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THE RESIDENCE TIME OF LARGE WOODY DEBRIS IN THE QUEETS RIVER, WASHINGTON, USA

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Abstract. Instream large woody debris (LWD) provides several critical functions in riverine ecosystems, including sediment and nutrient retention, salmonid habitat enhancement, and stable colonization sites for incipient floodplain vegetation. In this study, the size and species composition of LWD in the Queets River, Washington, USA, were examined and compared with the size and species composition of forest trees from which they originated, in order to determine a depletion rate for LWD in the active channel. Increment cores from instream LWD were crossdated against cores from riparian conifers to estimate the year each LWD piece was recruited to the river channel. Debris pieces that were decayed or otherwise incompetent to provide cores were dated using standard ^{14}C techniques. Hardwood species (*Alnus rubra, Populus trichocarpa,* and *Acer macrophyllum*) were better represented among riparian forests than among instream LWD, and conifers (*Picea sitchensis, Tsuga heterophylla, Pseudotsuga menziesii,* and *Thuja plicata*) were better represented among LWD than in the adjacent riparian forest, suggesting that hardwoods were depleted from the channel faster than conifers. The depletion rate of coniferous LWD from the channel followed an exponential decay curve in which 80% of LWD pieces were <50 yr old, although some pieces have remained for up to 1400 yr. Although most wood is depleted from the channel within 50 yr, some wood is apparently buried in the floodplain and exhumed centuries later by lateral channel migration. The calculated depletion constant of 0.030 is equivalent to a half-life of ~ 20 yr, meaning that virtually all of the wood will have disappeared within 50 yr. This rapid depletion suggests that harvesting large conifers from the riparian zones of large streams could have adverse impacts within three to five decades.

Key words: dendrochronology; large woody debris (LWD); Queets River watershed, Washington, USA; riparian ecosystem.

INTRODUCTION

The genesis and fate of large woody debris (LWD) has come under increased scrutiny since the late 1970s, when fishery biologists realized that LWD, which until that time had been deliberately removed from channels to improve fish passage, was in fact a primary determinant of habitat quality. Since that time dozens of studies and several literature reviews have documented the effects of LWD in streams (Harmon et al. 1986, Bisson et al. 1987, Sedell et al. 1988, Bilby and Bisson 1998). Other studies have shown that the size of LWD that remains lodged in streams depends primarily on the length of LWD relative to the width of the stream (Swanson et al. 1976, Lienkaemper and Swanson 1987, Bilby and Ward 1989). The distribution of LWD in large and small channels (Bilby and Ward 1989, 1991, Nakamura and Swanson 1993, 1994), and the processes by which LWD influences pool frequency and channel shape (Keller and Swanson 1979, Lisle 1981, Montgomery et al. 1996) have important implications for the quantity and distribution of fish habitat. The preference of certain life stages of fish for woody cover (Bustard and Narver 1975, Bisson et al. 1982, Tschaplinski and Hartman 1983) has recently taken on an enhanced significance in the face of endangered species listings for several stocks of salmon and trout. Similarly, the discoveries that salmon carcasses are a vital source of nutrients to stream and riparian ecosystems (Bilby et al. 1996, 1998), and that LWD is an important component in retaining those carcasses (Cederholm et al. 1989) have encouraged many efforts in adding or retaining LWD in streams. The sediment retention and gravel sorting that occur around LWD (Keller and Swanson 1979, Bilby 1981) are being touted as having a buffering effect against increased sediment loads caused by forest roads and poor agricultural practices. Likewise, debris dams serve as refugia for colonizing vegetation and in some rivers are instrumental in formation of the floodplain (Abbe and Montgomery 1996, Naiman et al. 1998). Finally, the effects of clearcut logging and riparian buffers on LWD supply (Grette 1985, Long 1987, McDade et al. 1990, Robison and Beschta 1990, Van Sickle and Gregory 1990, McHenry et al. 1998) have focused attention on the amount of LWD necessary to maintain the essential instream functions of LWD. Yet while many studies have docu-

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mented the functions and importance of LWD in depth, a few important questions about LWD remain either unexplored or insufficiently substantiated. The residence time of LWD in stream channels is one such question; the species composition of instream LWD is another.

The residence time of in-channel LWD has been estimated by a handful of studies that dated LWD based on the ages of saplings growing on LWD pieces, or by the scars left when trees fell into the channel (Swanson et al. 1976, Keller and Tally 1979, Murphy and Koski 1989). In some cases only 10% of LWD pieces in the channel could be dated with these methods, and the lag time for sapling colonization is still largely unknown. Most of the age estimates are from LWD in constrained, low-order channels flowing through old-growth coniferous forests in California, Oregon, and Alaska, and have indicated that key pieces can reside in streams for up to ∼260 yr (Keller and Tally 1979, Grette 1985, Murphy and Koski 1989). Regardless of the actual age of the wood, these studies have shown that debris can remain unmoved for 70–100 yr, and sometimes more (Swanson et al. 1976, 1984, Swanson and Lienkaemper 1978).

The rate at which LWD is removed from the channel through decay, transport, and burial is what is referred to in this study as the depletion rate. We use the term fall age, or age, to denote the number of years since a LWD piece was recruited to the channel. To be precise, the residence time can not be determined until a LWD piece disappears from the channel, but at that point it is not practically measurable. In this study we calculate the residence time from an empirically-derived cumulative distribution of the LWD ages. This requires that we take an aggregate, steady-state view and examine the accumulation of LWD in a river, assuming that over several decades, and over an entire watershed, wood is recruited to the channel at approximately the same rate that it is depleted. Both recruitment and depletion of LWD have been shown to vary dramatically over short periods (Harmon et al. 1986, Bilby and Bisson 1998), but it is assumed here that an equilibrium between recruitment and depletion must exist over the long term, at least in channels unaffected by timber harvest, channelization, and other anthropogenic disturbances. We view accumulation and depletion to be opposite sides of the same coin; what accumulates is what is not depleted. We thus assume that a time series which describes the rate of LWD accumulation also describes its converse: the depletion of LWD that would occur over time if recruitment were to end.

The depletion rate will vary for each type of stream, and is determined by factors relating to wood decay, the size of LWD relative to the stream, stream type (alluvial or constrained), disturbance history, and active burial. The purpose of this study is to determine the depletion rate of LWD in a large, alluvial river. The specific objectives are (1) to determine a depletion rate for key LWD pieces, (2) to examine the differences in depletion rate among common riparian species, and (3) to examine the age of LWD in relation to its size, species, decay class, and dependent vegetation. The results are intended for use with models of LWD recruitment (McDade et al. 1990) to determine the structure of riparian forests necessary to produce desired amounts of instream LWD over time. Comparisons of different species and their relative decay rates are intended to inform decisions regarding wood choices for instream LWD and species composition of riparian buffers.

METHODS

Field methods

Our research was conducted in the Queets River watershed, on the west slope of the Olympic Mountains in western Washington State, USA. The study sites were all within the confines of Olympic National Park and upstream of the Queets River road, in protected old growth forests. The Queets is a braided alluvial river with a drainage area of 1157 km^2 and an average annual runoff of 377 cm/m^2 at the Clearwater gage. Mean width of the active channel among the study sites is 165 m (range: 51–398 m). Width of the summer low-flow wetted channel is ∼20 m. Precipitation in the headwaters, on the glaciated west flank of Mt. Olympus, is the highest in the continental United States, at ∼610 cm annually (Phillips and Donaldson 1972). As a comparison, the Queets River has only 1/250th the drainage area of the Colorado River at Lees Ferry, Arizona, yet it carries approximately one-fourth of the annual runoff (Stockton 1975, Wiggins et al. 1998). The annual low-flow period occurs in July–September, and the highest floods are typically during combined rain and snowmelt events in winter. Of the ten largest floods on record for the Queets River (1930–present) all occurred between November and February. While the year-round mean flow is 120 m^3/s, the lowest flow on record is 8.5 m^3/s and flood peaks have surpassed 3000 m^3/s.

Abundant rainfall and mild winters along the Olympic coast combine to create a geographic optimum for many conifers, resulting in some of the largest specimens in the world for Sitka spruce, Douglas-fir, western hemlock, and black cottonwood (*Picea sitchensis, Pseudotsuga menziesii, Tsuga heterophylla,* and *Populus trichocarpa,* respectively) (Waring and Franklin 1979, Van Pelt 1994). Conifers in the Queets valley commonly reach heights of 60 m and diameters of 2 m or more. Valley bottom forests are characterized by a series of elevated terraces of fluvial and glacial origin, conspicuous coverage of epiphytic plants, abundant nurse logs, and intensive herbivory by Roosevelt elk (*Cervus elaphus*) (Fonda 1974, McKee et al. 1982, Schreiner et al. 1996). Whereas Sitka spruce is considered a seral species over most of its range, in the low valleys of the western Olympics it is often considered a climax dominant, due to the elk herbivory, floodplain soils, and its success in establishing on nurse logs (Harmon and Franklin 1983, 1989, Woodward et al. 1994).

Field sampling

Field sampling was carried out at 25 transects and four intensive sites. The 25 transects spanned the channel (orthogonal to the current) at 1-km intervals, upstream of the Queets River road. A riparian plot was established at each end of each transect to measure the overstory composition. Riparian plots were centered five meters inland from the edge of the active channel, and the diameter and species of the four closest trees (one per quadrant) were noted for each plot (Lindsey et al. 1958). Maximum plot diameter was 20 m, beyond which no trees were measured. Two data sets were taken at each plot, the first with a minimum tree diameter of 30 cm, for comparison with LWD at the four intensive sites, the second with a minimum diameter of 7.5 cm to describe riparian conditions at a finer resolution. Each plot was categorized according to its fluvial context—whether it was on the outside of a meander bend, on the inside point bar, or near the meander crossover. Approximate bankfull channel width was also measured at each transect.

The LWD sampling was carried out in two phases. The first phase consisted of sampling key LWD (minimum 60 cm diameter and 5 m length) and riparian vegetation at the 25 transects. The second phase sampled all LWD (minimum 30 cm diameter and 5 m length) for a minimum of 100 meters of active channel at four intensive sites. The key pieces were used to determine the ages of LWD; the LWD measured at the four intensive sites were for species and size comparisons with trees in the riparian zone.

The first three key pieces of LWD (60 cm diameter and 5 m length) at each of the 25 transects were sampled to determine age, species, length, diameter, decay class, and rootwad condition. Notes were also taken on the site context of each key piece, such as jam formation, burial, and the amount or absence of dependent vegetation. If possible, an increment core was extracted from each piece. Decayed LWD pieces that were not competent to produce an increment core in three attempts were classified in decay class 7 (Table 1). Fist-sized wood samples were cut from the outer diameter of deteriorated logs (decay classes 5–7) for species identification and radiocarbon dating. Every effort was made to collect wood samples that included the outermost wood layer (i.e., the annual ring formed immediately before the tree died). Whenever possible wood samples were taken from areas with bark or from smooth areas where the bark had sloughed away. In the case of rough or deteriorated surfaces the amount of missing wood was estimated in the field. In isolated cases, where at least part of a key member was surrounded or confined by persistent woody vegetation (typically alder saplings) increment cores were taken from saplings for annual ring counting. Rings of very young saplings (1–4 yr) were counted in the field. These ring counts were used to compare the age of LWD to the floodplain colonization dates of surrounding vegetation.

TABLE 1. Decomposition classes for categorizing LWD and associated root wads.

Decay class†		Root wad class	
Number	Description	Number	Description
1	Bark intact, limbs and twigs present	1	Dirt or previous vegetation intact
2	Bark intact, limbs and twigs absent	2	Medium roots (<2.54 cm) intact
3	Bark loose or 5% absent	3	Major roots (>10.16 cm) remaining
4	Bark 95% absent, surface firm	4	No root wad, upper broken bole
5	Surface deteriorating, center solid	B	Buried, not determined
6	Surface deteriorating, center patchy		
7	Surface deteriorating, center rotten		

† Classes 5–7 require sampling with an increment borer to assess interior wood condition.

The four intensive sites were chosen to characterize species composition of LWD (at the 30-cm threshold) and to demonstrate variations in LWD abundance in different channel types. Two of the intensive sites were on flat alluvial floodplains of sand and cobble, with large logjams and interspersed flood-deposited LWD. The other two sites were in narrower, bedrock-controlled transport reaches (Montgomery and Buffington 1993) where LWD was typically anchored to the stream bank slightly above the level of bankfull flow. Due to differences in debris abundance the two depositional reaches were surveyed for 100 lineal meters of active channel, while the sparser transport reaches were surveyed for 300–400 m (to obtain an adequate sample). All LWD pieces greater than the minimum size (30 cm) were sampled for species identification, volume, decay class, rootwad class, and position in the channel.

Each LWD piece was identified by species in the field where possible and identified independently in the laboratory from the increment core or wood sample. Macroscopic features such as wood color, grain texture, presence of resin ducts, and early-wood to late-wood transitions were frequently adequate to determine species. In other cases, especially for decayed pieces, microscopic examination of the cellular structure was necessary. The shape, number, and positioning of intervessel pits, and the presence or absence of fusiform rays, spiral thickenings, and ray tracheids were used to determine the species of otherwise indistinguishable woods (Panshin and DeZeeuw 1980, Hoadley 1990).

TABLE 2. Master chronologies used for crossdating LWD cores.

Species	Time span (calendar years)	Cores (number)	Mean sensitivity†	Series intercorrelation‡
Sitka spruce	1682–1996	23	0.195	0.421
Douglas-fir	1374–1996	8	0.222	0.495
Western hemlock	1678–1996	11	0.289	0.379
Western redcedar	1838–1996	4	0.247	0.247

† Mean sensitivity is a measure of the differences between sequential rings averaged over several series. Species with higher values exhibit stronger annual fluctuation and often crossdate with greater certainty; species with low sensitivity are relatively complacent with respect to climate.

‡ Series intercorrelation is a measure of the signal common among all series in a chronology (Fritts 1976, Briffa and Jones 1989). Higher intercorrelations denote greater agreement among standardized cores and a higher signal-to-noise ratio.

Crossdating

Increment cores from both LWD and from standing trees in the Queets valley were mounted, sanded, and the ring widths measured to the nearest 0.01 mm using standard dendrochronological techniques (Stokes and Smiley 1968, Phipps 1985). Ring width series from LWD that correlated significantly ($P < 0.001$) with living trees, especially those recently recruited to the channel or those providing exceptionally long records, were added to the master chronology for that species. Hardwoods common to the Queets River were undatable with an adequate degree of certainty, either due to missing or indistinct rings (typical of black cottonwood and bigleaf maple), rings that failed to correlate between trees or between cores from the same tree (black cottonwood and red alder), or to short lifespans that produced an insufficient number of rings for an accurate match (red alder). Master chronologies were compiled for coniferous species only (Table 2).

Ring-width series from coniferous LWD were standardized and matched against master chronologies to determine the year of formation for the last ring (and by association all earlier rings) in the core (Fritts 1976, Cook and Kairiukstis 1989). Initial ring matches between LWD cores and the master chronologies were obtained using the program CORREL (Yamaguchi and Allen 1992, Yamaguchi 1994). The initial electronic crossdating was verified visually on the wood core to match the significant marker years without the statistical interference of the more complacent intervening rings. Only after visual verification was a core accepted as dated, and in a few cases visual crossdating superseded statistical ring matching that had produced questionable dates. Samples from LWD for which no acceptable date could be found, or from which no increment core could be extracted, were shipped to the University of Texas radiocarbon laboratory for standard ^{14}C dating.

Radiocarbon dating of modern samples presents several ambiguities (Stuiver and Pearson 1993, Stuiver and Reimer 1993). One ambiguity particular to this study results from wood that was alive during the mid-1960s and was thus subjected to elevated ^{14}C concentrations from atmospheric nuclear tests. For these pieces of ''ultramodern'' wood a ranking procedure was based on the percentage of ^{14}C relative to the 1950 NBS standard. Each sample was matched with the ambient tropospheric ^{14}C level during the 1954–1970 period, as given by Nydal and Lövseth (1983) and Broecker and Peng (1994). Adjustments were made in some cases to account for multiple-year wood samples and a sharp peak in ambient ^{14}C in 1963. Four samples with known ultramodern dates (from the crossdating procedure) were also dated using the ^{14}C technique as an aid in calibration. In cases where LWD samples were dated as ultramodern, other factors such as crossdating, decay class, dependent vegetation, and ages of adjacent logs in the same debris jam were employed to determine whether the wood was to be calibrated on the rising end or the trailing end of the bomb carbon decay curve (Broecker and Peng 1994).

The resulting list of dates from all dating techniques (the year each LWD piece was recruited to the channel) was plotted as a cumulative distribution curve according to the number of pieces in the data set that had been recruited prior to that year. For example the most recent key piece fell in 1996 and had 68 accumulated pieces before it ($n = 69$). The oldest two pieces fell in approximately AD 565 and AD 658 and had zero and one prior piece, respectively. The cumulative distribution curve was used to fit various functions to the observed data. Curve fitting algorithms were not able to solve for optimal solutions when the earliest two dates (565 and 658) were included, so these were dropped from the procedure. Various models, including linear, logarithmic, inverse, power, and exponential functions were evaluated according to their mean square error and observed fit to the empirical data.

RESULTS

Comparisons between LWD and the riparian forest

The species composition of the aggregated riparian plots was compared to that of the LWD species identified in the laboratory. As Fig. 1 shows, the most common tree species (>30 cm diameter) in the riparian zone is red alder, followed by Sitka spruce and western

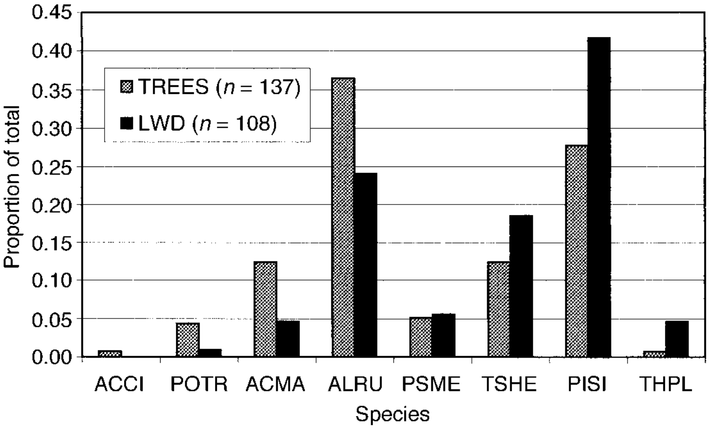

FIG. 1. Relative abundance of LWD vs. riparian trees, by species (30 cm diameter and larger). Species codes: ACCI, *Acer circinatum* (vine maple); ACMA, *Acer macrophyllum* (bigleaf maple); ALRU, *Alnus rubra* (red alder); PISI, *Picea sitchensis* (Sitka spruce); POTR, *Populus trichocarpa* (black cottonwood); PSME, *Pseudotsuga menziesii* (Douglas-fir); THPL, *Thuja plicata* (western redcedar); TSHE, *Tsuga heterophylla* (western hemlock).

hemlock, whereas the most common species of LWD (>30 cm diameter) is Sitka spruce, followed by red alder and western hemlock. Each of the hardwood species is better represented among standing trees than among LWD, and each of the conifers are better represented as LWD than among trees in the riparian zone. Several tree species do not occur in the sample in numbers adequate to draw statistical conclusions, yet they all follow the same general pattern between conifers and hardwoods.

Diameters of LWD were significantly larger than diameters of riparian trees as a whole, although comparisons were not consistent across all species (Table 3). When all LWD (>30 cm) were compared to all riparian trees (>30 cm), the LWD were significantly larger in diameter than the standing trees ($P = 0.006$), which was also true for red alder and Sitka spruce. However, the opposite trend was observed for western hemlock. Species that were poorly represented in the riparian zone showed ambiguous relationships between sizes of trees and sizes of LWD.

Sizes of LWD varied substantially between alluvial river reaches (Sites A and C) and transport reaches (Sites B and D). In the two transport reaches the LWD pieces were fewer, but not necessarily smaller, and in the two alluvial reaches the total volume of wood was greater, in one case by nearly an order of magnitude (Table 4). Volume calculations at each site were influenced by a few very large pieces. The maximum piece sizes were frequently near 100 m^3 and the mean piece size was typically more than three times the median. The exception to this pattern was at Site D, a constrained bedrock channel where several large old growth trees had been recruited from, and remained anchored to, the river bank. The inability of the channel to move these large pieces resulted in a greater overall LWD size and volume.

Residence time

Of the 75 LWD samples taken at 25 transects, 59 were dated using dendrochronological techniques, 19 were dated using ^{14}C, and eight were dated using a combination of techniques (including dependent vegetation) for comparison and calibration. Only the 69 conifers were consistently datable with these methods; the six hardwoods were generally either too small (too few rings for crossdating) or too young (ultramodern ^{14}C levels) to provide consistently accurate dates. Thus the depletion curve is based on conifers only. The time since recruitment of individual conifers ranged from

TABLE 3. Comparison of riparian tree diameters to in-channel LWD diameters at the 30-cm threshold.

	Riparian vegetation			In-channel LWD			Two-tailed *t* test	
Species	Number of trees	Percentage of trees	Mean diameter (cm)	Number of LWD	Percentage of LWD	Mean diameter (cm)	*t*	P
Vine maple	1	0.01	38.1	0	…	…	…	…
Black cottonwood	6	0.04	91.2	1	0.01	97.5	0.208	0.843
Bigleaf maple	17	0.12	75.8	5	0.05	68.0	−0.531	0.601
Red alder	50	0.36	41.9	26	0.24	48.6	2.495	0.015
Douglas fir	7	0.05	97.8	6	0.06	100.0	0.064	0.950
Western hemlock	17	0.12	89.4	20	0.19	68.1	−2.145	0.039
Sitka spruce	38	0.28	81.7	45	0.42	121.3	3.110	0.002
Western redcedar	1	0.01	126.5	5	0.05	94.0	−1.260	0.276
All combined	137		80.3	108		85.4	2.780	0.006

Note: Riparian tree diameters were smaller overall than LWD diameters, and diameter of Sitka spruce and red alder trees were smaller than Sitka spruce and red alder LWD, but other species (often with lower sample sizes) were more ambiguous or showed the opposite relationship.

TABLE 4. Comparison of LWD volumes between study sites.

Site†	LWD no.	Volume (m^3)	Vol./100 m‡	Volume (m^3) characteristics of LWD pieces			
				Mean	Median	Maximum	Minimum
A	31	374	374	12.08	3.28	97.14	0.49
B	9	127	32	14.14	3.37	60.61	2.60
C	53	1003	1003	18.93	4.60	109.94	0.48
D	8	134	45	16.80	10.42	54.04	4.33

Note: All volumes are in cubic meters of wood.

† Sites A and C are unconstrained alluvial channels; sites B and D are constrained bedrock channels.

‡ Vol./100 m is total site volume (m^3) per hundred meters of channel. Sites A and C were surveyed for 100 m. Site B was surveyed for 400 m, and site D for 300 m.

one year to over 1400 yr, with a mean age for all dated pieces of 84 yr and a median of 19 yr (Table 5). Most LWD (80%; 55 pieces) were <50 yr old, and half of those (24 pieces) had been recruited to the channel in the most recent decade. Eleven pieces were between 50 and 400 yr old, and two were over 1300 yr old (approximate recruitment in 565 AD and 658 AD).

The decay model that produced the best fit to the observed dates followed the form

$$Y = (67.02)\ e^{(-0.030t)} \tag{1}$$

where Y is the number of predicted LWD pieces in the channel, t is time in years, and 0.030 is the depletion rate. The reciprocal of the depletion rate gives a mean residence time of ~30 yr, but the wide variation in LWD ages indicates that individual pieces may reside in the channel for much longer periods. Over the 1599–1996 cumulative distribution curve the mean square error was lowest for the exponential function (MSE = 13.8) followed by the power function (MSE = 16.7), and the logarithmic (MSE = 20.8). As stated previously, the earliest two LWD dates had to be excluded for the curve fitting procedures to find an optimal solution. Over the most recent 50 yr the exponential curve fit the observed data (MSE = 6.92) much better than the power function (MSE = 16.8). For the years prior to about 1950 the exponential function underestimates and the power function overestimates LWD abundance relative to the observed data.

The depletion curve constructed from all LWD dates (Fig. 2) indicates that wood typically disappears from the active channel within the first five decades, after which some pieces may remain for several hundred years. A slight juncture at the fifth decade suggests that more than one process may be responsible for the retention of LWD in the channel. This conclusion is borne out in the field notes, which indicate that burial may be responsible for the longer residence times. Of the eleven oldest LWD pieces examined (all recruited prior to 1900) none were anchored to the bank or surrounded by dependent vegetation, and several were sitting exposed on active cobble bars in areas of recent channel migration. Although surface wood in many instances was highly decayed, four of the five oldest LWD samples (including two more than 1000 yr old) produced solid wood cores with the increment borer.

Decay class and dependent vegetation

Among the coniferous LWD, no significant relationship existed between LWD fall age and diameter, which is perhaps due to only examining key (>60 cm diameter) LWD pieces (Fig. 3). Several of the largest logs in the data set were recruited in the most recent decade, which works against the assumption that larger LWD pieces would be generally older, and three of the oldest logs were relatively small (<1 m diameter), which further obscures the relationship. Linear regressions between the diameter and fall age of LWD had a low coefficient of determination when all key pieces were included ($r^2 = 0.01$), a relationship which did not improve substantially when the two oldest specimens were removed from the sample ($r^2 = 0.03$), nor when

TABLE 5. Number of key LWD pieces depleted from the channel over time (depletion constant $k = 0.030$).

Reach	Current LWD (*n*)	LWD/ 100 m†	10 yr	20 yr	30 yr	40 yr	50 yr
Site A, alluvial	15	15	7	9	10	12	14
Site B, constrained	6	1	1	1	1	1	1
Site C, alluvial	32	32	14	19	22	25	30
Site D, constrained	8	3	1	2	2	2	3
Combined reaches	61	51	23	30	36	40	49
Proportion depleted			0.45	0.59	0.70	0.78	0.95

Note: Columns 4–8 depict the number of current pieces of wood (column 3) that would be depleted from 100 m of channel over the stated time period.

† LWD in constrained channels (sites B and D) was surveyed for more than 100 m to increase sample size.

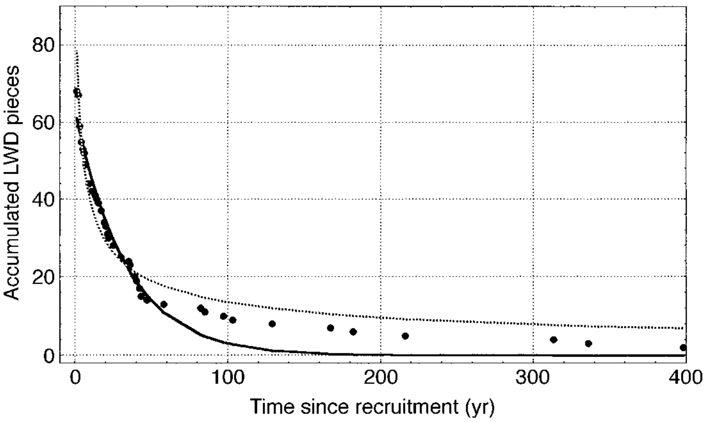

FIG. 2. Depletion curve for LWD recruited between 1599 and 1997, which excludes the two oldest pieces in the data set (recruited in ~565 and 658 AD). Curves were fitted to the data shown in the graph. The exponential function $Y = 67.019e^{(-0.030t)}$ (solid line) has a mean square error (MSE) of 13.8. The power function $Y = 135.913t^{(-0.499)}$ (dotted line) has an MSE of 16.7.

only those pieces that died after ~1920 were included ($r^2 = 0.002$).

The species of coniferous LWD was not significantly associated with fall age. Mean age of Sitka spruce LWD was 92 yr ($n = 50$), Douglas-fir was 91 yr ($n = 4$), western hemlock was 59 yr ($n = 14$), and the single western redcedar in the data set was 25 yr old. A single-factor ANOVA to test the difference between the mean fall age of Sitka spruce, western hemlock, and Douglas-fir revealed that the within-species variance far exceeded the between-species variance ($F = 0.097$, $P = 0.97$), therefore no intraspecific differences in age could be detected.

Decay class was not an accurate predictor of LWD age. Decay classes 1 and 2 were combined due to the similarity of characteristics and the low sample size in class 1. All of the LWD in decay classes 1 and 2 were <10 yr old, and all LWD in decay class 7 were >30 yr old, but classes 3–6 showed dramatically overlapping ages (Fig. 4). Decay class 5, which included the two oldest pieces of LWD in the data set, was significantly different from the other classes (Tukey hsd test, $F = 3.24$, $P = 0.011$), the remainder of which were homogeneous at the 0.05 significance level.

Dependent vegetation on or around LWD was a poor and often misleading indicator of residence time. Many LWD pieces that had 1–5 yr-old vegetation growing on or around them were discovered to have died and presumably recruited to the channel >20 yr previous. Few of the oldest pieces in the channel had any dependent vegetation whatsoever, and several pieces that had the densest or most advanced dependent vegetation had been recruited to the channel within the past two decades.

DISCUSSION

Species differences between LWD and riparian trees

Based on their relative frequency in the riparian zone, hardwoods are more likely to be depleted from

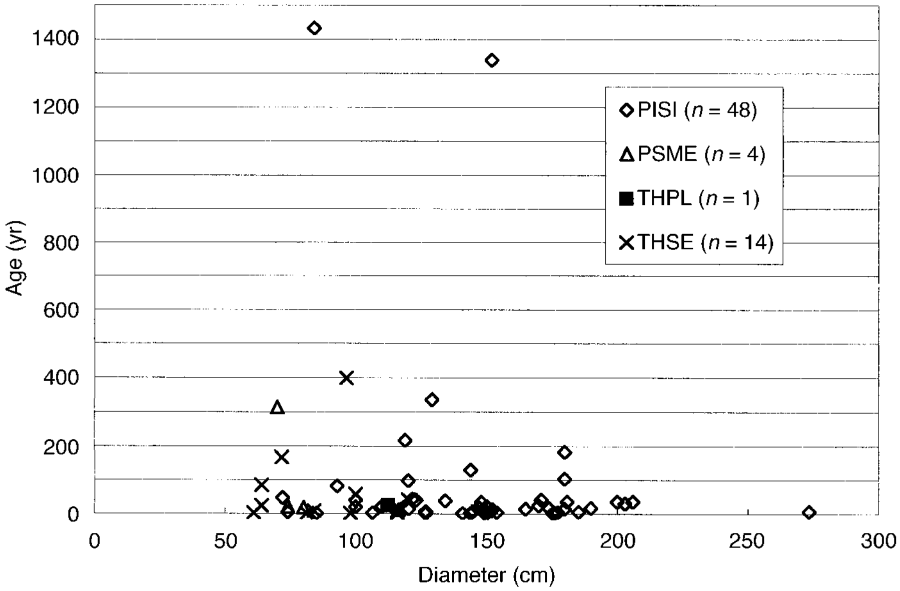

FIG. 3. Diameter of in-channel coniferous LWD vs. the time since recruitment, by species. Species codes are as in Fig. 1.

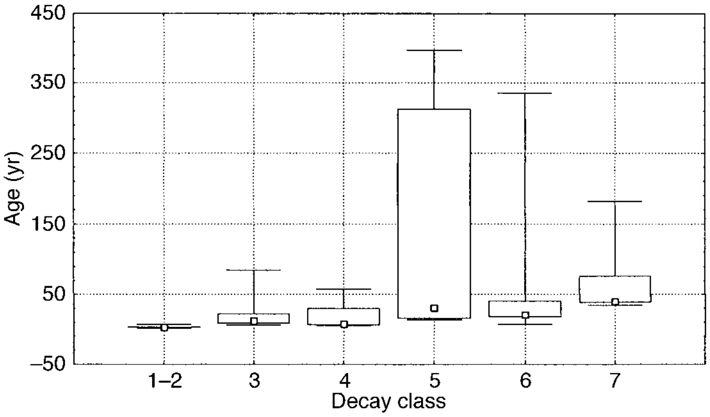

Fig. 4. Box and whisker plot of LWD ages grouped by decay class, showing median values, 25th and 75th percentiles, and range. Decay classes 1 and 2 were combined due to low sample size in class 2. Decay class is generally a poor predictor of wood age. The two oldest samples (age 1340 yr and 1430 yr, both in decay class 5) were removed from the data set to show greater resolution.

the channel than conifers. If recruitment to and transport from the active channel were approximately the same for each tree species then each species would have the same relative abundance in both the riparian zone and among LWD, but this is not the case. Fig. 1 demonstrated that each of the conifers is better represented among LWD than among trees in the riparian zone, and that each of the hardwoods is better represented among standing trees than among LWD. Conclusions on unequal LWD transport depend on an assumption that recruitment is both random and proportional to riparian species abundance. Although the sample sizes are not statistically valid in every case, Fig. 1 suggests that hardwood species are being transported from the channel, buried in the floodplain, or broken down to less than the measurement threshold faster than conifers.

Each of the species in Fig. 1 is plotted in order of the ratio of relative abundance among riparian trees against the relative abundance among LWD. The abscissa therefore represents a hypothetical ordination of the ''depletion resistance'' of each species. Thus black cottonwood is depleted from the channel more rapidly than Sitka spruce or western redcedar. Black cottonwood is also depleted more rapidly than red alder, despite the wide disparity in size. The arrangement of species in Fig. 1 also reflects published values on the decay resistance of various types of wood (Scheffer 1957, Scheffer and Cowling 1966, Aho and Cahill 1984, Harmon et al. 1986, Highley 1995), suggesting that wood decay is a significant factor in LWD residence time. The obvious anomaly in Fig. 1 is Douglas-fir, which is regarded as more decay resistant than both western hemlock and Sitka spruce. This anomaly might be attributable to one of the 50 riparian plots (Transect 7) which contained several large Douglas-fir, which may have skewed the riparian data and made Douglas-fir appear more abundant in the riparian zone than it actually is.

The depletion of hardwoods is apparently affected as much by wood decay as it is by tree size. Note that black cottonwood LWD was roughly the same size as Douglas-fir or western redcedar (Table 3), yet it followed the same general pattern that separates hardwoods from conifers. The same could also be claimed for bigleaf maple and western hemlock. Although the sample sizes were low, the fact that these hardwoods do not appear to behave the same as similarly-sized conifers suggests that decay resistance, and not transport, is perhaps responsible for their unequal relative abundance.

Depletion rate

The cumulative distribution curve in Fig. 2 shows a steep decline up to about the fifth decade and a gradual tapering thereafter, indicating that recent LWD recruits are relatively abundant and older pieces are relatively rare. An inflection in the curve at about 1950 (the 50-yr mark) might be expected in a system in which two separate physical processes were determining the transport and retention of LWD. One interpretation of the depletion curve is that most LWD is transported out of the system within the first three to five decades, but that a subset of LWD is buried or jammed in the river floodplain for perhaps hundreds of years, after which it can be exhumed and reintroduced to the active channel. This model of LWD transport would explain why some of the oldest LWD pieces were relatively undecayed (had they been buried in an anaerobic environment) while some of the more decayed pieces had died only a few decades ago. It would also explain why many of the oldest pieces were sitting unconstrained and unanchored on cobble bars in the middle of the active channel, evidently deposited by recent floods, while many of the younger recruits were held fast to the channel banks, entangled in LWD jams, or surrounded by dependent vegetation.

The exponential depletion curve (Eq. 1) fit the empirical data for the most recent five decades, after which it underpredicted LWD abundance. The power function also diverged from the empirical data after five decades. Burial, exhumation, and jam formation should work equally on both old wood and new, and channel migration may disturb established banks as well as recent depositions, so wood that is buried or jammed for short durations could fall into either the steep decline of wood (the most recent five decades) or more likely the recent end of the long, flat depletion of wood (around the turn of the 20th century). The jointed depletion curve (Fig. 2) gives rise to three possible depletion rates for LWD: one that governs all LWD in the channel (the one presented here), one that governs wood that is depleted rapidly, and another that applies to wood that remains in the channel for long periods due to burial and jamming. Because of the practical difficulty in separating wood that has been buried from wood that has remained exposed, we did not attempt to separate recent and ancient curves from the unified curve based on Eq. 1. What we find remarkable, however, is the existence of large, solid LWD pieces from 3 to 14 centuries old, many of which were lying exposed in the active channel. We can only assume that these LWD pieces spent much of their tenure buried in the floodplain, preserved from disintegration and aerobic decay.

Disturbances that might have recruited large pulses of LWD to the Queets channel do not seem to have made a significant contribution when viewed over a multidecadal time scale. Small variations in the LWD depletion curve, which are evident when the most recent fifty years are plotted, are insignificant on the 400-yr plot. A major fire in the upper Queets watershed in 1961 appears to have not had any effect on the supply of LWD, probably because the fire did not burn into the riparian zone (Pickford et al. 1977, Huff 1995). However, three of the eight largest floods on record for the Queets River occurred in 1954, 1955, and 1956 (Wiggins et al. 1998), which could be expected to cause substantial bank cutting and LWD recruitment. The second largest flood on record was in 1955, which reached a stage of 8.2 m above the gage datum at Clearwater, Washington, near the mouth of the river. An increase in LWD dating from the 1950s may be due to these floods. The period of record for the Queets River dates from 1930, with minor interruptions since that time. The third largest flood on record occurred in 1990, which could explain the high number of LWD pieces that were dated from that decade, from that year, and from the year following.

Regardless of the variations in or the interpretation of the depletion curve shape, the first decades of the curve show an unequivocal rapid depletion of LWD pieces from the channel (Fig. 2). The depletion may be due to transport, burial, breakup, or a combination of all three, but the curve clearly shows that most (80%) of the key pieces of LWD now resident in the active channel were living trees as recently as 1950. This trend is clear for all conifers combined and specifically for Sitka spruce; unfortunately other species were not adequately represented to draw similar conclusions. One implication of this curve is that if the riparian zone of the Queets River had been harvested in the last 50 yr, then most of the LWD now in the river would not have been available for recruitment. Moreover, since the minimum size of dated LWD was 60 cm in diameter, if the riparian buffers had been preferentially harvested to extract the merchantable timber, as many forest practice regulations currently allow, then most of the key LWD members in the Queets River would now be gone.

The depletion rate of LWD is an important factor in calculating the number of trees that must remain in riparian buffers after timber harvests. Eq. 1 can thus be used with data on the amount of LWD in various reaches to estimate the depletion of key pieces. The depletion constant (0.030) indicates the proportion of wood currently in the channel that will be depleted each year, when viewed on a multidecadal scale (i.e., ignoring pulses of depletion due to catastrophic events). Table 4 shows the number of key LWD pieces in four dissimilar reaches (two alluvial and two constrained) of the Queets River and the number of those pieces depleted over five decades. In order to maintain a long-term equilibrium of LWD in the channel, trees would need to be recruited at approximately the same rate as they are depleted.

Several caveats regarding Table 4 are in order. First, while Eq. 1 might be applied to many different types of channels (Murphy and Koski 1989), the depletion constant used here is from a large, mostly alluvial river and should probably be applied only to similar rivers. Further, the relationship between mean channel width and LWD length is crucial for determining LWD transport during floods, and the ratio of river width to LWD length is perhaps different for the Queets than for constrained rivers (mean bankfull width at study transects on the Queets is 165 m and the range is 51–398 m; mean key LWD length is 23.4 m and the range is 5.3–69.0 m). Similarly, the depletion constant used above was calculated from LWD throughout the river, but was applied to four study channels of two dissimilar types. Finally, alluvial channels trap wood from upstream, and constrained channels export LWD downstream, so it is not to be expected that the LWD resident in a channel was recruited from the riparian zone in that reach.

These caveats notwithstanding, the values in Table 4 may be useful in many restoration and monitoring efforts. Few rivers in North America are subject to the extreme flooding and have the large trees found on the Olympic Coast of western Washington, although it is possible that the relative sizes of LWD to the channel is duplicated in other rivers. Many of these other rivers, particularly those draining to Puget Sound, have been altered to obscure the amount of naturally-occurring LWD. Restoration efforts in these and other rivers may benefit from the approximate calculations in Table 4, as would other river systems for which a 0.03 depletion constant would probably represent an upper bound.

Other researchers have looked at various aspects of LWD in alluvial rivers and drawn conclusions similar to what is being inferred here. Several studies have dated LWD based on the ages of dependent vegetation (Swanson et al. 1976, Keller and Tally 1979, Murphy and Koski 1989) and have shown that LWD may remain unmoved or stable for up to 260 yr (Swanson et al. 1976, 1984, Swanson and Lienkaemper 1978, Murphy and Koski 1989). Eq. 1 is similar to a LWD depletion equation given by Murphy and Koski (1989), except that Eq. 1 was derived directly from dated wood, whereas Murphy and Koski (1989) calculated the depletion rates as the reciprocal of the weighted mean LWD age. Murphy and Koski (1989) assumed an exponential decay model and computed depletion rates of 0.016–0.011 in smaller channels (width 20–30 m) with smaller sized wood (61–90 cm diameter, 3 m minimum length). An extensive study by Grette (1985) in the Olympic Mountains showed that in smaller streams the depletion rate was such that streams logged without buffers would be totally depleted of LWD in $<$100 yr. Similar findings of rapid transport and decay have been put forth by Andrus et al. (1988) and Bilby and Ward (1991). The oldest instream LWD dated in this study is several times older than any yet reported in North America, although Nanson et al. (1995) has dated instream LWD in Tasmania at 2000 yr old and wood buried in the floodplain at $>$17 000 yr old. Becker (1986) has dated buried wood in the Rhine and Danube rivers at $>$10 000 yr old.

Decay class and dependent vegetation

In this study decay class was not a particularly good indicator of LWD age, except in the extremities. All LWD in decay classes 1 and 2 had been dead $<$10 yr, and almost all LWD in decay class 7 had been dead $>$30 yr. Age variation and overlap in the intermediate decay classes (3–6) was so high that the classes were virtually meaningless. Much of the oldest wood sampled, including the two pieces $>$1300 yr old, were remarkably undecayed and capable of producing a relatively solid increment core. By contrast, many of the younger (more recently deceased) LWD had residence times $<$10 yr, and were grouped in decay classes 3–6. Often these younger, decayed pieces were lodged in wet or shady areas where the surface wood appeared to decay relatively rapidly.

Caution should also be used in drawing precise conclusions on the age or residence time of LWD based on the age of dependent vegetation growing on or near the wood, especially in braided reaches where the wood is easily moved. Dates from the Queets River suggest that circumstantial evidence on the residence time of LWD is generally not very trustworthy. Much of the LWD sampled in this study had no dependent vegetation growing nearby, even though fall ages of ten to thirty years were common. Dependent vegetation seems to be less an indicator of residence time than of relative stability. In very few cases was the lag time between LWD deposition and vegetation colonization of the surrounding sand and cobble bars $<$10 yr, and almost half of the LWD population was resident for $<$10 yr. A study that disregarded such a large proportion of the LWD population would therefore underestimate the depletion constant by a substantial margin. It is uncertain whether the longer lag times were due to slow colonization or to unstable LWD that was being re-arranged during successive floods. None of the datable LWD pieces in this study that exceeded a residence time of 100 yr hosted any dependent vegetation more than a few years old.

Finally, none of the differences in the species, size, or recruitment date of LWD were attributable to the confluence of tributaries that might contribute LWD. This was in part intentional, since nearly all of the study sites and transects were chosen to reflect the actions of a large, alluvial river, and the emphasis on ‘‘key’’ LWD necessitated a minimum size threshold (60 cm diameter and 5 m length) that was not mobile in smaller tributaries except during major debris flows. With the exception of Tshletschy Creek, all tributaries to the Queets River in the study area were too small to transport substantial quantities of LWD at or above the measurement threshold (except during catastrophic debris flows), therefore the contribution of tributary channels in this study was minimized.

CONCLUSIONS

The size and abundance of LWD in any given forested channel depends on complex interactions between channel morphology, flood intensity, and riparian stand characteristics. Volumes of LWD in similar channels can vary widely, therefore no single amount of LWD can be prescribed for a given channel. However, it is possible to estimate the amount of LWD that must be recruited to the channel in order to maintain a desired level of wood in the stream. This study, conducted in an alluvial river with very large trees and extreme floods, represents one end of the spectrum for debris sizes and volumes. The depletion rate for LWD pieces calculated from this data is higher than previously published depletion rates, which were crafted from smaller channels with smaller wood. The depletion curve shows the half-life of LWD to be ~20 yr, and thus nearly all wood now in residence will be exported, buried, or broken down within three to five decades. Also, comparisons between LWD and riparian stands shows that hardwoods are depleted from the channel more rapidly than conifers. Although smaller LWD from both conifers and hardwoods may be appropriate for smaller channels (Beechie 1998), on large rivers the protection of river structure and salmonid habitat would dictate preserving the largest conifers in the riparian zone for future LWD recruitment. While much of the LWD will probably be flushed from or buried in the channel in a few decades, some pieces may remain active, or become active again, after several hundred years. Thus the current management of riparian zones, whether harvested or not, could have a lasting effect on river environments for many years to come.

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