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Wood retention and transport in tropical, headwater streams, La Selva Biological Station, Costa Rica

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ABSTRACT

Wood in tropical streams has the potential to be more mobile than wood in otherwise similar temperate streams because of the warm and humid conditions that promote decay and the more frequent and flashier floods of the tropics. To test this hypothesis, we monitored all large wood pieces for 2.3 years in 10 50-m-long reaches of old-growth headwater streams in La Selva Biological Station, Costa Rica. Annual wood retention rates for pieces ranged from 0.55 to 0.91 among the sites, and retention rates by volume ranged from 0.67 to 0.99. Assuming steady state wood load, which is reasonable for La Selva, these rates are equivalent to mean residence times of 2.2–10.6 years for pieces, and 3.0–83.2 years for a volume of wood. Calculating mean residence time from the weighted average of retention rates gives an average residence time of 4.9 years for a piece of wood and 6.9 years for a volume of wood. These values are less than those reported for old-growth temperate forests, supporting our hypothesis. Mobility of individual pieces was best predicted by piece length relative to stream width (l_r, higher l_r led to lower mobility), channel gradient (s, higher s led to higher mobility), and piece integration into the channel (unattached pieces were 2.6 times more mobile than attached, ramp, or bridge pieces). Temporal variation in retention rates was well explained by variation in peak flow. All four of these factors have also been observed to influence mobility in the temperate zone. The higher mobility of wood in our study site relative to the temperate rainforest of the Pacific Northwest may be explained by the flashy and frequent floods, the high decay rate, or the branching morphology of the native trees; but differentiating the role of these factors, particularly flow and decay, will be complicated by their covariation across climates.

1. Introduction

A growing body of research has established that in-stream wood can be important to both the geomorphology and ecological function of a broad range of temperate zone streams. Most geomorphic effects of wood occur around stationary pieces or jams within the channel that deflect or impound flow. Such pieces may do any or all of the following: (i) increase resistance to flow (Curran and Wohl, 2003; Wilcox and Wohl, 2006), (ii) deflect flow toward channel margins (Daniels and Rhoads, 2003), (iii) shield channel margins (Brooks et al., 2003), (iv) form steps and pools (Richmond and Fausch, 1995; Beechie and Sibley, 1997; Gurnell and Sweet, 1998), (v) induce pool scour (Fausch and Northcote, 1992; Baillie and Davies, 2002), (vi) trap sediment or nutrients (Smith et al., 1993; Hart, 2002; Faustini and Jones, 2003), (vii) force avulsions (Maser and Sedell, 1994), and (viii) increase overbank flow (Jeffries et al., 2003). Ecologically, the presence of wood usually leads to increased stream habitat complexity (Bisson et al., 1987; Fausch and Northcote, 1992; Kail, 2003). Wood also promotes retention of both fine particulate organic matter (FPOM) (Daniels, 2006) and coarse particulate organic matter (CPOM) (Bilby and Likens, 1980; Webster et al., 1994), which are major sources of energy and nutrients in many streams. The wood hosts macroinvertebrates (Anderson et al., 1978) and provides substrate for algae, fungi, and microbes that contribute to the basal layer of aquatic food webs (Maser and Sedell, 1994; Tank and Webster, 1998).

In order to perform most of these functions, the wood must remain stable; and the duration of piece stability reflects the degree of influence the piece will have on fluvial processes and channel morphology. In this sense, we expect to see a correlation between wood residence time and geomorphic effectiveness. For example, a frequently moving piece of wood is less likely to cause persistent storage of CPOM or induce deep scour (Daniels, 2006). And, although jams may persist even if the individual pieces turn over quickly (thereby maintaining flow deflection characteristics) a jam that frequently loses wood will likely pass even coarse sediment as well (Haschenburger and Rice, 2004). Moreover, wood depletion rate is a necessary component of a comprehensive wood budget (Benda and Sias, 2003). Finally, wood mobility is an important factor to consider

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when balancing the needs of natural stream function and infrastructure protection and maintenance (Comiti et al., 2006; Mazzorana et al., 2009). For these reasons, quantification of wood mobility in terms of retention rates or residence times is desirable. Numerous researchers have considered wood residence time in temperate zone streams using techniques such as dendro-chronology (Keller and Tally, 1979; Murphy and Koski, 1989; Dahlström et al., 2005; Powell et al., 2009), radiocarbon dating (Hyatt and Naiman, 2001; Guyette et al., 2002), wood input monitoring (Lienkaemper and Swanson, 1987), and wood transport monitoring (Berg et al., 1998; Wohl and Goode, 2008).

Few studies have considered in-stream wood in tropical settings. Wood loads in La Selva Biological Station, Costa Rica, a tropical rainforest, are lower than in the temperate rainforests of the Pacific Northwest (Cadol et al., 2009). In the previous paper, we inferred that the lower wood loads reflect increased mobility of in-stream wood because both regions have equally large trees and because primary productivity is expected to be as high or higher in the tropical rainforest as in temperate forests (Raich et al., 1991; Melillo et al., 1993), although errors are potentially large in these estimates of productivity (Clark et al., 2001). Here we test the inference of greater mobility of wood in old-growth tropical forest streams relative to analogous temperate forest streams.

Rates of wood transport in tropical streams may be different for several reasons, including decay and flow characteristics. Decay rates are typically higher in the tropics because of the high rate of biological activity, high microbial diversity, and year-round warm and moist conditions (Panshin et al., 1964; Zabel and Morrell, 1992). Higher decay rates hasten the breakdown of immobile key pieces of wood into smaller pieces that can be transported by the flow. Tropical forest floor wood decay rates are several times higher than those from temperate zones (Harmon et al., 1986; Clark et al., 2002), making it unlikely that wood in tropical streams does not decay faster than wood in temperate streams, although the reduction in decay rates caused by submergence in anoxic conditions (Triska and Cromack, 1980) or the decay-resistant compounds present in the wood of many tropical trees may influence relative in-stream decay. Although runoff production is dependent on both soil anisotropy and rainfall regime (Elsenbeer, 2001; Godsey et al., 2004), stormflow is generally greater and flashier in the tropics than most temperate zone climates, which may also lead to higher wood mobility. Rapid streamflow generation during storms may be driven by overland flow caused by rapid reductions in hydraulic conductivity of the soils with depth (Godsey et al., 2004) as well as by high infiltration rates resulting from the presence of fractures and abundant macropores that enable rainfall to be quickly routed through the subsurface in the shallow aquifer adjacent to the channel (Hendrickx et al., 2005). In the study area, we have observed overland flow on trails within several meters of ridge crests during common, high intensity rainfall events. Tropical storms have the potential to deliver intense rainfall, which combines with the flashy discharge regime to create an event-driven aquatic ecosystem (Smith et al., 2003). Typically, the extremely high values of unit discharge result in large hydraulic forces that create well-developed downstream hydraulic geometry and frequent mobilization of coarse bed material (Wohl, 2005) and presumably wood as well.

Dendro-chronology techniques cannot be used to find the age distribution of in-stream wood in tropical settings because of the lack of annual growth rings, so we established a regimen of flagging and monitoring of in-stream wood in old-growth rainforest catchments in La Selva Biological Station. Our primary objective is to document wood retention and transport over a period of slightly more than two years in headwater stream segments spanning a range of values for stream gradient, substrate type, and channel morphology. We hypothesize that the study streams will exhibit shorter retention times for in-stream wood than temperate headwater streams with similar characteristics.

2. Study site

All stream reaches in this study were located in old-growth forest within La Selva Biological Station, a rainforest preserve operated by the Organization for Tropical Studies in northeastern Costa Rica (10°26′ N., 84°00′ W.) (Fig. 1). La Selva encompasses 16 km^2 of forest classified as tropical wet forest in the Holdridge system (Hartshorn and Peralta, 1988), approximately evenly divided between old-growth and second-growth. The 730 ha of old-growth primary forest has not been logged. Elevations within the preserve range from 30 to 150 m. The southern end of La Selva is adjacent to Braulio Carillo National Park, which extends into the heart of the Central Volcanic Cordillera of Costa Rica, a large area of intact primary forest that includes the volcanoes Poaz (2704 m), Barva (2906 m), and Irazu (3423 m). The northern border of La Selva is formed by the Río Sarapiquí, flowing east and draining 432 km^2, and the Río Puerto Viejo, flowing west and draining 370 km^2. These two rivers join at La Selva and flow north to the Río San Juan. La Selva is the terminus of a peninsula of preserved forest that extends to the edge of the Caribbean lowlands. The surrounding land has been cleared for pastures and plantations. La Selva is located at the northeastern edge of the foothills of the Central Volcanic Cordillera, at the distal end of the underlying andesitic lava flows (Alvarado, 1990, in Kleber et al., 2007). The land to the north and east is a flat coastal plain.

The three primary streams of La Selva are El Surá, El Salto, and Quebrada Esquina, with drainage areas of 4.8 km^2, 8.5 km^2, and 2.3 km^2, respectively; all are tributary to the Río Puerto Viejo (Fig. 2). The basins of the Surà and Salto are entirely within Braulio Carillo National Park and La Selva, whereas the lower Esquina forms the eastern border of La Selva. Most of the watershed of the Esquina beyond La Selva is forested, but the lowermost portion is pastureland.

Rain falls throughout the year, and a dry season is effectively absent because of the prevalence of condensation drip nearly every night. Mean annual precipitation from 1963 to 2008 was 4365 mm, with the driest month on average being March with 168 mm and the wettest months being July and December with 533 mm and 458 mm, respectively (Organization for Tropical Studies, 2010). Standard annual deviation of precipitation from 1963 to 2008 was 700 mm. Mean annual temperature is 26 °C and monthly average temperature fluctuates by <5 °C, whereas daily temperature typically fluctuates by at least 10 °C. Hurricanes seldom reach the area, but intense rains are generated from November to January by the establishment of a cold front and polar trough that penetrates the air mass over the Caribbean Sea to as low as 10°N. (Janzen, 1983). Although hillslopes are frequently steep, typically 0.4 m/m but up to 1 m/m, we observed no evidence for landslides during our extensive field work, perhaps because hillslope length is rarely >50 m.

Channel spanning jams are relatively rare at La Selva, with seven found in 30 50-m-long study reaches, resulting in an average of 4.7 jams/km of channel (Cadol, et al., 2009). These seven jams contain 11% of the total number of wood pieces found in all 30 reaches, although within the reaches that contained channel spanning jams 38–67% of pieces were in jams. If the definition of a jam is broadened to include any group of at least three wood pieces in contact with one another, then 42% of the surveyed pieces were in jams.

All stream corridors are densely vegetated, with smaller woody vegetation immediately adjacent to the active channel. Trees at La Selva can reach 50 m in height, and over 300 hardwood species have been identified at La Selva (Hartshorn and Hammel, 1994). Over 80% of these have ≤1 individual per hectare with diameter at breast height (dbh) ≥ 10 cm (Lieberman and Lieberman, 1994). Nonetheless, the forest is dominated by the species *Pentaclethra macroloba*, which accounts for 13% of all stems and 38% of all aboveground biomass (Clark and Clark, 2000). *Pentaclethra* can reach 40 m in height and is relatively resistant to decomposition, with fallen trees remaining on the forest floor for 20 years (Janzen, 1983). Trees in the old-growth

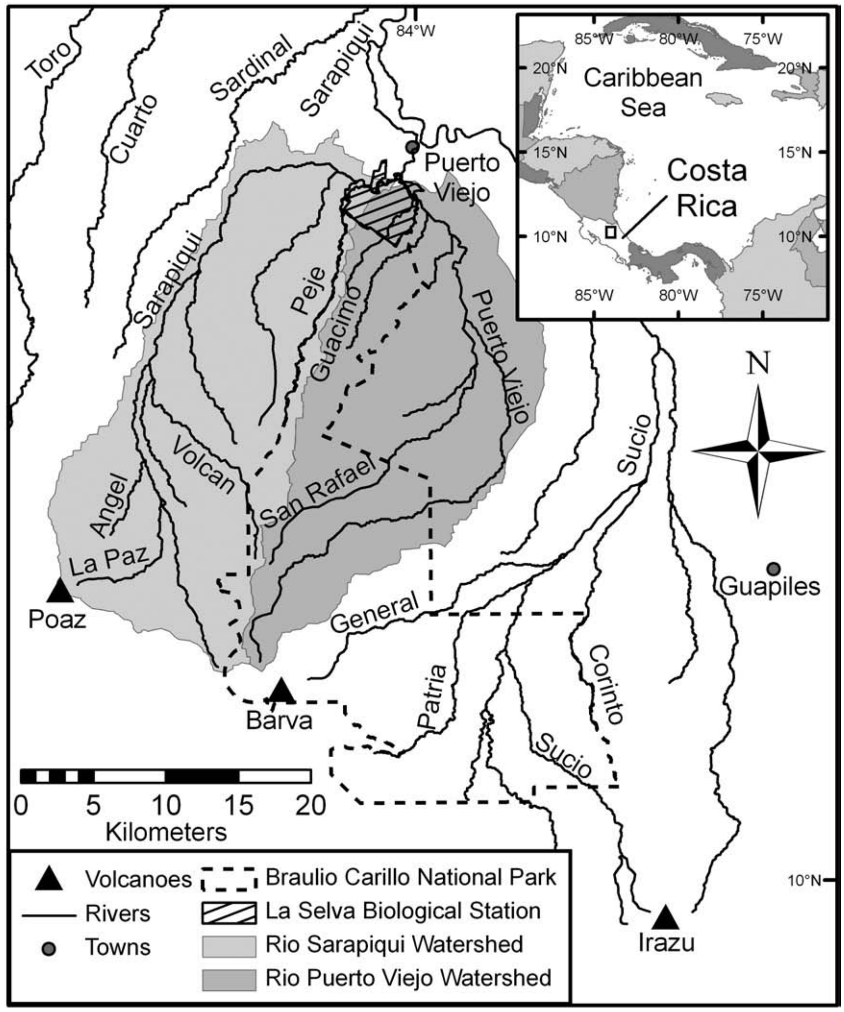

Fig. 1. Map showing the location of La Selva Biological Station within the upper Río Sarapiquí drainage basin.

portion of La Selva have a mean dbh of ~20 cm, and the mean number of stems per hectare is ~450 (Clark and Clark, 2000). Stem turnover is ~2%/y for trees at least 10 cm dbh (Lieberman, et al., 1990) in spite of the lack of disturbances such as hurricanes or landslides. Turnover time of coarse woody debris (CWD; pieces of dead wood >10 cm in diameter) on the forest floor is circa 9 years (Clark et al., 2002). Fallen CWD averages 22.8 m^2/ha, which is comparable to the basal area of living trees at 23.6 m^2/ha (Clark et al., 2002). Wood density ranges from 0.35 to 0.98 g/cm^3 among the various tree species found in La Selva (Clark and Clark, 1999), which extends to higher densities than the range of 0.3–0.7 g/cm^3 cited by Braudrick and Grant (2000) as typical for wood density values found in forested streams of the temperate zone.

3. Methods

3.1. Wood monitoring

All pieces of large wood (wood with diameter ≥ 0.1 m and length ≥ 1 m) in the study reaches were monitored for 2.3 years, with resurveys taking place approximately every 4 months. Surveys were done in July and November of 2007; March, June, and November of 2008; and February, June, and November of 2009. Ten representative study reaches (Fig. 2) were selected for monitoring from an initial group of 30 reaches surveyed in March 2007 (Cadol et al., 2009). These reaches were selected to cover the full range of bed material size and gradient observed in the full data set, while also providing for relatively easy access. Each reach was ~50 m long, with gradients ranging from 0.2 to 6.2%, channel widths ranging from 4.9 to 13.4 m, and drainage areas ranging from 0.3 to 6.8 km^2 (Table 1). Additional reach information and images are available in Cadol et al. (2009). Reaches that are 50 m long may not be representative of the full streams of which they are a part, as a result of local variations in gradient or confinement. But by monitoring reaches from a broad range of local gradients, bed material size distributions, and drainage areas, this study attempts to describe the range of variability of wood dynamics, as well as the typical or average behavior.

In the initial survey, all large wood pieces were flagged, numbered, and the end points surveyed with a total station. The total length (l_w), length within the active channel (l_{bf}), and midpoint diameter (d_w) of each piece was recorded, as was its position in the stream (attached, unattached, ramp, bridge) and its qualitative decay class (1–7). We delineated the active channel at the edge of dense vegetation where there was a break in slope. This level is similar in concept to the bankfull channel, although it appears to be flooded multiple times each year. Attached pieces included pieces that were buried in streambed sediment, pinned under rocks, and pinned under larger logs or in channel spanning jams; unattached pieces were loose within the channel; ramp pieces had one end within the channel and one end on the bank above the active channel; and bridge pieces had each end resting on opposite banks of the channel. The decay scale was modified from Grette (1985) with minimum criteria of: 1—leaves present; 2—small branches present, bark intact; 3—only large branches present, bark mostly intact; 4—bark rotting; 5—bark absent,

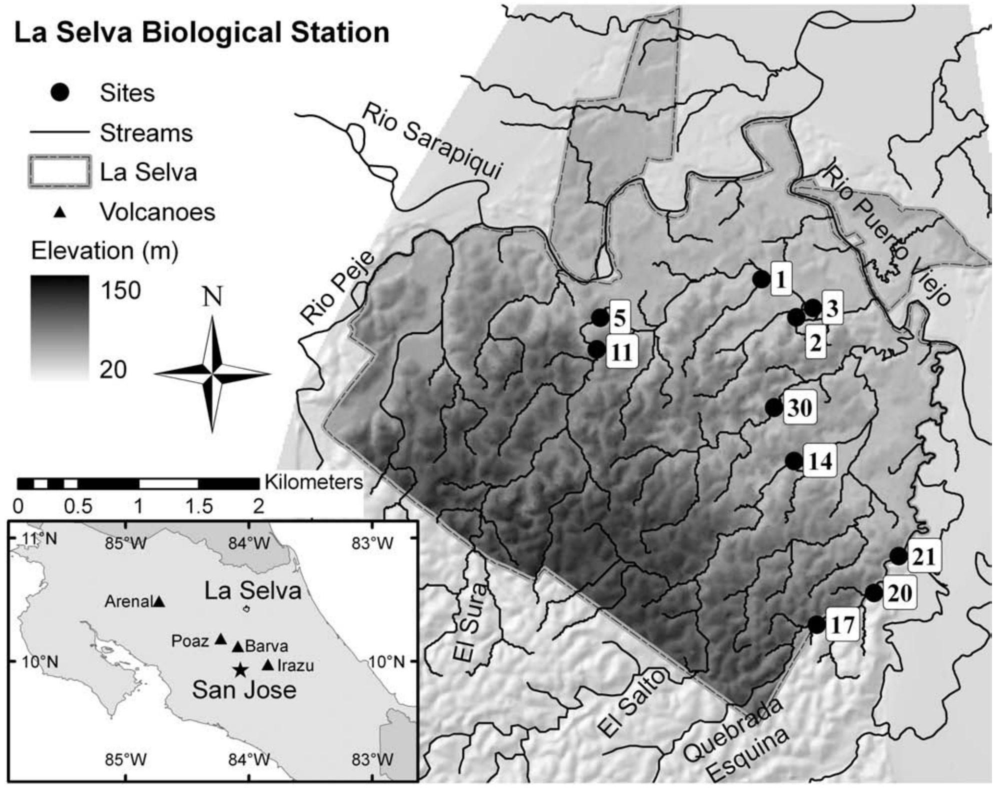

Fig. 2. Map of the primary drainages of La Selva, showing the locations of the 10 study reaches in which wood was monitored.

surface slightly rotted; 6—surface extensively rotted, center solid; and 7—center rotted. No attempt was made to identify species. In all subsequent surveys all new pieces were flagged, numbered, measured, and described. All pieces that already had flags were reflagged and described, but not remeasured unless they had broken since the previous survey. All pieces were resurveyed with a total station. Some low gradient sites had very deep silt deposits that may have contained hidden wood. Although all of the large wood in these reaches was likely found over the duration of the study, the measured wood loads should be considered minimum values.

3.2. Decay samples

Recently fallen samples of three common trees of La Selva, *Cecropia* (probably *Cecropia peltata*, trumpet-wood), *Pentaclethra macroloba*, and *Dipteryx panamensis*, were obtained in July 2007. These species typically have specific weights of 0.26–0.34, 0.50–0.60, and 0.72–0.86, respectively (Jiménez et al., 2002). *Cecropia* is common in high disturbance areas such as stream corridors and grows quickly to heights of up to 20 m, with diameters typically 20–30 cm (Jiménez et al., 2002). *Pentaclethra* is a subcanopy tree that is common on alluvial soils (Jiménez et al., 2002) and is the most common tree at La Selva (Clark and Clark, 2000). *Dipteryx* is an emergent and canopy tree with prominent buttresses that grows well in flat areas with alluvial soil and can reach heights up to 60 m (Jiménez et al., 2002). We were able to obtain two pieces of *Cecropia*, each 20 cm in diameter and approximately 1 m long, and one piece each of *Pentaclethra* and *Dipteryx*, both 25 cm in diameter and 1 m long. The *Pentaclethra* and *Dipteryx* samples were cut in half parallel to the long axis, resulting in a total of six samples, two of each species. The pieces were attached vertically to bridge piers with wire cables at two sites, one sample of each species at each site. The pieces were situated so that the lower portion was sunken in sediment, the middle portion was submerged at typical base flow stage, and the upper portion was typically exposed but very frequently submerged during floods. The surface strength of the wood was measured with a bank penetrometer over 28 months on the same schedule as the surveys. In November 2009 the pieces were removed from the streams. Cross sections ~8 cm wide were cut out of the pieces, one each from the top, middle, and bottom of each piece. The volume of each slice was found by measuring the width of each slice with a tape measure and calculating the cross-sectional area from digital photographs using ArcGIS. Each slice was weighed wet, then put in an oven at 70 °C to dry for 3 days and weighed again dry. Wet and dry densities were calculated from these values.

Table 1
Study reach characteristics.

Site #	Stream name	Stream gradient (%)	Drainage area (km^2)	Active channel width (m)	Dominant bed material
1	Taconazo	0.24	0.28	7.3	Sand
2	Arboleda	0.22	0.40	7.3	Silt
3	Surá	0.24	4.79	8.1	Sand
5	Surá	1.22	3.36	10.3	Boulder
11	Surá	6.16	3.26	13.4	Boulder
14	Salto	0.97	6.77	7.8	Sand
17	Esquina	3.20	1.64	8.3	Boulder
20	Esquina	1.00	2.18	7.7	Gravel
21	Esquina	0.75	2.27	8.2	Cobble
30	Saltito	0.30	1.20	4.9	Sand

3.3. Stream discharge gaging and flow characterization

We installed a vented pressure sensor stage gage at one of the sites (site 5, Surá) that recorded stage every 15 min from 21 November 2007 to 18 July 2009. A stage–discharge relationship was established using the best fit power function of 8 salt-slug conductivity discharge measurements taken over the widest range of discharges available at site 5 during our time in the field. On 18 July 2009, the installation was destroyed by a flood, although a nonvented sensor being used as a backup at the site was recovered in November 2009. Estimated peak flow at failure was 10 m^3/s, but it may have been as high as 20 m^3/s, with uncertainty caused by extrapolation of the stage–discharge relationship beyond 1.25 m^3/s, the highest discharge measured in the field. Drainage area at the site is 3.36 km^2, meaning runoff production during the flood was likely between 3 and 6 $m^3/s/km^2$. The second largest flood recorded was estimated to have a peak flow of 4.4 m^3/s on 23 November 2008.

We compared flow characteristics at La Selva with those at HJ Andrews Experimental Forest in Oregon, USA, a temperate zone site with both a long stream gage record available online (Johnson and Rothacher, 2009) and published wood retention data (Lienkaemper and Swanson, 1987). We considered the cumulative distributions of discharge, maximum depth at the gage site, and estimated cross section average depth at one riffle in El Surá at La Selva and one in Mack Creek at HJ Andrews near their respective gages. We estimated riffle depth at these sites from discharge records using a surveyed cross section from each site and the Mannings equation, $Q = n^{-1}AR^{2/3}s^{1/2}$, where Q is discharge in m^3/s, n is the Mannings resistance coefficient, A is cross-sectional area in m^2, R is hydraulic radius in m, and s is channel gradient. The Mannings n coefficient was visually estimated at Mack Creek ($n = 0.07$) and calibrated to match measured stage and discharge at El Surá ($n = 0.08$). Given the difficulty of estimating n values in steep channels (Wohl, 2000), n was assumed to be constant despite changing stage. The uncertainty in estimating depth caused by this simplifying assumption is likely to be $<10\%$ and thus negligible in the comparison conducted here between different field areas. Cross section average depth (d_{ave}) for each stage was calculated as $d_{ave} = A/w$, where w is top width. We also considered the ratio of daily mean flow to daily peak flow (Q_{mean}/Q_{max}) as a measure of flashiness. A low value of Q_{mean}/Q_{max} indicates that the peak flow for that day was much higher than the mean and that stage rose and fell quickly, whereas a high value of Q_{mean}/Q_{max} near 1 indicates that flow was nearly constant that day.

3.4. Retention rates and mean residence times

The percentage of logs retained within each study reach was calculated for every time interval, from ~4 months (sample size, $N, = 7$) to ~28 months ($N = 1$). The mean retention rate for time intervals that were approximately equal was calculated, for example all ~4 month time intervals were grouped together even though actual intervals between visits ranged from 3 to 5 months. Retention rates weighted by piece volume (v) were also calculated for all time intervals, calculating piece volume as $v = l_{bf}\pi(d_w/2)^2$. We converted the average retention rates for each time interval into an equivalent yearly retention rate using the formula $r_1 = r_x^{(1/x)}$ where r_1 is the yearly retention rate, r_x is the observed retention rate over time interval x, and x is the time interval in years.

If the wood load is assumed to approximate a steady state, which is reasonable at La Selva considering the lack of landslide-introduced wood, the undisturbed history of the sites, and the frequent flooding relative to the study period (Cadol et al., 2009), then short-term wood retention rates can be extrapolated into mean residence times. In systems with a constant introduction rate and a constant depletion rate, which is complementary to the retention rate, the cumulative age distribution of wood can be described with an exponential decay function of the form $c = e^{(-rt)}$ were c is the cumulative distribution function (CDF) of wood relative to time, i.e., the proportion of wood older than t, r is the depletion rate, and t is the age. Mean residence time in this case is the inverse of the depletion rate. Depletion rates, CDFs, and mean residence times can be calculated in terms of the number of wood pieces, wood volume, wood mass, and carbon content, among others. We calculated residence times in terms of wood pieces and wood volume.

3.5. Logistic regressions

A logistic regression analysis was performed using the R statistical software package version 2.5.1 in order to assess the wood and stream variables that best predict the likelihood of a piece being transported out of the study reaches. We considered the wood piece variables total length (l_w), diameter, (d_w), decay class (c_d), and type (t, a categorical variable), the stream variables gradient (s), drainage area (A_d), active channel width (w), average active channel depth (d), relative stream power (Ω, calculated as the product of gradient and drainage area), relative unit stream power (ω, calculated as stream power divided by width), and 84th percentile of grain size (d_{84}), and the hybrid variables wood diameter to bankfull depth ratio (d_r), and wood length to bankfull width ratio (l_r). We found s, w, and d from field surveys of the channels, A_d from a LiDAR derived digital elevation model (DEM) of La Selva and the surrounding area, and d_{84} from a pebble count of 100 clasts at each site. We also considered site variability that was not captured in the measured stream variables by including a categorical variable for each site. Variables that had log-normal distributions were log transformed prior to analysis, which included l_w, d_w, l_r, d_r, and s. The response variable was a categorical transport variable, in which 0 indicated that the piece was retained in the reach and 1 indicated that the piece had been transported out of the reach.

Models were primarily evaluated using the Akaike Information Criterion (AIC) as calculated by the general linear modeling function in R, which helps choose the most parsimonious model by balancing predictive power with the number of variables included in the model (Akaike, 1973). Many models had similarly low AIC values, so models were also evaluated using the percent of logs that were correctly classified as transported or retained by the model. To evaluate this classification power, the fitted transport likelihood returned by the logistic regression for each wood piece was rounded to 0 (i.e., retained) if the value was <0.5, and rounded to 1 (i.e., transported) if the value was ≥ 0.5. The proportion of pieces that were both observed to have been transported and predicted to have been transported was combined with the proportion of pieces that were both observed to have been retained and predicted to have been retained, giving the total proportion of pieces that were accurately classified by the model. Models were only considered if all individual variables were significant in the model at $p<0.05$. When multiple models performed similarly well in both evaluations, the one with the fewest variables was selected.

The models that performed best in the evaluations included categorical site variables. Because these variables by definition represent variation between sites that is not explained by the variables measured in the field and because their estimated parameters may simply encompass random variation thereby artificially inflating the power of the model, we also performed model selection on all models that excluded categorical site variables. Excluding these site variables generally led to a minimal loss in classification power.

We excluded those pieces which were first observed in the study reaches in November 2009 from the retention analysis because these pieces that were first observed during this final survey never had an opportunity to be transported in the study period. Even if one of these pieces was extremely prone to transport and would have been transported within 4 months, it was classified as retained simply because we were unable to resurvey the reaches subsequent to its emplacement.

4. Results

4.1. Wood retention rates and residence times

The number of wood pieces and the volume of wood did not show any consistent trends through time across the study reaches (Fig. 3), although the wood piece depletion rate during each interval between

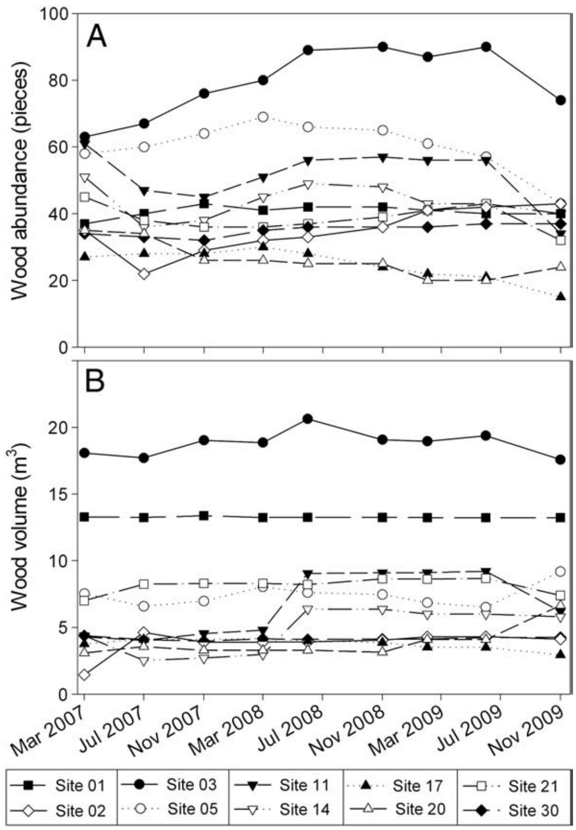

Fig. 3. Variation in wood load in the 10 study reaches during the study period, in terms of (A) piece abundance and (B) total in-stream wood volume. No consistent trends through time were observed.

surveys correlated very well with peak discharge at the stream gage site (Fig. 4). We interpret this lack of trend as supporting the assertion that wood load is in a steady state at La Selva, with abundance fluctuating around a mean. If this assertion is accurate, then we may extrapolate the observations of wood retention rates over the 28-month period of July 2007–November 2009 into much longer estimated mean retention times.

Yearly retention rates for wood pieces ranged from 0.41 to 0.92, depending on the study reach and the time interval considered (Table 2). Averaging the yearly retention rates calculated from the various time intervals within each site gives a range of 0.55–0.91

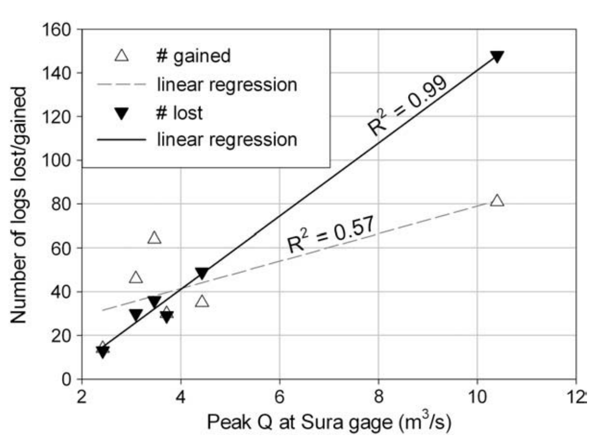

Fig. 4. Wood piece loss and gain relative to peak discharge at the gage on El Surá at site 05. Stage at El Surá was recorded at 10-minute intervals. The highest discharge measurement used to establish the stage–discharge relationship was 1.25 m^3/s, so all peaks reported here are estimates based on extrapolation using a power function.

among the sites. In terms of wood volume, the average retention rates ranged from 0.67 to 0.99 among the sites (Table 3). Average residence times for pieces range from 2.2 to 10.6 years among the 10 reaches, with an average for all reaches of 4.9 years.

Average residence times by volume range from 3.0 to 83.2 years, which includes one high outlier, site 1 on the Taconazo (Table 3). This was the smallest study reach by discharge, and the wood load was dominated by two very large pieces that bridged the channel, one 65 cm in diameter and one 150 cm in diameter. We should note that because residence times are calculated as the inverse of depletion rates, as the retention rate approaches 1 and the depletion rate approaches zero, small measurement errors lead to large errors in calculated residence time. If an observed depletion rate of 0.5 has ± 0.01 uncertainty, then the mean residence time of 2 years will have ± 0.04 years uncertainty; but if a depletion rate of 0.1 has ± 0.01 uncertainty, then the mean residence time of 10 years will have about ± 1 year uncertainty, and a rate of 0.012 (which is the observed depletion rate in site 1, Taconazo) with ± 0.01 uncertainty will lead to mean residence times that could range from 45 to 500 years. In general, the percent uncertainty is equal. Because the wide variation of residence times is caused by the random location of very large pieces and because small measurement errors in such a situation will lead to large residence time errors, we do not think a simple average of the 10 residence times will necessarily represent mean residence time in the study area. Therefore, we calculated a mean retention rate weighted by the volume of wood in each reach, which results in a retention rate by volume of 0.855. This is equivalent to a mean residence time of 6.9 years, which is shorter than the simple average of the 10 residence times of 14.7 years.

We have very limited data with which to constrain the uncertainty involved in scaling up our observed depletion rates either spatially or temporally. We surveyed the longitudinal position of all large wood along 1150 m of Quebrada Esquina, which also contained three of the long-term study reaches. The average number of pieces in 50-m sections was 34, with a standard deviation of 10.6 ($N = 23$), which compares well with the average number of pieces in the three Esquina study reaches (32). The wood frequency in the study reaches thus appears representative of the full channel, but this is still not direct information on the variability of retention rates. The only long-term data set for temporal uncertainty analysis is precipitation. Mean annual precipitation from 1963 to 2008 was 4365 mm, with a standard deviation of 700 mm. Precipitation during the 3 years of the study was 4077 mm (2007), 4191 mm (2008), and 4826 mm (2009), all within half the standard deviation of the mean. The average maximum monthly precipitation in each year over the period of record was 727 mm, standard deviation 194 mm. For the 3 years of the study, the maximum monthly precipitation of each year was 619 mm in November 2007, 550 mm in August 2008, and 658 mm in July 2009, all less than the record average. Thus, the study may have occurred during a period with lower than average flow and higher than average retention.

The relationship between estimated mean residence times and the stream variables s, A_d, Ω, and ω at the 10 study reaches can be described with power functions with exponents of -0.34, -0.24, -0.20, and -0.21 and coefficients of determination of 0.62, 0.26, 0.58, and 0.52, respectively (Fig. 5). No multivariate models for mean residence time using these four stream variables were found in which all variables included in the model were significant at a 0.05 confidence level. Logistic models of wood retention and mean residence times will be considered later.

4.2. Wood decay

Surface resistance of the wood pieces affixed to the bridge piers showed consistent vertical trends. The wood became more solid moving down the piece, except when the irregular presence of bark interfered. The resistance of the *Pentaclethra* and *Dipteryx* pieces could

Table 2
Average retention rates for wood pieces.

Site #	Stream name	Retention rates (average rate for interval length, equivalent annual rate)							Average annual retention rate	Equivalent mean residence time (years)
		4 months	8 months	12 months	16 months	20 months	24 months	28 months		
1	Taconazo	0.96, 0.88	0.92, 0.89	0.90, 0.90	0.88, 0.91	0.85, 0.90	0.78, 0.88	0.73, 0.87	0.89	9.1
2	Arboleda	0.90, 0.74	0.85, 0.79	0.81, 0.81	0.76, 0.81	0.69, 0.80	0.63, 0.80	0.55, 0.77	0.79	4.7
3	Surá	0.87, 0.66	0.83, 0.75	0.79, 0.79	0.75, 0.80	0.70, 0.81	0.63, 0.79	0.51, 0.75	0.76	4.2
5	Surá	0.88, 0.67	0.82, 0.74	0.76, 0.76	0.71, 0.77	0.64, 0.77	0.56, 0.75	0.45, 0.71	0.74	3.8
11	Surá	0.79, 0.49	0.72, 0.61	0.66, 0.66	0.58, 0.67	0.48, 0.65	0.37, 0.61	0.26, 0.56	0.61	2.5
14	Salto	0.89, 0.72	0.82, 0.74	0.75, 0.75	0.71, 0.77	0.67, 0.78	0.65, 0.81	0.53, 0.76	0.76	4.2
17	Esquina	0.74, 0.41	0.63, 0.51	0.54, 0.54	0.48, 0.58	0.43, 0.60	0.39, 0.63	0.29, 0.58	0.55	2.2
20	Esquina	0.85, 0.61	0.76, 0.66	0.67, 0.67	0.62, 0.70	0.58, 0.72	0.54, 0.73	0.44, 0.70	0.68	3.2
21	Esquina	0.86, 0.64	0.82, 0.75	0.79, 0.79	0.76, 0.81	0.71, 0.81	0.63, 0.80	0.53, 0.76	0.77	4.3
30	Saltito	0.96, 0.88	0.94, 0.91	0.91, 0.91	0.88, 0.91	0.86, 0.91	0.85, 0.92	0.76, 0.89	0.91	10.6

Table 3
Average retention rates for a unit wood volume.

Site #	Stream name	Retention rates (average rate for interval length, equivalent annual rate)							Average annual retention rate	Equivalent mean residence time (years)
		4 months	8 months	12 months	16 months	20 months	24 months	28 months		
1	Taconazo	0.996, 0.987	0.991, 0.987	0.989, 0.989	0.986, 0.990	0.982, 0.989	0.974, 0.987	0.970, 0.987	0.988	83.2
2	Arboleda	0.85, 0.60	0.78, 0.69	0.74, 0.74	0.67, 0.74	0.57, 0.71	0.47, 0.68	0.19, 0.49	0.67	3.0
3	Surá	0.94, 0.82	0.91, 0.87	0.89, 0.89	0.87, 0.90	0.87, 0.92	0.84, 0.91	0.79, 0.91	0.89	9.1
5	Surá	0.90, 0.74	0.85, 0.79	0.80, 0.80	0.76, 0.81	0.70, 0.81	0.61, 0.78	0.45, 0.71	0.78	4.5
11	Surá	0.85, 0.61	0.81, 0.73	0.77, 0.77	0.71, 0.77	0.58, 0.72	0.43, 0.66	0.23, 0.53	0.68	3.2
14	Salto	0.94, 0.83	0.90, 0.86	0.84, 0.84	0.82, 0.86	0.74, 0.84	0.75, 0.86	0.69, 0.86	0.85	6.7
17	Esquina	0.90, 0.73	0.85, 0.79	0.80, 0.80	0.77, 0.82	0.72, 0.82	0.70, 0.84	0.65, 0.83	0.80	5.1
20	Esquina	0.94, 0.82	0.89, 0.84	0.84, 0.84	0.80, 0.85	0.79, 0.87	0.77, 0.88	0.73, 0.88	0.85	6.8
21	Esquina	0.93, 0.81	0.89, 0.84	0.84, 0.84	0.78, 0.83	0.76, 0.85	0.72, 0.85	0.64, 0.83	0.84	6.1
30	Saltito	0.98, 0.94	0.96, 0.95	0.95, 0.95	0.93, 0.95	0.92, 0.95	0.92, 0.96	0.89, 0.95	0.95	19.4

not be differentiated using a bank penetrometer because they were both more resistant than the maximum pressure we could measure. The *Cecropia* pieces were always less resistant than either of the others at all vertical locations. During removal, the upper 10–25 cm of both *Cecropia* pieces fell apart under their own weight. The other pieces were still quite sound, and cross sections had to be cut with a chainsaw.

The wet densities of the pieces after removal from the streams were all about 1 g/cm^3 or greater (Table 4). Slices 11–18 were dried in a separate oven than slices 1–10, and the oven used for slices 11–18 may not have held its temperature properly, possibly explaining the wide variation between dry densities of the same species. Generally, dry density decreased moving up each log (Fig. 6), but trends varied. The slices were not fully dry after 3 days in the ovens and some of the variation in trends may have been caused by uneven drying. If we had been able to fully dry each piece, the trends might have been more consistent.

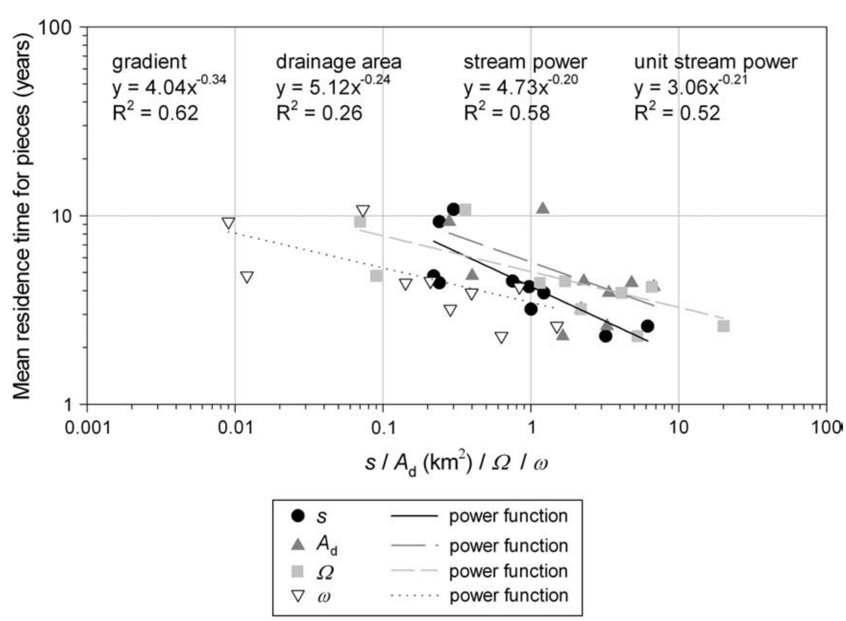

Fig. 5. Mean residence time for in-stream wood pieces in the 10 study reaches plotted against gradient (s), drainage area, (A_d), stream power (Ω, calculated as the product of s and A_d, using A_d as a surrogate for discharge), and unit stream power (ω, calculated as Ω divided by the reach average active channel width). Gradient has the highest coefficient of determination (R^2).

Table 4
Decay results.

Piece #	Stream	Species[a]	Vertical location	Wet density (g/cm^2)	Dry density (g/cm^2)
1	Surá	Cec.	Top	0.910	0.239
2	Surá	Cec.	Mid	0.984	0.329
3	Surá	Cec.	Low	1.028	0.291
4	Surá	Dip.	Top	1.273	0.896
5	Surá	Dip.	Mid	1.227	0.861
6	Surá	Dip.	Low	1.334	0.937
7	Surá	Pent.	Top	1.089	0.373
8	Surá	Pent.	Mid	1.167	0.523
9	Surá	Pent.	Low	1.238	0.576
10	Salto	Cec.	Top	0.879	0.244
11	Salto	Cec.	Mid	0.992	0.453
12	Salto	Cec.	Low	1.035	0.526
13	Salto	Dip.	Top	1.379	1.057
14	Salto	Dip.	Mid	1.137	0.873
15	Salto	Dip.	Low	1.279	0.901
16	Salto	Pent.	Top	1.040	0.632
17	Salto	Pent.	Mid	1.190	0.619
18	Salto	Pent.	Low	1.265	0.739

[a]Species abbreviations: Cecropia (Cec.), Dipteryx (Dip.), Pentaclethra (Pent.).

4.3. Statistical modeling of wood retention

As a precursor to modeling, we analyzed how the percent of wood that was transported varied with the potential controlling piece variables length (l_w), diameter (d_w), decay class (c_d), and type (t). We present here the results of the analyses that excluded the pieces that were found in November 2009, as discussed earlier. The likelihood of a piece of wood being lost correlates well with d_w (Fig. 7A) and the natural logarithm of l_w (Fig. 7B); it does not correlate well with c_d (Fig. 7C). The four type classes have distinct wood loss rates, with unattached pieces being removed at the highest rate, followed by attached, ramp, and bridge (Fig. 7D).

The best logistic model of the data included the continuous variables $\ln(l_r)$ and $\ln(s)$, and the categorical (dummy) variables t_u (1 if unattached, 0 otherwise) and $site_{03}$ (1 if in site Sura03, 0 otherwise). The variables l_r and s were log transformed because of their apparent log-normal distribution. This model correctly predicted the status, either retained or transported, of 72% of the pieces (Figs. 8A and B).

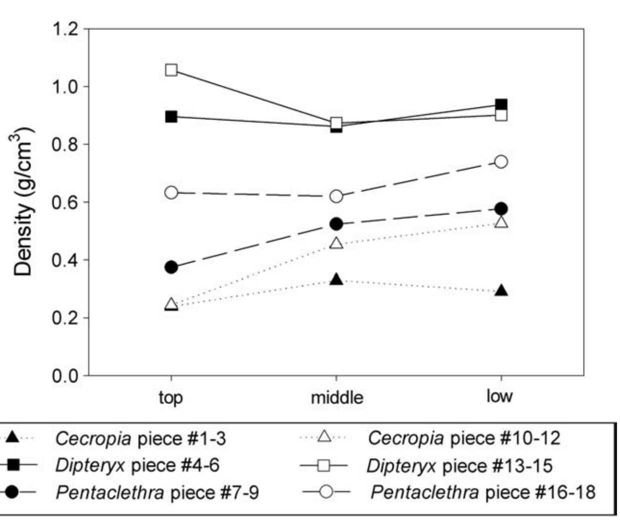

Fig. 6. Density of wood after 2.3 years affixed to bridge piers in El Surá and El Salto. The 1-m long pieces were oriented vertically such that the lower portion was sunken in sediment, the middle portion was nearly always submerged, and the top was above the water surface at base flows but submerged during floods. After removal from the streams, 8-cm-thick slices were cut from the top, middle, and bottom of the pieces using a chainsaw. The densities reported here were calculated after the pieces were dried in ovens for 3 days at 70 °C. Piece numbers refer to Table 4.

The best logistic model that excluded categorical site variables included the continuous variables $\ln(l_r)$ and $\ln(s)$ and the categorical variable t_u. It correctly predicted the status of 70% of the pieces (Fig. 8C). The likelihood of transport given by the model agrees well with the observed transport rates. For example, the 38 pieces given a transport probability between 0.50 and 0.55 by the model had an observed transport rate of 0.50 (Fig. 8D). Interpreting the estimated parameters of the model ($\beta_{\ln lr} = 0.920$, $\beta_{\ln s} = 0.493$, $\beta_{tu} = 0.964$), we find that the odds of transport are halved for every doubling of relative log length (l_r), the odds of transport are doubled for every fourfold increase in gradient (s), and the odds of transport increase by a factor of 2.6 if a piece is unattached relative to the other types. Odds (o) and probability (p) are related by the equation $o = p(1-p)^{-1}$.

4.4. Comparison of flow characteristics

We found that floods were flashier at La Selva than at HJ Andrews Experimental Forest, Oregon, as indicated by lower values of Q_{mean}/Q_{max} at La Selva on days with high discharge (Fig. 9). Floods that exceeded 0.4 m^3/s/km^2 were 4–10 times more common at La Selva than at HJ Andrews (Table 5). Flows of a given frequency were deeper in El Surá, Costa Rica, than in Mack Creek, Oregon (Fig. 10). This is in part because of the lower width-to-depth ratio in El Surá, which may be influenced by the dense bank vegetation, deeply weathered bedrock, or frequent floods. Flow depth at the gage exceeded 0.5 m 2.8 d/y on average at Mack Creek, but 150.6 d/y at El Surá; d_{ave} at the surveyed riffles never exceeded 0.5 m at Mack Creek over 30 years of records, but exceeded 0.5 m six times at El Surá in 1.66 years (Table 6). In-stream wood was smaller on average at La Selva, and d_{ave} at the riffle exceeded the diameter of the largest piece once (during the flood that destroyed the stream gage) when the average depth was estimated to be 0.89 m. This largest piece, 9.05 m long and 0.73 m in diameter, had been previously observed upstream of the study reach and was transported approximately 35 m during the flood, even though its relative length (l_r) was>1. In contrast, the largest diameter observed in Mack Creek was 2.2 m, which is much greater than the highest estimated average depth over the surveyed riffle (0.46 m). The comparison between HJ Andrews and La Selva is instructive, but not perfect — in part because HJ Andrews receives about 2.5 m of precipitation annually (Lienkaemper and Swanson, 1987), whereas La Selva receives 4.37 m annually (Organization for Tropical Studies, 2010).

5. Discussion

5.1. Wood retention controls

Piece size relative to channel size, especially l_r, was important for modeling wood mobility, as predicted by flume work (Braudrick and Grant, 2001) and observed in other field studies across a wide range of climatic conditions (Lienkaemper and Swanson, 1987; Berg et al., 1998; Jacobson et al., 1999; Daniels, 2006). The logarithmic nature of the relationship between length and mobility has also been observed in the temperate zone (Berg et al., 1998). Stream gradient and relative stream power were both good predictors of mean residence times (Fig. 5), but the logistic regression models tended to perform significantly better with gradient. Drainage area added little information to the models, and gradient and stream power were highly correlated. This may be an artifact of the limited sample size of stream reaches, or it may reflect variability in the drainage area–discharge relationship within the study area. Transbasin subsurface flow is known to occur at La Selva as groundwater from higher in the mountains emerges in seeps and springs (Genereux and Jordan, 2006). This could mean that the actual influence of discharge on wood mobility is not captured by using drainage area as a surrogate.

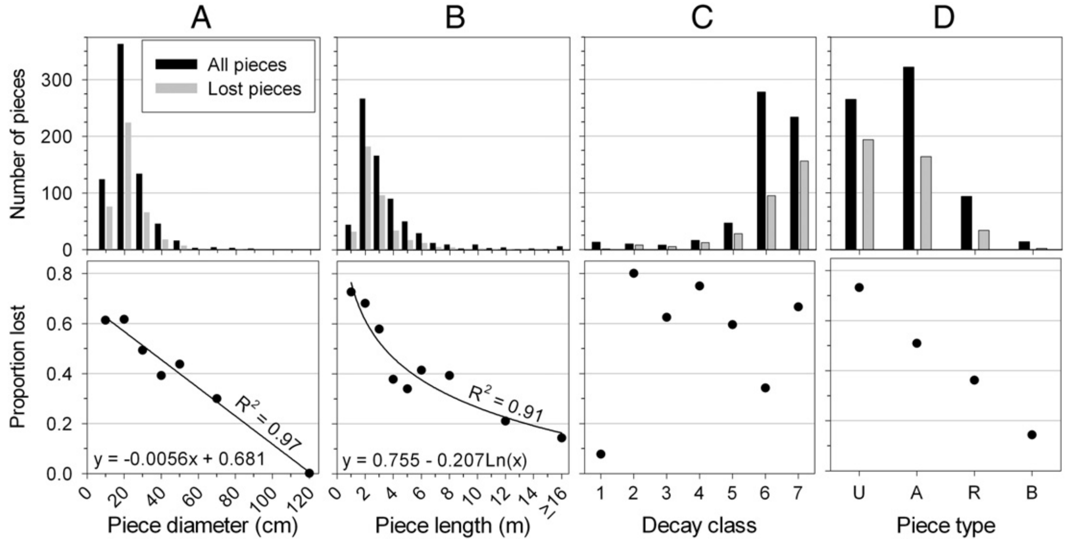

Fig. 7. The distribution of found and lost pieces and the proportion lost of all surveyed pieces sorted by (A) diameter, (B) length, (C) decay class, and (D) boundary interaction type. Types are U — unattached, A — attached, R — ramp, and B — bridge (see methods section for type description). Pieces that were first observed in November 2009 were excluded from these analyses because there was no opportunity to observe transport of these pieces.

Decay class was not correlated with the likelihood of a piece being retained within the study reaches. However, we did observe that *Cecropia* pieces that are exposed to repeated wetting and drying disintegrate within 2.5 years and that *Pentaclethra* pieces in the same position can lose over one-third of their mass in 2.5 years. The lack of correlation may be because newly fallen pieces are not preferentially located in low energy portions of the stream; whereas older, more decayed pieces that are still present are generally restricted to those that are in locations that favor wood retention or are incorporated in jams. In this way, a winnowing process may be contributing to equal mobility of the pieces across age classes and thus decay classes. As pieces in low energy positions decay, the stability provided by position may be overcome by loss of structural integrity. Decay rate may thus contribute to differences in retention rates between temperate and tropical streams without decay class being a predictor of transport within either region.

Peak stream discharge explains nearly all of the temporal variation in retention rates observed at La Selva (Fig. 4), a finding similar to that of Wohl and Goode (2008). However the lower correlation between flow and piece gain suggests that while fluvial activity dominates

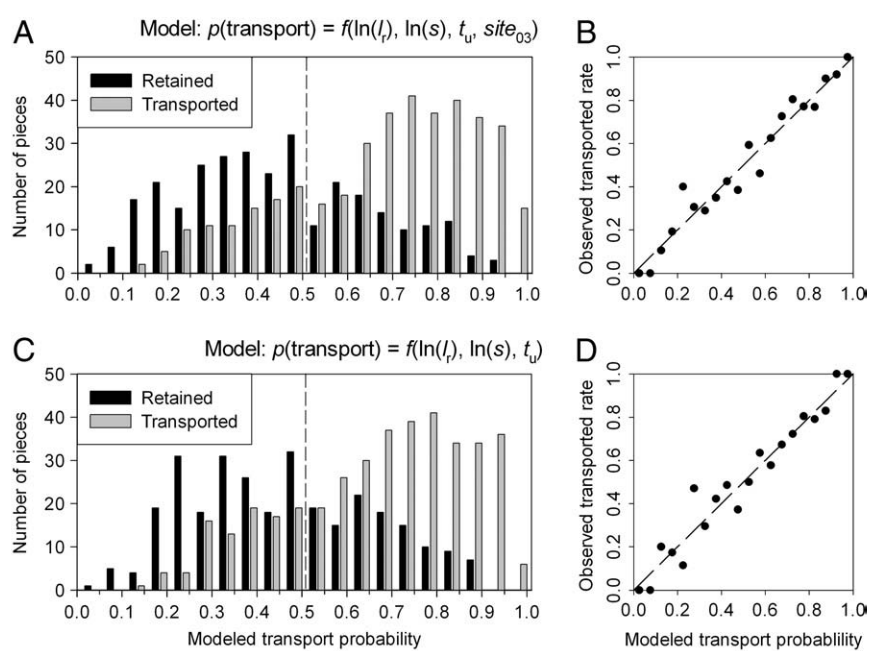

Fig. 8. (A) Results of the best model that includes categorical site variables. The continuous variables in this model are the natural log of relative piece length (l_r, piece length divided by channel width) and the natural log of stream gradient (s); and the categorical variables are whether the piece is unattached (t_u) and whether the piece is in site 03 ($site_{03}$). This model gives 65% of the pieces that were observed to be retained in the reaches a probability of transport <0.5, and 77% of the pieces that were observed to be transported out of the reaches a probability of transport ≥ 0.5. (B) The proportion of pieces observed to have been transported within each modeled transport probability class for the model in part A. The dashed line shows a 1:1 correlation. (C) Results of the best model that excluded categorical site variables. The variables selected for this model were ln(l_r), ln(s), and t_u. This model gives 62% of the pieces that were observed to be retained in the reaches a probability of transport <0.5, and 76% of the pieces that were observed to be transported out of the reaches a probability of transport ≥ 0.5. (D) The proportion of pieces observed to have been transported within each modeled transport probability class for the model in part C. The dashed line shows a 1:1 correlation.

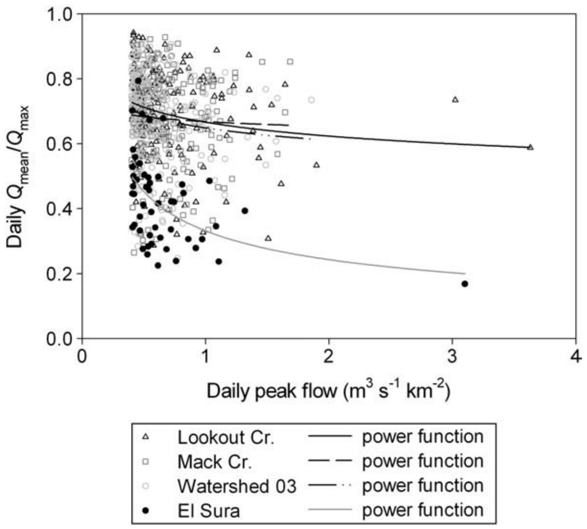

Fig. 9. Ratio of Q_{mean}/Q_{max} for all days with peak flow of >0.4 $m^3/s/km^2$. Note that all three streams in HJ Andrews Experimental Forest (Lookout Cr., Mack Cr, and Watershed 03) had similar trends in spite of the wide range of drainage areas (62.40, 5.81, and 1.01 km^2, respectively). In contrast, El Surá in La Selva (drainage area 3.36 km^2) had much lower average values of Q_{mean}/Q_{max} for a given unit discharge. Q_{mean}/Q_{max} is used here as a measure of flashiness, with high values indicating that peak flow was sustained for nearly the full day and that the flood was not flashy, and low values indicating that the peak flow was sustained for much less than a day and that the flood was flashy. The largest El Surá flow may exaggerate the true flashiness because the gage was destroyed and the record ends with the peak. However, even if the peak discharge had been sustained for the remainder of the day, the Q_{mean}/Q_{max} ratio would still only have been 0.38.

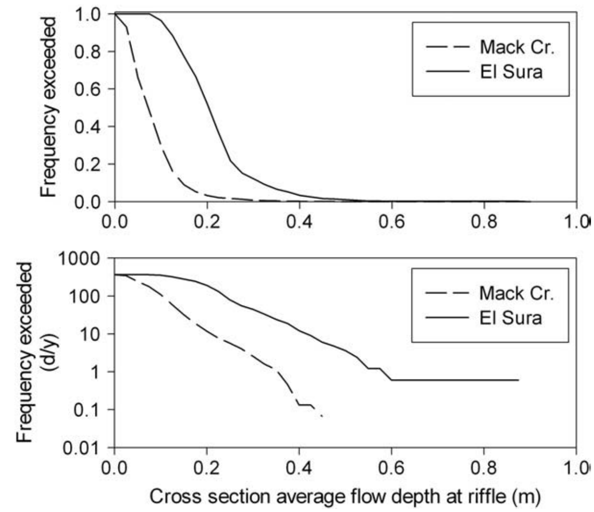

Fig. 10. Proportion of days for which average depth over a riffle exceeds a given value. Depth was calculated from discharge records using surveyed cross sections and the Mannings equation. The Mannings n coefficient was visually estimated at Mack Cr., in HJ Andrews Experimental Forest, Oregon ($n = 0.07$), and calibrated to match measured stage and discharge at El Surá, in La Selva Biological Station, Costa Rica ($n = 0.08$).

piece export it has less influence on piece recruitment into the reach. We did not observe a major influence of preconditioning, as seen in a Pacific Northwest stream (Lienkaemper and Swanson, 1987), where short-term mobility rates were reduced in the times following flows high enough to redistribute newly fallen pieces. Precipitation at La Selva varies relatively little from year to year, either in total rainfall (4375 ± 700 mm, mean ± standard deviation) or distribution (minimum monthly precipitation is 103 ± 61 mm and falls between February and April 93% of years; maximum monthly precipitation is 734 ± 196 mm and falls between May and August 60% of years and between November and December 30% of years). This low variation in rainfall combined with the observed correlation between discharge and wood retention rate supports the assertion that the wood load of the streams of La Selva is approximately steady state. A wide range of peak flows were observed in the two years of gage data, but there is no way of knowing if the full range of conditions present at La Selva were documented in the study period, or if wood load conditions approximate steady state over longer time periods. In part this is because of the lack of long-term gage records, although the long-term precipitation record may provide insight into the representativeness of the study period. Precipitation during the study period was slightly below the long-term average, as noted in the previous section, and thus flow during the study period may be below average as well. There has been one recorded hurricane strike at La Selva, in the early 1960s, which would certainly fall outside of our observations, although the rarity of these events is one of the characteristics of La Selva that supports the conclusion that steady state conditions prevail.

Steady state wood load is likely only possible because of the rarity of landslides. The lack of a landslide influence on wood dynamics at La Selva is in contrast with the Rìo Chagres, Panama, where wood delivery is dominated by large, landslide-triggering tropical storms (Wohl, et al., 2009). After high recurrence interval storm events, landslide-delivered wood forms large jams along the Rìo Chagres that are estimated to persist for 2 years, but the high transport capacity of the river keeps it nearly wood-free in the intervening periods. The steady state dynamics we describe for La Selva, and thus the retention rates and mean residence times presented here, should not be assumed to transfer to all wet tropical settings, and certainly should not be applied to streams in the dry or seasonal tropics without further investigation.

We found a variation of up to 0.25 in wood retention rates depending on of the length of time interval analyzed (Table 2). Part of this variation is because pieces that both enter and exit the study reach in the interval between surveys are not recorded, although

Table 5
Comparison of La Selva and H.J. Andrews study sites.

	HJ Andrews, Oregon			La Selva
	Lookout Cr.	Mack Cr.	Watershed 03	El Surá
Drainage area (km^2)	62.40	5.81	1.01	3.36
Record length (years)	59.2	30	57	1.66
# of days with flow > 0.4 $m^3/s/km^2$	186	215	226	52
Average events/year	3.1	7.2	4.0	31.4

Table 6
Frequency of flow depths at Mack Creek and El Surá, relative to wood size.

	Mack Creek, OR	El Surá, CR
Length of record (years)	30	1.66
Days with max depth at gage > 0.5 m	84	250
Average # of events/year	2.8	150.6
Events with x-sec average depth at riffle > 0.5 m	0	6
Average # of events/year	0.0	3.6
Events with x-sec average depth at riffle > 0.4 m	4	20
Average # of events/year	0.1	12.0
Length of reach in which wood was surveyed (m)	1000	50
Mean wood diameter (m)	0.36	0.20
Events with ave. d at riffle > mean wood diam	27	314
Average # of events/year	0.9	189.2
84th percentile wood diameter (m)	0.60	0.30
Events with ave. d at riffle > 84th perc. wood diam	0	74
Average # of events/year	0.0	44.6
95th percentile wood diameter (m)	0.84	0.40
Events with ave. d at riffle > 95th perc. wood diam	0	20
Average # of events/year	0.0	12.0
Maximum wood diameter (m)	2.2	0.73
Events with ave. d at riffle > max. wood diam	0	1
Average # of events/year	0	0.6

more frequent sampling increases the chances of including these pieces. This effect will lead to lower retention rates for shorter sample intervals. However, in this study we also found lower retention rates for the longest sample intervals. This is because the greatest wood loss occurred in the first and last intervals between the eight surveys, probably driven by natural variation in intersample peak discharge. Both of these low retention intervals were July–November, the rainiest season. Intermediate intervals averaged higher retention rates than the longer intervals because they included more samples that did not cover the two low retention intervals, driving up the average. These two artifacts in the data highlight the ability of sampling interval to affect retention estimates using our method and the need for long-term monitoring to capture the range of interannual and seasonal variation in retention rates.

5.2. Comparison of tropical and temperate zone residence times

The estimated mean residence time found for wood across all the study reaches was 4.9 years for a piece of wood and 6.9 years for a unit volume of wood, which is shorter than most estimates from the temperate zone, particularly estimates from old-growth forests (Table 7), although not all studies to which we compare our data were conducted on similar sized streams or used similar methods. Mean residence times of wood may not meaningfully reflect stream processes if disturbances prevent the attainment of steady state (Dahlström et al., 2005). Therefore we have attempted to limit comparison to undisturbed field sites. Disturbance is likely to lead to shorter residence times, as in the case of the Rocky Mountains of Colorado where Wohl and Goode (2008) found a mean residence time of 3.4 years. The Colorado study streams were in forests that do not appear to have fully recovered from logging in the late 19th century, which likely contributed to the small piece sizes relative to unlogged forests in the region and the short residence times. Natural disturbances such as fires also complicate interpretation of wood residence time findings, although they do not affect La Selva. In a fire-influenced landscape in western Alberta, Canada, Powell et al. (2009) found mean ages since death of 45 and 55 years for pine- and spruce-dominated areas, respectively. In such situations, the dominant age class may reflect time since last stand-replacing fire rather than fluvial or decay processes.

The longest reported mean residence time (350 years mean carbon residence time; similar to wood residence time by mass) and maximum residence time (9485 years) were found in a meandering stream reach in Missouri, USA (Guyette, et al., 2002). The oldest residence times are likely the result of wood burial and exhumation as the channel migrates across its floodplain and were only able to be quantified by the use of radiocarbon dating. This process may be active in the floodplains of the Río Sarapiquí and Río Puerto Viejo at our field site, but not in the steep valleys of the smaller streams.

Estimates of mean residence time for old-growth forests in the temperate zone primarily come from the Pacific Northwest region, USA, and are summarized by Hassan et al. (2005). Difficulties in comparison arise because of the variety of minimum piece size criteria used, the wide range of channel sizes, and the variety of dating methods (Table 7). Mean residence time ranges from 30 y (Hyatt and Naiman, 2001) to 100 y (Keller and Tally, 1979), and as low as 12 years in some individual reaches (Lienkaemper and Swanson, 1987). In comparison, logged catchments in western Washington lost about half of their old-growth-derived wood within 5–11 years (Bilby and Ward, 1991; McHenry et al., 1998), although some of this change may be a direct impact of logging practices.

Mean wood residence time at La Selva is thus shorter than values reported for old-growth temperate rainforests of the Pacific Northwest–in spite of the comparable rainfall total and runoff production in rainforests of the two regions–and similarly large trees that can attain heights of >50 m and diameters of >2 m. However, the analysis of flow shows that discharge is flashier, floods are more common, and flow depths greater than wood diameter are more frequently attained at La Selva than at HJ Andrews. Pieces appear to be smaller on average at La Selva, possibly because of the branching morphology of most tropical trees as opposed to the straight-boled conifers of the Pacific Northwest. Tropical trees may contribute more small pieces to streams by dropping branches that are then more mobile than the main boles or by breaking at the more numerous branching sites upon falling.

Higher tropical decay rates may also contribute to the difference in residence time. Winter in the temperate zone slows decay, whereas the nearly constant temperature of the tropics enables year-round decay. Coarse woody debris (CWD, pieces with a diameter of ≥10 cm) on the forest floor of La Selva have a mean residence time of about 9 years (Clark et al., 2002); whereas in a temperate rainforest study site in the Olympic Peninsula of Washington, spruce and hemlock CWD had mean residence times of 90–100 years (Graham and Cromack, 1982). In HJ Andrews Experimental Forest, mean residence time for CWD is 60–90 years (Harmon and Hua, 1991). Decay rates of many temperate conifer species are summarized by Harmon et al. (1986) and generally range from 30 to 90 years, but can be as high as 250 years. It is unclear whether wood decay rate differences will be of the same magnitude in streams as on the forest floor. Full submersion reduces decay, as documented by the pieces which we introduced into the channel and monitored, and may reduce the influence of the

Table 7
Site characteristics and mean in-stream wood residence times of selected studies.

Study site	Forest type	Minimum piece size		Channel width (m)	Mean residence time (years)	Methods	Reference
		Diam. (cm)	Len. (m)				
Redwoods National Park, Calif.	Redwood, old-growth	10		6–19	~100	Age of trees germinated on piece	Keller and Tally, 1979
Southeast Alaska	Hemlock–spruce, old-growth	10	3	8–31	~54	Age of trees germinated on piece	Murphy and Koski 1989
HJ Andrews Experimental Forest, Ore.	Douglas fir–hemlock, old-growth	10	1.5	3–24	12–83	Observation of wood input	Lienkaemper and Swanson, 1987
Olympic Peninsula, Washington	Hemlock–spruce–Douglas fir, old-growth	60	5	165	30	Dendro-chronology, radiocarbon	Hyatt and Naiman, 2001
Medicine Creek, Missouri	*Quercus–Carya–Acer*, gallery forest	25		Not reported est. ~2	350 (carbon)	Dendro-chronology, radiocarbon	Guyette et al., 2002
Rocky Mtn. foothills, Alberta	Pine- or spruce-dominated, ~100 years. fire recur. int.	10	1	0.8–3.5	45–55	Dendro-chronology	Powell et al., 2009
Rocky Mtns., Colorado	Sub-alpine, logged ~100 years ago	5	1	4.3–6.5	4.3–6.3	Observation of wood export	Wohl and Goode, 2008
La Selva, Costa Rica	Tropical, old-growth	10	1	5–13	5 (piece); 7 (volume)	Observation of wood export	This study

temperature and microbe factors that lead to higher decay on the forest floor in the tropics. And, depending on the sediment dynamics of the stream, abrasion of the wood by particles suspended in the flow may accelerate in-stream wood decay and overwhelm climate differences. Direct measurement of in-stream decay in both temperate and tropical sites may help to determine whether decay is an important control on mobility differences between the two zones.

6. Conclusions

The data show that relative piece length (l_r) is the best single predictor of individual piece transport in the streams of La Selva, with the likelihood of transport doubling if l_r is halved. Unattached pieces are significantly more mobile than other types, taking relative length into account. Stream gradient is the best stream variable for predicting wood mobility on a reach scale, with higher gradients leading to greater mobility. Most temporal variation in retention rates can be explained by variation in peak discharge, with higher peak flows leading to lower retention rates. These results are similar to those documented for wood in headwater streams of the temperate zone. We found annual piece retention rates from 0.55 to 0.91 and annual volume retention rates from 0.67 to 0.99. Assuming wood load is in a steady state, an assertion that the data support, these retention rates are equivalent to mean residence times of 2.2–10.6 years for pieces (with an average of 4.9 years) and 3.0–83.2 years for a unit volume of wood (with a weighted average of 6.9 years). The site with the longest residence time by volume had a time over four times longer than the next longest site (19.4 years). This long age was controlled by the random inclusion of two unusually large bridges. For this reason we propose that the residence time calculated from the weighted average retention rate across all 10 reaches best reflects the character of wood dynamics in this study area. These residence times are generally shorter than those reported for temperate rainforests, as well as other temperate zone environments, and thus support our hypothesis. Flashier tropical flow regimes, branching tropical trees, and higher tropical decay rates are all reasonable explanations for this difference. Comparable data on in-stream wood decay rates from both temperate and tropical sites could help confirm or counter the inference of decay rate differences. Because decay rate and flashiness both tend to correlate with temperature, sites with low decay and high flashiness or high decay and low flashiness are expected to be rare, making it difficult to separate the influence of the two factors. Because of the shorter residence times, wood may be less important in controlling the physical structure of headwater tropical streams compared to temperate zone streams. However, it does not exclude the possibility that wood is important for ecosystem function, as a nutrient source or as a stable substrate in sandy low gradient reaches. If it is determined that wood is necessary for tropical stream ecosystem function, then efforts to maintain wood recruitment into the streams will likely be more effective than introducing engineered log structures. Artificial wood structures are likely to be either quickly removed by flow or decay or, if they are built strongly enough to persist, may perform channel shaping functions not as commonly associated with wood in the tropics as in the temperate zone, and possibly less important to the tropical aquatic ecosystems.

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References

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), 2nd International Symposium on Information Theory. Akademia Kiado, Budapest, pp. 267–281.
Anderson, N.H., Sedell, J.R., Roberts, L.M., Triska, F.J., 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. American Midland Naturalist 100 (1), 64–82.
Baillie, B.R., Davies, T.R., 2002. Influence of large woody debris on channel morphology in native forest and pine plantation streams in the Nelson region, New Zealand. New Zealand Journal of Marine and Freshwater Research 36, 763–774.
Beechie, T.J., Sibley, T.H., 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams. Transactions of the American Fisheries Society 126 (2), 217–229.
Benda, L.E., Sias, J.C., 2003. A quantitative framework for evaluating the mass balance of in-stream organic debris. Forest Ecology and Management 172 (1), 1–16.
Berg, N., Carlson, A., Azuma, D., 1998. Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California. Canadian Journal of Fisheries and Aquatic Sciences 55 (8), 1807–1820.
Bilby, R.E., Likens, G.E., 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61 (5), 1107–1113.
Bilby, R.E., Ward, J.W., 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Canadian Journal of Fisheries and Aquatic Sciences 48 (12), 2499–2508.
Bisson, P.A., Bilby, R.E., Bryant, M.D., Dollof, C.A., Grette, G.B., House, R.A., Murphy, M.L., Koski, K.V., Sedell, J.R., 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. In: Salo, E.O., Cundy, T.W. (Eds.), Streamside Management: Forestry and Fishery Interactions. University of Washington, Institute of Forest Resources, Seattle, pp. 143–190. Contribution No. 57.
Braudrick, C.A., Grant, G.E., 2000. When do logs move in rivers? Water Resources Research 36 (2), 571–583.
Braudrick, C.A., Grant, G.E., 2001. Transport and deposition of large woody debris in streams: a flume experiment. Geomorphology 41 (4), 263–283.
Brooks, A.P., Brierley, G.J., Millar, R.G., 2003. The long-term control of vegetation and woody debris on channel and flood-plain evolution: insights from a paired catchment study in southeastern Australia. Geomorphology 51 (1–3), 7–29.
Cadol, D., Wohl, E., Goode, J.R., Jaeger, K.L., 2009. Wood distribution in neotropical forested headwater streams of La Selva, Costa Rica. Earth Surface Processes and Landforms 34 (9), 1198–1215.
Clark, D.A., Clark, D.B., 1999. Assessing the growth of tropical rain forest trees: issues for forest modeling and management. Ecological Applications 9 (3), 981–997.
Clark, D.B., Clark, D.A., 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. Forest Ecology and Management 137 (1–3), 185–198.
Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Tomlinson, J.R., Ni, J., Holland, E.A., 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. Ecological Applications 11 (2), 371–384.
Clark, D.B., Clark, D.A., Brown, S., Oberbauer, S.F., Veldkamp, E., 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. Forest Ecology and Management 164 (1–3), 237–248.
Comiti, F., Andreoli, A., Lenzi, M.A., Mao, L., 2006. Spatial density and characteristics of woody debris in five mountain rivers of the Dolomites (Italian Alps). Geomorphology 78 (1–2), 44–63.
Curran, J.H., Wohl, E.E., 2003. Large woody debris and flow resistance in step-pool channels, Cascade Range, Washington. Geomorphology 51 (1–3), 141–157.
Dahlström, N., Jonsson, K., Nilsson, C., 2005. Long-term dynamics of large woody debris in a managed boreal forest stream. Forest Ecology and Management 210 (1–3), 363–373.
Daniels, M.D., 2006. Distribution and dynamics of large woody debris and organic matter in a low-energy meandering stream. Geomorphology 77 (3–4), 286–298.
Daniels, M.D., Rhoads, B.L., 2003. Influence of a large woody debris obstruction on three-dimensional flow structure in a meander bend. Geomorphology 51 (1–3), 159–173.
Elsenbeer, H., 2001. Hydrologic flowpaths in tropical rainforest soilscapes—a review. Hydrological Processes 15, 1751–1759.
Fausch, K.D., Northcote, T.G., 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49 (4), 682–693.
Faustini, J.M., Jones, J.A., 2003. Influence of large woody debris on channel morphology and dynamics in steep, boulder-rich mountain streams, western Cascades, Oregon. Geomorphology 51 (1–3), 187–205.
Genereux, D.P., Jordan, M., 2006. Interbasin groundwater flow and groundwater interaction with surface water in a lowland rainforest, Costa Rica: a review. Journal of Hydrology 320 (3–4), 385–399.

Godsey, S., Elsenbeer, H., Stallard, R., 2004. Overland flow generation in two lithologically distinct rainforest catchments. Journal of Hydrology 295 (1–4), 276–290.
Graham, R.L., Cromack, K., 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Canadian Journal of Forest Research 12, 511–521.
Grette, G.B., 1985. The Role of Large Organic Debris in Juvenile Salmonid Rearing Habitat in Small Streams. University of Washington.
Gurnell, A.M., Sweet, R., 1998. The distribution of large woody debris accumulations and pools in relation to woodland stream management in a small, low-gradient stream. Earth Surface Processes and Landforms 23 (12), 1101–1121.
Guyette, R.P., Cole, W.G., Dey, D.C., Muzika, R.-M., 2002. Perspective on the age and distribution of large wood in riparian carbon pools. Canadian Journal of Fisheries and Aquatic Sciences 59 (3), 578.
Harmon, M.E., Hua, C., 1991. Coarse woody debris dynamics in two old-growth ecosystems. Bioscience 41 (9), 604–610.
Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, J.K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133–302.
Hart, E.A., 2002. Effects of woody debris on channel morphology and sediment storage in headwater streams in the Great Smoky Mountains, Tennessee–North Carolina. Physical Geography 23 (6), 492–510.
Hartshorn, G.S., Hammel, B.E., 1994. Vegetation types and floristic patterns. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., Hartshorn, G.S. (Eds.), La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, pp. 73–89.
Hartshorn, G.S., Peralta, R., 1988. Preliminary description of primary forests along the La Selva–Volcan Barva altitudinal transect, Costa Rica. In: Almeda, F., Pringle, C. (Eds.), Tropical Rainforests: Diversity and Conservation. California Academy of Science, San Francisco, pp. 281–295.
Haschenburger, J.K., Rice, S.P., 2004. Changes in woody debris and bed material texture in a gravel-bed channel. Geomorphology 60, 241–267.
Hassan, M.A., Hogan, D.L., Bird, S.A., May, C.L., Gomi, T., Campbell, D., 2005. Spatial and temporal dynamics of wood in headwater streams of the Pacific Northwest. Journal of the American Water Resources Association 41 (4), 899–919.
Hendrickx, J.M.H., Vega, D., Harrison, J.B.J., Calvo-Gobbett, L.E., Rojas, P., Miller, T.W., 2005. Hydrology of hillslope soils in the Upper Rìo Chagres watershed, Panama. In: Harmon, R.S. (Ed.), The Rìo Chagres, Panama: A Multidisciplinary Profile of a Tropical Watershed. Springer, Dordrecht, The Netherlands.
Hyatt, T.L., Naiman, R.J., 2001. The residence time of large woody debris in the Queets River, Washington, USA. Ecological Applications 11 (1), 191–202.
Jacobson, P.J., Jacobson, K.M., Angermeier, P.L., Don, S.C., 1999. Transport, retention, and ecological significance of woody debris within a large ephemeral river. Journal of the North American Benthological Society 18 (4), 429–444.
Janzen, D.H., 1983. Costa Rican Natural History. University of Chicago Press.
Jeffries, R., Darby, S.E., Sear, D.A., 2003. The influence of vegetation and organic debris on flood-plain sediment dynamics: case study of a low-order stream in the New Forest, England. Geomorphology 51 (1–3), 61–80.
Jiménez, Q.J., Rojas, F.R., Rojas, V.C., Rodriguez, L.S., 2002. Timber Trees of Costa Rica: Ecology and Silviculture. InBio, Instituto Nacional de Biodiversidad. 361 pp.
Johnson, S.L., Rothacher, J., 2009. Streamflow from small watersheds at the H.J. Andrews Experimental Forest. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR. [Database]. Available: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=HF004 (11 January 2010).
Kail, J., 2003. Influence of large woody debris on the morphology of six central European streams. Geomorphology 51 (1–3), 207–223.
Keller, E.A., Tally, T., 1979. Effects of large organic debris on channel form and fluvial process in the coastal redwood environment. In: Rhodes, D.D., Williams, G.P. (Eds.), Adjustments of the Fluvial System: Proceedings of the 10th Annual Geomorphology Symposium, State University of New York, Binghamton. NY. Kendall/Hunt Publishing Co., Dubuque, IA, pp. 169–197.
Kleber, M., Schwendenmann, L., Veldkamp, E., Rosner, J., Jahn, R., 2007. Halloysite versus gibbsite: silicon cycling as a pedogenetic process in two lowland neotropical rain forest soils of La Selva, Costa Rica. Geoderma 138 (1–2), 1–11.
Lieberman, M., Lieberman, D., 1994. Patterns of density and dispersion of forest trees. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A., Hartshorn, G.S. (Eds.), La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, pp. 106–119.
Lieberman, D., Hartshorn, G.S., Lieberman, M., Peralta, R., 1990. Forest dynamics at La Selva Biological Station, 1969–1985. In: Gentry, A.H. (Ed.), Four Neotropical Rainforests. Yale University Press, New Haven, CT, pp. 509–521.
Lienkaemper, G.W., Swanson, F.J., 1987. Dynamics of large woody debris in streams in old-growth Douglas-fir forests. Canadian Journal of Forest Research 17 (2), 150–156.
Maser, C., Sedell, J.R., 1994. From the Forest to the Sea: The Ecology of Wood in Streams, Rivers, Estuaries, and Oceans. St. Lucie Press, Delray Beach, FL. 200 p.
Mazzorana, B., Zischg, A., Largiader, A., Hübl, J., 2009. Hazard index maps for woody material recruitment and transport in alpine catchments. Natural Hazards and Earth System Sciences 9, 197–209.
McHenry, M.L., Shott, E., Conrad, R.H., Grette, G.B., 1998. Changes in the quantity and characteristics of large woody debris in streams of the Olympic: Peninsula, Washington, USA (1982–1993). Canadian Journal of Fisheries and Aquatic Sciences 55 (6), 1395–1407.
Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. Nature 363, 234–240.
Murphy, M.L., Koski, K.V., 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. North American Journal of Fisheries Management 9 (4), 427–436.
Organization for Tropical Studies, 2010. La Selva Daily Rainfall, 1963–2009. Clark, D.A. (Ed.), http://www.ots.ac.cr/meteoro/default.php?pestacion=2.
Panshin, A.J., De Zeeuw, C., Brown, H.P., 1964. Textbook of Wood Technology. McGraw-Hill Book Co., New York. 643 pp.
Powell, S.R., Daniels, L.D., Jones, T.A., 2009. Temporal dynamics of large woody debris in small streams of the Alberta foothills, Canada. Canadian Journal of Forest Research 39, 1159–1170.
Raich, J.W., Rastetter, E.B., Melillo, J.M., Kickligheter, D.W., Steudler, P.A., Peterso, B.J., 1991. Potential net primary productivity in South America: application of a global model. Ecological Applications 1 (4), 399–429.
Richmond, A.D., Fausch, K.D., 1995. Characteristics and function of large woody debris in sub-alpine Rocky Mountain streams in northern Colorado. Canadian Journal of Fisheries and Aquatic Sciences 52 (8), 1789–1802.
Smith, R.D., Sidle, R.C., Porter, P.E., Noel, J.R., 1993. Effects of experimental removal of woody debris on the channel morphology of a forest, gravel-bed stream. Journal of Hydrology 152 (1–4), 153–178.
Smith, G.C., Covich, A.P., Brasher, A.M.D., 2003. An ecological perspective on the biodiversity of tropical island streams. Bioscience 53 (11), 1048–1051.
Tank, J.L., Webster, J.R., 1998. Interaction of substrate and nutrient availability on wood biofilm processes in streams. Ecology 79 (6), 2168–2179.
Triska, F.J., Cromack, K., 1980. The role of wood debris in forests and streams. In: Waring, R.H. (Ed.), Forests: Fresh Perspectives from Ecosystem Analysis. Oregon State University, Corvallis, OR, pp. 171–190.
Webster, J.R., Covich, A.P., Tank, J.L., Crockett, T.V., 1994. Retention of coarse organic particles in streams in the southern Appalachian Mountains. Journal of the North American Benthological Society 13 (2), 140–150.
Wilcox, A.C., Wohl, E.E., 2006. Flow resistance dynamics in step-pool stream channels: 1. Large woody debris and controls on total resistance. Water Resources Research 42 (5) W05418-W05418.
Wohl, E., 2000. Mountain Rivers. American Geophysical Union Press, Washington, D.C.
Wohl, E., 2005. Downstream hydraulic geometry along a tropical mountain river. In: Singh, V.P., Harmon, R.S. (Eds.), The Río Chagres, Panama: A Multidisciplinary Profile of a Tropical Watershed. Springer, Dordrecht, The Netherlands, pp. 169–188.
Wohl, E., Goode, J.R., 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. Water Resources Research 44 W09420-W09420.
Wohl, E., Ogden, F.L., Goode, J., 2009. Episodic wood loading in a mountainous neotropical watershed. Geomorphology 111 (3–4), 149–159.
Zabel, R.A., Morrell, J.J., 1992. Wood Microbiology: Decay and Its Prevention. Academic Press, San Diego. 467 pp.