>
<td>500</td>
<td>199</td>
<td>54</td>
<td>1</td>
<td>Douglas-fir</td>
</tr>
</tbody>
</table>

*Refers to Fig. 1.
†Valley floor width divided by Active channel width.
‡ Only trees >0.1 m diameter at breast height (DBH) measured
constraints $< 2.5$, and $\bar{\theta} = 56^\circ$ (95% CI = 48°–64°) for sites with constraints $\geq 2.5$.

The second resolution was based on differences in fall directionality observed for individual trees in the two valley side slope categories (moderate side slopes (<40%) and steep side slopes (>40%)). We set average fall direction ($\bar{\theta}$) to 90° in eq. 3 in both side slope categories to reflect the central tendency in field data for tree falls to have fallen towards the stream regardless of side slope (Table 3). However, to reflect differences in variability of tree fall according to valley side slope found in our data, we set $\sigma$ to 75° in eq. 6 for wood recruitment from steep side slopes, while $\sigma$ was set to 41° in the scenario with moderate side slopes (Table 3).

Recruitment based on random tree fall directions produced the least amount of large wood among the six model scenarios (Figs. 4A and 5A). Direct fall towards the channel produced three times more large wood (number of boles) than from random fall directions, while 1.8 times more wood was expected to be recruited from moderate side slopes (<40%) than from random fall directions (Fig. 5A). On the other hand, 76% and 57% of the amount of large wood recruited from direct fall towards the channel would be expected to be recruited from side slopes <40% and side slopes >40%, respectively. Also, 1.5 times more wood by number of tree boles was expected to be recruited to a stream reach with uniform steep side slopes on both banks versus a reach with uniform moderate side slopes.

The cumulative percent curves indicated a spatial dimension of large wood recruitment based on tree fall directionality in riparian forests (Figs. 4B and 5B). For example, our model predicts that the forest within a distance of 0.5 tree height upslope of the stream will contribute 50% of the potential input of the entire stand, if all riparian trees fall directly toward the channel (solid line, Figs. 4B and 5B). This would be reduced to 21% for random fall (dotted line, Figs. 4B and 5B). In contrast, this only would be reduced to 43% and 41% on stream reaches with constraints <2.5 and constraints $\geq 2.5$, respectively. In scenarios based on side slope, a forest within a distance of 0.5 tree height upslope of the stream would produce 47% of the maximum potential input on steep side slopes (>40%) and 35% on moderate side slopes (<40%). Differences among the cumulative recruitments of the six falling scenarios steadily increase with distance from the channel. For the full stand ($z = h$), riparian forests in valleys with constraints <2.5 are predicted to deliver 68% of the maximum stand potential, while valleys with con-
strains ≥2.5 would produce 64% (Fig. 5B). In comparison, steep side slopes are predicted to deliver 80% of the maximum potential, while forests on moderate side slopes and flat terrain (random fall) deliver 56% and 32%, respectively (Fig. 5B).

**Discussion**

Previous studies have suggested that prevailing storm winds provide sufficient information to accurately predict large wood recruitment to streams from riparian forests (e.g., Steinblums et al. 1984; Andrus and Froelich 1992; Ott 1997). While this approach may be appropriate in locations where pathways of storms are well known (e.g., coastal areas of the Pacific Northwest), many areas of concern to land managers are located in remote landscapes where complex topographic features create uncertainty in force and direction of damaging winds (Gratkowski 1956). Our data do not support the hypothesis that riparian tree fall directionality is directly related to wind direction. Tree fall directionality was similar on both sides of the stream channel at the majority of our sites (17 sites), which encompassed a broad geographic area and diverse environmental conditions. At the remaining four sites, tree fall directionality was oriented upstream, indicating that wind funneling up the valley may have been an important process in years preceding our surveys. We conclude that the complexity of wind in highly dissected landscapes make accurate model predictions of large wood recruitment based on wind direction in these areas unlikely in the near future. Instead, incorporating relationships between fall directionality and physical features of the riparian zone into process-based models should provide more accurate predictions of large wood recruitment to these systems.

The central overall tendency for directional tree fall towards the stream most likely is related to growth forms of riparian trees. Specifically, we believe that (1) undercutting of root mass by channel erosion processes, (2) light exposure to the natural canopy opening over a stream, and (3) soil movements on hillslopes all influence tree fall direction relative to the stream channel by shifting a tree’s center of gravity towards the stream. Bank undercutting displaces root mass towards the stream, resulting in the characteristic lean com-
monly observed in riparian trees on margins of the active channel (Lienkaemper and Swanson 1987). Trees also develop more branch mass toward canopy openings as a result of phototropic growth (Bustos-Letelier 1994). Additionally, landslides and soil creep on hillslopes result in downhill tree lean and pistol-butt growth forms (Fantucci 1999; Welty et al. 2002). Our observations of tree fall directions on steep side slopes (>40%) and constrained valley segments (constraint ≤2.5) are consistent with these hypothesized influences. However, there were exceptions to general towards-the-channel fall directionality for individual species on moderate side slopes (<40%) and at sites with relatively unconstrained valleys (constraint ≥2.5). These exceptions demonstrate the importance of complementing modeling studies with field data. While our results indicate that some degree of preferential tree fall towards the stream is an appropriate first approximation in recruitment modeling, performing periodic field surveys to validate this model parameter is critical to assess accuracy of model predictions.

Edaphic, topographic, and hydrologic characteristics of riparian zone landforms probably are related to the greater variability in tree fall directions on moderate valley side slopes than on steep side slopes. The categorization of tree fall directionality by side slope (bank slope perpendicular to

Table 3. Fall directions for trees pooled among sites in the Pacific Northwest, USA.

<table>
<thead>
<tr>
<th>Species</th>
<th>Valley slope (%)</th>
<th>n</th>
<th>No. of sites*</th>
<th>Geometric mean DBH (m)†</th>
<th>Fall direction (degrees)‡</th>
<th>Average (SD)</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Engelmann spruce</td>
<td>&lt;40</td>
<td>82</td>
<td>5</td>
<td>0.27 (0.24–0.31)</td>
<td>–52 (84)</td>
<td>Undefined</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>39</td>
<td>5</td>
<td>0.23 (0.19–0.27)</td>
<td>84 (51)</td>
<td>47 to 122</td>
<td></td>
</tr>
<tr>
<td>Douglas-fir (coastal)</td>
<td>&lt;40</td>
<td>116</td>
<td>11</td>
<td>0.29 (0.25–0.35)</td>
<td>76 (57)</td>
<td>26 to 126</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>139</td>
<td>11</td>
<td>0.44 (0.37–0.51)</td>
<td>84 (35)</td>
<td>63 to 104</td>
<td></td>
</tr>
<tr>
<td>Douglas-fir (interior)</td>
<td>&lt;40</td>
<td>30</td>
<td>4</td>
<td>0.25 (0.18–0.36)</td>
<td>9 (61)</td>
<td>–57 to 74</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>75</td>
<td>6</td>
<td>0.22 (0.19–0.24)</td>
<td>84 (36)</td>
<td>60 to 108</td>
<td></td>
</tr>
<tr>
<td>Lodgepole pine</td>
<td>&lt;40</td>
<td>27</td>
<td>2</td>
<td>0.22 (0.17–0.30)</td>
<td>70 (63)</td>
<td>1 to 141</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>37</td>
<td>2</td>
<td>0.17 (0.12–0.17)</td>
<td>54 (46)</td>
<td>18 to 90</td>
<td></td>
</tr>
<tr>
<td>Red alder</td>
<td>&lt;40</td>
<td>120</td>
<td>11</td>
<td>0.23 (0.20–0.26)</td>
<td>89 (75)</td>
<td>–59 to 236</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>58</td>
<td>10</td>
<td>0.31 (0.27–0.34)</td>
<td>82 (39)</td>
<td>60 to 102</td>
<td></td>
</tr>
<tr>
<td>Western hemlock</td>
<td>&lt;40</td>
<td>44</td>
<td>7</td>
<td>0.20 (0.17–0.24)</td>
<td>71 (64)</td>
<td>6 to 135</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>56</td>
<td>7</td>
<td>0.22 (0.19–0.25)</td>
<td>73 (47)</td>
<td>36 to 111</td>
<td></td>
</tr>
<tr>
<td>Western larch</td>
<td>&lt;40</td>
<td>30</td>
<td>3</td>
<td>0.46 (0.39–0.53)</td>
<td>–3 (62)</td>
<td>–70 to 65</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>26</td>
<td>3</td>
<td>0.44 (0.35–0.56)</td>
<td>58 (43)</td>
<td>26 to 90</td>
<td></td>
</tr>
<tr>
<td>Western redcedar</td>
<td>&lt;40</td>
<td>86</td>
<td>10</td>
<td>0.34 (0.29–0.40)</td>
<td>80 (79)</td>
<td>Undefined</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>98</td>
<td>11</td>
<td>0.37 (0.31–0.44)</td>
<td>77 (39)</td>
<td>51 to 104</td>
<td></td>
</tr>
<tr>
<td>All species</td>
<td>&lt;40</td>
<td>535</td>
<td>21</td>
<td>0.29 (0.27–0.31)</td>
<td>90 (76)</td>
<td>66 to 114</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;40</td>
<td>528</td>
<td>21</td>
<td>0.31 (0.28–0.33)</td>
<td>89 (41)</td>
<td>84 to 95</td>
<td></td>
</tr>
</tbody>
</table>

*95% confidence intervals in parentheses.
†Frequency of sites were species in each slope category occurred.
‡Upstream, 0° and 360°; toward stream, 90°; downstream, 180°; away from stream, –90° and 270°.
the channel) is more useful viewed in terms of different landforms represented in each class. The majority (63%) of riparian trees on moderate side slopes (<40%) were located on fluvial landforms (terraces, floodplains, and margins of active channels), while 91% of trees on steep side slopes (>40%) were located on hillslopes. Trees rooting next to streams typically grow in poorly drained soils with high water tables and, as a consequence, tend to have shallow, wide-spread root systems (Harlow and Harrar 1968; Lienkaemper and Swanson 1987). A 40% side slope is equivalent to an 18° side slope, which is a reasonable characterization of topographic conditions on margins of active channels, floodplains, and terraces observed in this study. Moderate side slope conditions may result in a lower force threshold for tree fall as compared with steep hillslopes (Alexander and Buell 1955; Gratkowski 1956; Swanson and Lienkaemper 1987; McDade et al. 1990). Trees on fluvial landforms also are exposed to a greater range of disturbance types than hillslope trees, with the possibility of major floods, bank failures, and other hydrologic and meteorological disturbances (Lienkaemper and Swanson 1987; Gregory et al. 1991). We propose that the diversity of tree fall mechanisms on fluvial landforms resulted in greater variability of fall directions on moderate side slopes (<40%). While tree fall mechanisms also can be diverse on steeper hillslopes, tree growth form appeared to have an overriding influence on variability of fall directions on side slopes >40%.

Red alder and the coastal form of Douglas-fir were the only two species that exhibited significant differences in DBH between side slope categories, with larger trees on moderate side slopes than on steep side slopes. This observation is consistent with fluvial landforms comprising side slopes <40%, where flood disturbances occur and tree mortality rates are higher relative to upland stands (Gregory et al. 1991; Acker et al. 2003). While these differences could provide of a confounding species × tree size effect on tree fall directionality, we do not believe this to be the case for two reasons. (1) Fall directionality for both red alder and
Douglas-fir on the different side slope categories was similar to that of the other six species (which did not exhibit significant differences in tree DBH among side slope categories).

(2) Fall directionality across all sites was more strongly associated with physical features of the riparian zone than with structural characteristics (density and basal area) of the riparian forest. Thus, while tree size may influence the relative importance of different mechanisms of tree fall, our data indicate that tree size did not have an influence on the directionality of tree fall at our sites.

Red alder is the only angiosperm represented in this analysis and has a different growth form, wood grain, and rooting structure than gymnosperms (Harlow and Harrar 1968; Haygreen and Bowyer 1996). Differences in tree fall directionality might also be expected as a result of these traits. Instead, we found a pattern consistent with that of the conifer species (Table 3). Distinguishing recruitment of deciduous wood from that of conifer wood is important for determining residence time and the functional role of wood in streams (Harmon et al. 1986). However, the use of one pattern (different fall directionality based on side slope) in recruitment modeling probably provides accurate estimates of large wood input from species considered in this study.

Model results at the two levels of resolution from field data (valley constraint and side slope steepness) indicate two important considerations for large wood recruitment modeling. (1) Small to moderate differences in mean tree fall direction (i.e., different valley constraint scenarios) do not impact predictions of large wood recruitment to the same degree as differences in fall direction variability (i.e., differences based on side slope). (2) Assessing controls on variability of tree fall directionality is a critical component of accurately modeling large wood recruitment. Small relative differences in recruitment between the two valley constraint classes indicated that a single fall directionality for all valley constraints would be adequate. Yet, modeling at the resolution of valley side slope indicated that significant differences in large wood recruitment occur according to valley topography. Valley constraint is a coarse-scale descriptor of the stream valley and does not explicitly describe slope topography. In fact, only 21% of the variance was explained in a linear regression model between constraint and site-averaged valley side slope (p = 0.04). Thus, we believe that the influence of slope topography on fall directionality provides more significant insight into large wood recruitment dynamics.

Streams in steep-sided valleys were predicted to receive a greater percentage of wood from farther away from the channel than streams in more moderately sloping or flat terrain. If riparian forest structure and species composition are assumed to be constant, we would expect a greater overall amount of wood, by number of tree boles, recruited to streams with steep banks than to those with gently sloped banks. However, a recent study (Acker et al. 2004) indicated that unconstrained reaches (gently sloped banks) may, in fact, provide more large wood to the channel because of greater extensive lateral channel migration and higher tree mortality rates, thus acting as a source to constrained reaches. Our model does not explicitly incorporate differences in tree fall mechanisms among reach types or differences in riparian forest dynamics. A next step in wood recruitment modeling is to incorporate spatially explicit information on distribution of bank slope topography and dynamics of riparian forest productivity and mortality.

Our findings may be useful in modeling large wood recruitment to streams in regions outside of the Pacific Northwest. However, several factors need to be considered. We believe that differences in fall directionality based on side slope mainly characterized topographic differences between fluvial landforms and hillslope landforms in this study. Moderate side slopes (<40%) characterized all but 12% of identified fluvial landforms, while steep side slopes (>40%) characterized 71% of identified hillslope landforms. If slope characteristics of fluvial and hillslope landforms are significantly different in a particular region, then additional field surveys are needed to verify that behavior of fall directionality according to side slope is consistent with our findings. Also, use of one tree fall directionality pattern for all species in each of the two side slope classes applies only for species surveyed in this study. Different tree species (both angiosperms and gymnosperms) in other geographic regions may have unique fall patterns based on local disturbance regime, growth response to topographic conditions, physiological characteristics, and surrounding forest structure. Lastly, tree fall directionality along large river systems and associated with catastrophic disturbances are not characterized in this study. Implications from this study are most applicable to small- to medium-size streams (second- to fourth-order) in mountainous regions where sustained large wood recruitment from riparian forest mortality is the significant management concern.

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