Journal of Hydrology 462–463 (2012) 67–76

Contents lists available at ScienceDirect

Journal of Hydrology

journal homepage: www.elsevier.com/locate/jhydrol

A two end-member model of wood dynamics in headwater neotropical rivers

Ellen Wohl [a,*], Susan Bolton [b], Daniel Cadol [a], Francesco Comiti [c], Jaime R. Goode [a,1], Luca Mao [d]

[a] Department of Geosciences, Colorado State University, Ft. Collins, CO 80523-1482, USA
[b] School of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195-2100, USA
[c] Faculty of Science and Technology, Free University of Bozen-Bolzano, via Leonardo da Vinci 7, 39100 Bolzano, Italy
[d] Department of Land and Agro-Forest Environments, University of Padua, Viale dell'Università 16, Legnaro (PD), 35020, Italy

ARTICLE INFO

Article history:
Available online 1 March 2011

Keywords:
Large woody debris
Costa Rica
Panama
Landslides
Logjams
Wood recruitment

SUMMARY

Geomorphic and ecological effects of instream wood have been documented primarily along rivers in the temperate zones. Instream wood loads in tropical rivers might be expected to differ from those in analogous temperate rivers because of the higher transport capacity and higher rates of wood decay in the tropics. We use data from four field sites in Costa Rica and Panama to demonstrate that wood loads are consistently lower in tropical rivers, despite substantial variations among tropical sites as a result of differences in mechanisms of wood recruitment. We develop a model of wood dynamics (recruitment, transport, and retention) based on differences in dominant wood recruitment mechanism. The steady-state end-member reflects sites where gradual recruitment of wood through individual tree fall creates a relatively consistent wood load through time and development of logjams is minimal. The episodic end-member reflects sites dominated by episodic mass recruitment via landslides or blowdowns. This facilitates formation of transient logjams, so that wood loads exhibit substantial spatial and temporal variation along the channel network. The model presented here should also apply to headwater streams in the temperate zone, although existing documentation suggests that jams are more persistent along streams in the temperate zone.

1. Introduction

An extensive literature documents the geomorphic and ecological effects of wood in rivers of the temperate zones. Within the channel, wood increases frictional resistance to flow and channel-boundary roughness (Keller and Tally, 1979; Curran and Wohl, 2003). Individual wood pieces and jams create localized flow separation that reduces velocity, increases flow depth, and enhances local bed and bank scour (Berg et al., 1998; Linstead, 2001; Manners et al., 2007). Wood facilitates storage of sediment and organic matter, and thus alters the grain-size distribution of the bed surface (Faustini and Jones, 2003; Haschenburger and Rice, 2004; Comiti et al., 2008a) and the type and dimensions of bedforms present (MacFarlane and Wohl, 2003; Montgomery et al., 2003). The ecological effects of wood include increased substrate and habitat diversity and stability (Maser and Sedell, 1994), shorter pool spacing (Montgomery et al., 1995), greater pool volume (Fausch and Northcote, 1992; Mao et al., 2008), and greater retention and processing of nutrients (Bilby and Likens, 1980; Warren et al., 2007). Wood also affects channel planform and valley-bottom process and form when wood jams facilitate avulsion or the formation of anastomosing channels (Collins and Montgomery, 2002; O'Connor et al., 2003). Wood can increase channel width and lateral mobility (Brooks and Brierley, 2002), and can enhance overbank flooding and associated sediment deposition across the floodplain (Jeffries et al., 2003).

The literature documenting these geomorphic and ecological effects has for decades been dominated by studies from the northwestern United States and southwestern Canada. Most of the Pacific Northwest region is a temperate rainforest with many large, long-lived species of trees and relatively low-intensity seasonal rains or snowmelt. Because these forest and climate characteristics are likely important first-order controls on the recruitment and retention of instream wood, we expect wood dynamics in other regions to differ. Documenting these differences provides insight for understanding regional distinctions in the geomorphic and ecological functions of instream wood and for optimizing stream management strategies. Within the past decade, studies representing sites in other portions of North America (Richmond and Fausch, 1995; Downs and Simon, 2001; Marcus et al., 2002; Warren et al., 2007), as well as Europe (Piégay and Gurnell, 1997; Piégay et al., 1999; Gurnell et al., 2000; Linstead, 2001; Dahlström and Nilsson, 2004; Wyzga and Zawiejska, 2005; Comiti et al., 2006), Asia (Gomi et al., 2006; Seo and Nakamura, 2009), South America (Andreoli et al., 2007; Comiti et al., 2008a; Mao et al., 2008; Iroumè

* Corresponding author. Tel.: +1 970 491 5298; fax: +1 970 491 6307.
E-mail address: ellenw@cnr.colostate.edu (E. Wohl).
[1] Present address: USDA Forest Service, Rocky Mountain Research Station, 322 E. Front Street, Suite 401, Boise, ID 83702, USA.

0022-1694/$ - see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.jhydrol.2011.01.061

et al., 2010), Africa (Jacobson et al., 1999; Pettit and Naiman, 2006), Australia (Webb and Erskine, 2003) and New Zealand (Baillie and Davies, 2002; Meleason et al., 2005) have begun to provide greater insight into geographic diversity in the dynamics of instream wood. The majority of these studies come from sites in the temperate zones, where variations in mesoscale hydroclimatology and forest structure create differences in the volume and function of instream wood that can drive regionally targeted management strategies rather than extrapolation from different regions (Magilligan et al., 2008). Relatively little remains known, however, of high-latitude (e.g., boreal forest, but see Mao et al., 2008 for subantarctic forests) or low-latitude (e.g., tropical rainforest) environments, which might differ significantly from temperate environments. Our objective in this paper is to synthesize the results from several recent studies along neotropical forest streams in Costa Rica and Panama.

This paper focuses on what is commonly known as large woody debris, typically defined as pieces greater than 1 m in length and 10 cm in diameter. Because 'debris' can have negative connotations, we refer to logs as instream wood when at least some portion of the log lies within the bankfull channel. Instream wood dynamics include (i) recruitment of wood into the channel through processes ranging from mass introductions during landslides or blowdowns to individual treefall resulting from bank erosion or tree mortality, (ii) transport of wood within the channel or between the channel and adjacent floodplains, and (iii) retention of wood within the channel, which involves both storage and processes of alteration such as decay, physical breakage, ingestion by organisms, or abrasion by sediment in transport. Together, these processes govern the wood budget for a channel segment by determining inputs and outputs of wood through time and the volume of wood stored within the channel at any given location or time. Investigators have only recently begun to quantify wood budgets for temperate streams. Benda and Sias (2003), for example, propose the following budget equation for changes in wood storage S_c (expressed either in m^3 per ha of channel bed area or in m^3 per 100 m of channel length) over a length of channel x through time t:

$$\Delta S_c = [L_i - L_o + Q_i/\Delta x - Q_o/\Delta x - D]\Delta t \quad (1)$$

where L_i is lateral wood recruitment, L_o is loss of wood to overbank deposition and channel movement, Q_i is fluvial transport of wood into the channel segment, Q_o is fluvial transport out of the segment, and D is decay. Lateral wood recruitment can be further specified in terms of different recruitment processes:

$$L_i = I_m + I_f + I_{be} + I_s + I_e \quad (2)$$

where I_m is background forest mortality, I_f is toppling of trees following fires and during windstorms, I_{be} is punctuated inputs from bank erosion, I_s is wood delivered by hillslope mass movements (landslides, debris flows), and I_e is exhumation of buried wood (Benda and Sias, 2003).

Although it is difficult to fully quantify each of the parameters in Eqs. (1) and (2), in part because of their spatial and temporal variability, these equations can provide a conceptual framework for examining how the relative magnitude of each parameter varies between sites and through time. The magnitude of Q_i and Q_o, for example, may be small relative to L_i in headwater sites with limited fluvial transport capacity. Wood transport rates are also very difficult to estimate as well as to measure (MacVicar et al., 2009).

Some variables included in Eqs. (1) and (2) may not differ consistently between temperate and tropical environments. Background tree mortality, for example, does not appear to differ among tropical, temperate, and boreal forests (Hartshorn, 1990; Lieberman et al., 1990; Lugo and Scatena, 1996; Scatena et al., 2005). Instream wood dynamics in tropical rivers, however, might be expected to differ from wood dynamics in rivers of the temperate zone for at least two reasons; hydrology and wood decay (Douglas and Guyot, 2005). Tropical rivers are typically subject to intense rainfall that can produce values of unit discharge (up to 30–40 $m^3 s^{-1} km^{-2}$; Cadol et al., 2009; Wohl et al., 2009) higher than those typical of temperate rivers. Short duration, high-magnitude floods can also occur more frequently and have a greater cumulative duration than floods of analogous transport capacity in temperate rivers (Wohl and Jaeger, 2009). The net effect is greater transport capacity for wood in streams of a given drainage area, particularly in small headwater rivers (Covich and Crowl, 1990; Cadol and Wohl, 2010). Although relatively little is known of wood decay rates in rivers of any environment (Harmon et al., 1986; Hyatt and Naiman, 2001; Spänhoff and Meyer, 2004; MacVicar et al., 2009), studies of wood turnover time on forest floors in different environments indicate that wood decays much more rapidly in tropical environments. Decay rates of logs on a forest floor are on the order of >100 years in cold boreal/subantartic climates (Frangi et al., 1997), 50–100 years in dry climates (O'Connell, 1997; Ellis et al., 1999), 10–100 years in humid temperate climates (Boyce, 1961; Harmon, 1982), and less than 10 years in the tropics (Delaney et al., 1998; Clark et al., 2002; Lewis et al., 2004; Beard et al., 2005). Waterlogged instream wood may decay more slowly as a result of prolonged anaerobic conditions (Harmon et al., 1986; Beard et al., 2005), but the relative rates of decay between these regions based on forest-floor decay rates likely hold for instream wood. The characteristics of the hydrograph that, along with position with respect to the streambed, control the timing, duration, and frequency of wetting and drying of instream wood, likely also play a role in decay rates, such that the characteristic flashy hydrographs of tropical streams may enhance decay rates.

In the context of Eq. (1), therefore, tropical rivers might be expected to have higher values of Q_i, Q_o, and D than otherwise similar temperate rivers. Whether these differences lead to significantly different values of S_c or ΔS_c depends partly on L_i and L_o. In the synthesis presented here, we demonstrate that volume of wood stored per unit area of channel (S_c) is consistently lower for the headwater neotropical rivers studied, and annual turnover of wood (ΔS_c) is consistently higher, relative to analogous temperate rivers, despite substantial variations in L_i (lateral input rates) between study sites. L_o (lateral export towards the floodplain) is negligible in the laterally confined reaches that are the focus of these studies.

We also propose that differences in L_i between sites create what can be conceptualized as a two end-member model of wood dynamics in headwater neotropical streams. One end-member is represented by sites where gradual recruitment of wood through individual tree mortality creates a relatively steady-state condition with respect to S_c at a site through time. Although individual pieces of wood are relatively mobile, there is sufficient supply of wood via L_i and Q_i to replace wood lost through Q_o or D. The other end-member is represented by sites where wood recruitment occurs primarily through mass movements such as landslides and debris flows, or through mass recruitment associated with hurricanes that create catastrophic tree mortality (Lugo and Scatena, 1996). Episodic point sources of wood recruitment facilitate formation of logjams that temporarily store sediment and create very high values of S_c, but the persistence of these features within the channel is much shorter than the recurrence interval of the input process, so that S_c fluctuates dramatically through time and space along the channel network. We present data from four field areas to support this end-member model.

2. Study areas

The primary description of each of the four study sites (Fig. 1) we use in this synthesis is contained in the references cited for that

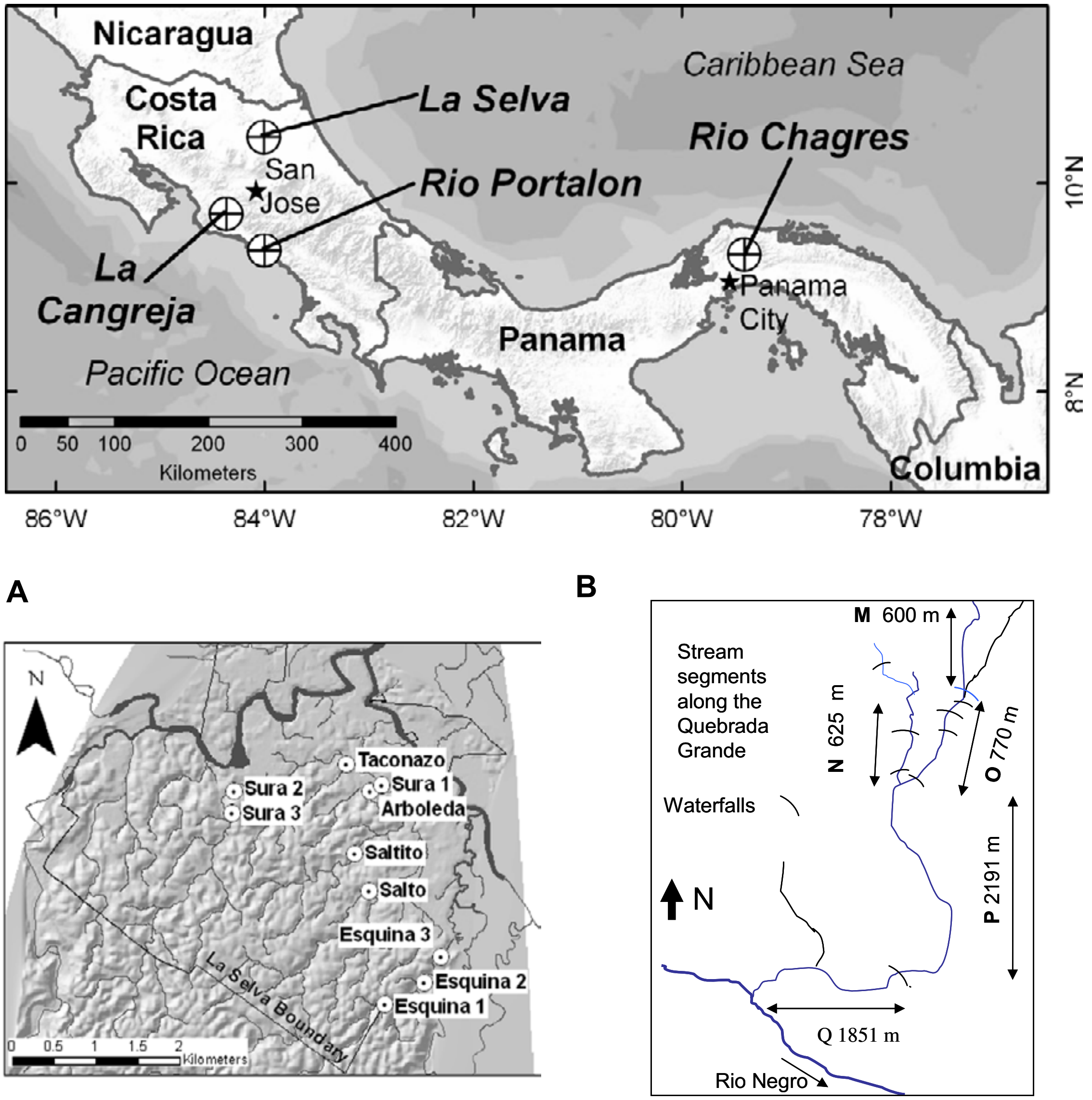


Fig. 1. Location map of Costa Rica and Panama showing general location of study sites relative to one another. Inset maps show details of multiple reaches at (A) La Selva and (B) La Cangreja.

study site. Here we briefly describe the salient characteristics of each site, which are also listed in Table 1.

2.1. Upper Rio Chagres, Panama

The Upper Rio Chagres is divided by a reservoir, Lake Alhajuela. The portion upstream from the reservoir, the Upper Rio Chagres, drains 414 km^2 of mountainous terrain in central Panama. The reservoir does not trap wood or influence upstream wood loads. Bedrock geology in the Upper Chagres is a mixture of volcanic and intrusive rocks of Cretaceous to Upper Tertiary age that are highly deformed and chemically altered (Wörner et al., 2005). The channel is narrowly confined between steep slopes and in many places bedrock is exposed along the stream banks or bed (Fig. 2A). Morphology varies from pool-riffle to step-pool across bed gradients of 0.0014–0082 m/m (Wohl, 2005). Bed sediment at the study sites is dominated by cobbles and small boulders (D_{50}, 19–20 cm, D_{84}, 33–40 cm).

About 70% of the Upper Rio Chagres catchment is in Parque Nacional Chagres and 98% of the catchment is covered by old-growth forest. Diversity of tree species is extremely high and individual trees can attain a height of 30 m and a diameter of 2.2 m (R. Condit, Smithsonian Tropical Research Institute, pers. comm., 2003). Wood is introduced to the channel network via bank erosion (a relatively minor source), landslides along the valley walls of the main channel, and tributary inputs from landslides and bank erosion along the tributary.

Mean annual precipitation at the mouth of the catchment is 2590 mm, of which 90% falls during the May–December wet season (Houseal, 1999). Discharge near the mouth of the upper catchment typically varies between 10 and 20 m^3/s during the dry season, with multiple flood peaks over 1000 m^3/s during the wet season. Mean annual peak flow is 1049 m^3/s and the flood of record was 3780 m^3/s in November 1966. Small landslides occur episodically on the steep slopes in association with heavy rainfall.

A tropical air mass thunderstorm on 10 July 2007 produced a flood across the upper basin that peaked at 720 m^3/s at a headwaters gage draining 17.5 km^2 and 1710 m^3/s at a downstream gage draining 414 km^2. Landslides caused by the heavy rainfall facilitated the formation of large logjams along portions of the channel where transport capacity of wood was reduced by a change in-channel geometry such as a bend, channel expansion, or single

Table 1
Characteristics of study sites.

Stream	A[a] (km^2)	Estimated Q_p[b] ($m^3/s/km^2$)	No. of study reaches	S[c] (m/m)	w[d] (m)	d[e] (m)	L_{wood}[f] (m)	d_{wood}[g] (m)	Primary wood recruitment process[h]	Wood load[i] (m^3/100 m)	Wood load[i] (m^3/ha)
Rio Chagres, Panama	16–60	4–41	3	0.005–0.02	15–94	~2–5	15.1	0.52	I_s	Not available	Not available
Rio Portalón, Costa Rica	17	20	7	0.015–0.05	16–23	~1.5–3	6.2	0.37	I_s and I_{be}	1.5	7.4
Taconazo, La Selva	0.3		1	0.0024	7.3	0.8	4.7	0.26	I_m and Q_i	26.4	363 (366, 362)
Arboleda, La Selva	0.4		1	0.0022	7.3	0.9	3.2	0.12	I_m and Q_i	3	107 (129, 41)
Sura 1, La Selva	4.8		1	0.0024	8.1	1.1	4.1	0.21	I_m and Q_i	34.7	427 (469, 399)
Sura 2, La Selva	3.4	3	1	0.0122	10.3	0.8	2.9	0.23	I_m and Q_i	15	143 (177, 126)
Sura 3, La Selva	3.3		1	0.0616	13.4	1.0	3.1	0.16	I_m and Q_i	7.4	79 (109, 47)
Salto, La Selva	6.8		1	0.0097	7.8	1.0	3.2	0.16	I_m and Q_i	7.8	108 (144, 57)
Esquina 1, La Selva	1.6		1	0.0320	8.3	0.9	3.6	0.20	I_m and Q_i	7.3	87 (96, 68)
Esquina 2, La Selva	2.2		1	0.0100	7.7	0.6	4.0	0.15	I_m and Q_i	15.1	95 (164, 76)
Esquina 3, La Selva	2.3		1	0.0075	8.2	0.5	4.6	0.18	I_m and Q_i	20.9	174 (185, 150)
Saltito, La Selva	1.2		1	0.0030	4.9	0.7	2.5	0.21	I_m and Q_i	10.1	196 (207, 187)
Quebrada Grande 1, La Cangreja Q 2003	8.2		3	0.005–0.04	11.4	0.8	3.6	0.21	I_m and Q_i	1 (3,0)	8.8 (10.3, 0)
Quebrada Grande 2, La Cangreja P 2003	4.6	3	3	0.01–0.13	12.7	0.8	3.6	0.35	I_s and Q_i	12 (24, 2)	95 (188, 16)
Quebrada Grande 3, La Cangreja O 2003	3.9		2	0.005–0.31	8.1	0.6	5.0	0.36	I_s and Q_i	5 (6, 3)	55 (90, 32)
Quebrada Grande 4, La Cangreja M 2003	2.9	1	2	0.04–0.78	7.8	0.4	3.6	0.28	I_s and I_f	16 (22, 9)	205 (272, 121)
Quebrada Grande 5, La Cangreja N 2003	0.2		2	0.015–0.46	6.9	0.7	4.5	0.2	I_f and I_s	17 (20, 14)	247 (294, 200)

[a] Drainage area at study site.
[b] Estimated maximum peak discharge per unit drainage area.
[c] Channel bed gradient.
[d] Average bankfull channel width.
[e] Average bankfull channel depth.
[f] Average wood piece length.
[g] Average wood piece diameter.
[h] Variables as in Eq. (2).
[i] Average value of wood volume per unit area of channel surface; maximum and minimum in parentheses.

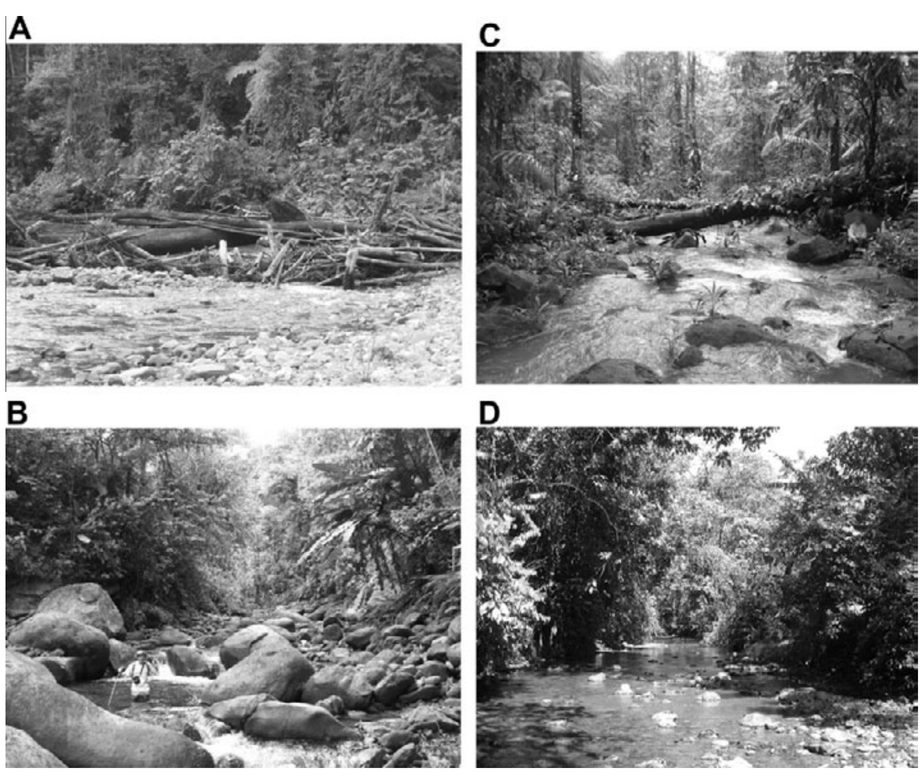


Fig. 2. Representative photographs of stream characteristics at the four study sites. Downstream view of a large jam on the Rio Chagres. Jam is at the upstream end of a channel bend that has split flow around an island. Person at right for scale. (B) Upstream view of a site along the Rio Portalón. Person at lower center of view for scale. (C) Downstream view of El Sura at site 3, La Selva. Seated person at right for scale. (D) La Cangreja.

large mid-channel bar. Individual jams exceeded 5 m in height and 2400 m^2 in area, and stored more than 8000 m^3 of sediment (Wohl et al., 2009). Jams surveyed during field work in February 2008 were largely gone by March 2009. This, coupled with observations of almost no instream wood throughout the main channel and tributaries of the Upper Chagres during extensive field work in 2002, despite the occurrence of a 20-year flood and associated landslides in 2000 (Wohl et al., 2009), suggests that even very large logjams last less than 2 years in this catchment.

The jams are likely destroyed by the combined effects of extremely high fluvial transport capacity and rapid wood decay. Multiple lines of evidence indicate the high fluvial transport capacity. First, despite numerous, closely spaced small (estimated $\leqslant$ 270 m^3) landslides along the main channel, fans at landslide toes or tributary junctions were absent during field work in February 2008. Second, one-dimensional hydraulic modeling of the July 2007 flood indicates that flow variables greatly exceeded the threshold conditions for transport of coarse-grained bed sediment and wood. Third, gage records from the flood indicate peak unit discharges as high as 41 $m^3/s/km^2$ over the five hours of the main flood peak (Wohl et al., 2009).

Although limited studies document wood decay in Panama, they suggest extremely high decay rates relative to temperate environments. Bultman and Southwell (1976) summarized the results of a 13-year study of decay in heartwood stakes from various Panamanian tree species exposed at sites near the canal. Twenty-seven percent of the species exhibited heavy to very heavy decay within 2.5 years, and this percentage rose to 63% by 7.5 years and 80% by 13 years.

2.2. Rio Portalón, Costa Rica

The Rio Portalón is a small (17 km^2), mountainous basin on the western side of Costa Rica that is underlain by Tertiary-age turbidites (Méndez Herrera and Esquivel, 2006). Bed slope ranges between 0.015 and 0.05 m/m, whereas bankfull width varies between 16 m and 23 m. Reach scale morphology is plane-bed style following Montgomery and Buffington's (1997) classification, with several rapids and occasional step and pool units. Channel bed sediments are very coarse, being dominated by boulders, up to 2–3 m in diameter, with large cobbles interspersed among them (Fig. 2B).

Mean annual precipitation in the area is about 3500 mm. Landslides and debris flows are widespread on the steep slopes adjacent to the confined channel network and hillslope instability is exacerbated by the passage of tropical storms such as Hurricane Rita in September 2005. Landslides and debris flows triggered by Rita supplied the main channel and tributaries of the Rio Portalón catchment with large quantities of sediment and large (up to 2 m in diameter and 30 m in height) mature trees that are very abundant in the old-growth rainforest covering the riparian corridor as well as of most of basin area (Mao and Comiti, 2010). Residents of the catchment claimed that the temporary formation of a large logjam along a confined portion of the Portalón during the hurricane created a flood surge once it collapsed. Residents also noted that most of the wood transport occurred during the flood peak and reported that a similar event occurred in the Rio Portalón about 50 years earlier. Peak discharge for the 2005 event was estimated around 350 m^3/s (i.e., about 20 $m^3/s/km^2$; Mao and Comiti, 2010). During a channel survey conducted in September 2008, Mao and Comiti (2010) found very little wood within the channel margins (7 m^3/ha), in contrast to the large amount (order of 10^3–10^4 m^3) transported during the 2005 event and deposited downstream as the channel becomes unconfined on the coastal plain where the village of Portalón is located. There several houses were destroyed and a bridge collapsed due to wood clogging. These observations suggest that wood dynamics in the Rio Portalón strongly resemble those in the Rio Chagres, with recruitment primarily through landslides and temporary storage of large volumes of wood within the channel, followed by rapid removal and relatively low in-channel wood loads until the next major recruitment event.

2.3. Streams at La Selva Biological Station, Costa Rica

La Selva Biological Station lies on Costa Rica's Atlantic margin at elevations of 34–110 m, at the transition from the low, steep foothills of the Cordillera Central to the Sarapiquí coastal plain. The foothills are underlain by andesitic lava flows originating from the volcanoes of the Central Cordillera (Kleber et al., 2007). The primary drainages of the biological station are El Surá, El Salto, and Quebrada Esquina. These streams and their tributaries have segmented longitudinal profiles that reflect the underlying topography of low-gradient valley bottoms, steep segments where the streams cross the fronts of the lava flows onto alluvial terraces, and low-gradient segments on the terraces. Lower gradient reaches (0.002–0.003 m/m) typically have pool-riffle or dune-ripple morphology formed in silty fine sand, whereas steeper segments (0.007–0.06 m/m) have pool-riffle or step-pool morphology formed in gravel- to boulder-size bed sediment distributions where D_{84} ranges from 110–940 mm (Fig. 2C).

The 1600-ha research reserve includes 730 ha of old-growth forest classified as Tropical Wet Forest in the Holdridge system (Clark et al., 1998). Hurricanes seldom reach the area, but intense rains are generated from November to January. Mean annual precipitation averages 4.3 m and rain falls throughout the year; a dry season is effectively absent (Organization for Tropical Research, 2007). Floods recur frequently and are of short duration. At a small weir draining 0.3 km^2, rainfall flows more than doubled the base flow 19 times during a 3-month period of the January–March drier season. For these flows, the rising limb typically lasted one hour and the falling limb averaged 10 h. At a second gage with slightly larger (3.4 km^2) drainage area, peak unit discharge exceeds 3 $m^3/s/km^2$ (Cadol and Wohl, 2010).

Despite the locally steep slopes adjacent to stream reaches, mass movements such as landslides and debris flows have not been observed at La Selva either during our spatially extensive field work (Cadol et al., 2009) or by other researchers continuously active at La Selva since the 1970s (D. Clark, pers. comm., March 2007). The channels are sufficiently close to the coastal plain to limit total relief and substantial groundwater drainage may prevent the slopes from reaching a saturation level that would promote slope failure. Lateral channel mobility is limited by steep slopes along many of the channels and floodplain development is minimal, so that individual tree fall (L_i) and transport from upstream (Q_i) are the primary mechanisms of wood recruitment, with Q_i likely dominant (Cadol et al., 2009).

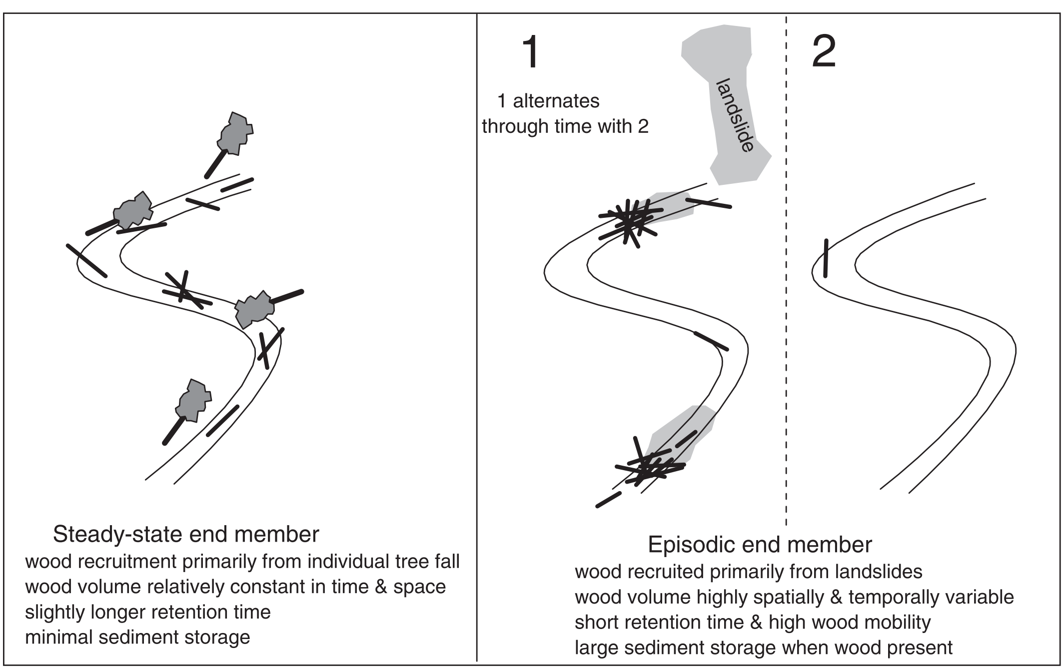
Wood surveys along 30 forested headwater stream segments in March 2007 revealed that, despite some very high wood loads (up to 400 m^3/ha, Table 1), jams are relatively rare and are only effective at trapping sediment in moderate energy, gravel-bed channels (Cadol et al., 2009). Only seven channel-spanning jams were found in 30 stream reaches surveyed, each of which was 50 m long. For comparison, such jams average 5.4/100 m in old-growth of the Colorado Front Range (Wohl and Cadol, 2011) and 6.1 jams/100 m in southern Argentina (Mao et al., 2008). Statistical analyses suggest that the variables of wood diameter/flow depth, stream power, the presence of backflooding from larger rivers to which the study streams are tributary, and channel width/depth ratio correlate significantly with wood load (Cadol et al., 2009). Subsequent visits to a subset of 10 of these survey sites approximately once every 4 months during the succeeding 2.3 years indicate that wood retention rates by piece range from 0.55 to 0.91 among the sites, which equates to mean residence times of 2.2–10.6 years (average 4.9 years) for pieces (Cadol and Wohl, 2010). Although these values are very small relative to many headwater sites in temperate zones, they are slightly longer than those for the Rio Chagres. Perhaps more importantly, the repeat surveys suggest that wood load at the La Selva sites is essentially in steady-state based on the absence of significant trends or changes in wood volume during the period of resurveys. Mobility of pieces at the La Selva sites correlates most strongly with the ratio of piece length/channel width, channel gradient, and piece type (unattached pieces are more mobile than pieces attached to the stream bed or banks). Temporal variation in piece mobility correlates well with variation in peak flow (Cadol and Wohl, 2010).

2.4. Streams at La Cangreja National Park, Costa Rica

La Cangreja National Park is located in Puriscal County west of San Jose, Costa Rica. The park protects 2200 ha of remnant forest classified as basal wet tropical forest and premontane wet transitioning to rainy tropical forest with elevations ranging from 300 m to 1300 m. Mean annual precipitation is around 4000 mm. Most of the headwater streams originating in the park drain to the Rio Tulin, but a few drain into the Rio Candelaria. Channels contain abundant bedrock and are frequently confined by steep hillslopes. Watershed lithology is a mix of marine sediments and basalts, with the harder basalt layers forming many waterfalls. Channel types vary from plane-bed to step-pool (Fig. 2D). Channel sediment in Segment Q (Fig. 1) is primarily large gravels and small cobbles. Segments O and N are primarily bedrock and segments P and M are a mix of boulders and bedrock.

Vegetation and stream habitat plots were established in 2003 during the dry season and have been resurveyed about every 3 years (S. Bolton, unpub. data). Wood data were collected in 2003, 2006 and 2009. Data from the 2003 baseline survey along the Quebrada Grande are reported in this paper. The Quebrada Grande basin above the lowest survey reach is about 823 ha. Following a walking survey of the stream, the mainstem was divided into 4 segments and 1 tributary which were then randomly surveyed for habitat characteristics. The Quebrada Grande is gaged in reaches P and M (Table 1). The streams exhibit a flashy response to the typically intense rainfall, with sharp rising and falling limbs. Flow levels can change more than 0.5 m in an hour. With the exception of the two lowest surveyed reaches, the stream runs through mature forest. Although jam wood volumes are larger than individual pieces, individual wood pieces are more common than jams. Frequent small debris flows from the steep hillslopes contribute wood and sediment, but much of this is flushed during the rainy season. The largest inputs of wood occur from infrequent but severe windstorms, with most of the rest coming from debris flows and downstream transport. Even in the low-gradient plane-bed reaches, very large pieces of wood can be transported. A very large tree (0.75 m diameter, >8 m long with attached root) was retained less than 3 years before being transported totally out of the basin.

In 2009, a windstorm the size of which most locals had never seen and some reported as maybe happening 50 years ago blew all the leaves off the trees, destroyed many roofs and contributed large amounts of wood to the streams. Preliminary analysis of wood volumes following the windstorm indicates wood loads 2–90 times greater than amounts measured in 2003. We measured 60 individual pieces and 23 jams. Early rainy season storms began transporting this wood, suggesting that it will be relatively transient at the study sites.



$$\Delta S_c = [L_i - L_o + Q_i/\Delta x - Q_o/\Delta x - D]\Delta t \qquad \mathbf{\Delta S_c} = [\mathbf{L_i} - L_o + \mathbf{Q_i}/\Delta x - \mathbf{Q_o}/\Delta x - D]\Delta t$$

$$L_i = \mathbf{I_m} + I_f + I_{be} + I_s + I_e \qquad L_i = I_m + I_f + I_{be} + \mathbf{I_s} + I_e$$

Fig. 3. Schematic illustration of the two end-member model of wood dynamics. Size of symbols for variables from Eqs. (1) and (2) represents their relative importance in the respective end-members. Gray shading in the channel for the episodic end-member indicates sediment storage upstream from the jam. Some of the streams in the four study areas are sinuous, some are straight, but all are single-thread channels. Logjams were observed at both channel bends and in straight channel segments.

3. Two end-member model

The two end-member model schematically illustrated in Fig. 3 reflects the characteristics of wood dynamics discussed above. The *steady-state end-member*, typified by the La Selva sites, has gradual but steady recruitment through individual tree fall. Recruitment rate is sufficiently high to maintain relatively unchanging wood loads through time, despite rapid decay and high capacity for fluvial transport of instream wood. Individual logs and small jams create relatively little sediment storage within the channel.

The *episodic end-member*, typified by the Rio Chagres, Rio Portalón, and La Cangreja sites, has frequent, low magnitude recruitment through individual tree fall, but superimposed on this are large episodes of bulk recruitment via landslides or blowdowns that recur at varying time intervals. While this mass-recruited wood is present in the channel, wood storage is spatially nonuniform and large volumes of sediment can be stored in the channel, but only for short periods of time. Logjams form at sites of reduced velocity and transport capacity, including tributary junctions, meander bends, channel expansions, and at the head of islands or bars. Logjams at these study sites are similar in that all are a type of allochthonous/transport jam known as 'flood jams' in the classification proposed by Abbe and Montgomery (2003). At the tropical study sites, the logjams are transient features that do not persist as long as the recurrence interval between mass recruitment events, so that instream wood loads vary with time and space. Contributing to this variability is reduced wood recruitment as trees regrow in patches of forest largely cleared by landslides or hurricanes. Wood is likely to be more mobile in this end-member, as evidenced by the lower wood loads at these sites, relative to La Selva, during intervals when logjams are not present.

The key differences between the end-members are the dominant recruitment mechanism and the transport capacity. The steady-state end-member is dominated by individual tree fall and gradual turnover of wood via removal of specific pieces. The episodic end-member is dominated by mass recruitment followed by complete removal of wood within a short time period, as well as sufficiently high transport capacity to mobilize wood recruited via individual tree fall between mass recruitment events. Transitional states might exist between these end-members at sites with (i) lower values of Q_i and Q_o that would allow logjams to persist over timespans closer to the recurrence interval of landslides (this would presumably result in much high values of S_c) or (ii) very small, infrequent, or widely spaced landslides that contribute to recruitment but to a lesser degree than in the episodic end-member (this would likely result in spatial and temporal variability in S_c that is intermediate between the end-members). Further field research in neotropical headwater streams can help to quantify the differences in rates of recruitment, retention and transport between end-member sites and to determine whether transitional states exist.

4. Discussion and conclusions

When applying this end-member model to other tropical sites, we propose that the dominant mechanism of wood recruitment is a more important factor than transport capacity, although this constitutes a hypothesis that can be tested with further field work. Some support for this interpretation comes from work done on a catchment draining 1.1 km^2 in Malaysia. More than a decade of field surveys in this catchment indicate that landslides create logjams that last an average of 12 months before extreme discharges that float the wood and *in situ* rotting of large logs in the jam cause the jam to break up (Douglas and Guyot, 2005). The fact that stream flows in even a very small catchment are capable of floating key logs within jams and thus dispersing the jam suggests that transport capacity is not likely to provide a useful means of discriminating end-members of wood dynamics in tropical environments.

Limited transport capacity in small catchments is likely to exert a more important control in temperate environments. Long-term studies in England's Highland Water catchment, for example, document persistence of individual logjams for periods of more than a decade, even in the absence of mass wood recruitment (e.g., Sear et al., 2010). An important characteristic of the Highland Water site is the presence of an extensive floodplain. One site characteristic that might influence wood transport and storage, but that does not vary substantially among our study sites, is lateral confinement of the channel. Flow depth continues to increase with discharge in a laterally confined channel. This rapidly increases the hydrostatic forces of buoyancy and lift and the hydrodynamic force of drag exerted on instream wood and facilitates transport. In a laterally unconfined channel with low banks and a broad floodplain, flow depth increases much more slowly with discharge as excess water spreads across the floodplain. Consequently, the hydraulic forces exerted on instream wood do not increase as much for a given increase in discharge, and both individual pieces of wood and logjams are likely to remain longer within a particular channel segment. We are not aware of any data on wood loads in neotropical rivers with extensive floodplains, but we can envision two possible scenarios: (1) High volumes of precipitation create sufficient stream flow and transport capacity that individual wood pieces and jams are readily transported even in the presence of a floodplain that attenuates peak discharges. In this case, wood recruitment mechanism differentiates end-members in our model. (2) Peak discharges are sufficiently attenuated by floodplains to limit transport capacity. This could result in gradual wood inputs clustering into logjams and/or greater persistence of logjams. In this case, our end-member model is not as useful in differentiating wood dynamics. In either scenario, wood recruitment could still occur via individual treefall upstream and within the portion of the catchment that has a floodplain. Mass recruitment could occur from blowdowns throughout the catchment or from landslides in steeper portions of catchment upstream from the floodplain. This 'thought exercise' suggests that it would be very useful to document wood dynamics in floodplain neotropical rivers.

Similarly, braided rivers occur in both laterally confined and floodplain tropical rivers. Our focus on single-thread channels reflects data available from the four study sites described in this paper. The ability of channel-spanning jams to form in association with single large islands or bars along the Rio Chagres suggests that such jams could also form in laterally confined braided channels with mass wood recruitment, although field data from braided channels are necessary to test this hypothesis.

The end-member model proposed here may also have biogeographical implications in that episodic end-member sites are more likely to occur in montane catchments and areas subject to hurricanes, whereas the steady-state end-member sites are more likely to be lowland forests and those rarely influenced by hurricanes. The latter type of site is particularly widespread in South America, Africa and southeastern Asia.

The contrasting end-members presented here also apply to laterally confined, unmanaged headwater streams in the temperate zone, where both gradual (Wohl and Goode, 2008) and episodic (May and Gresswell, 2003) recruitment processes have been demonstrated (Table 2). Studies of wood dynamics through time at sites in the Colorado Front Range, USA support the idea that wood load does not vary significantly from year to year at sites with gradual recruitment, despite substantial transport of individual pieces into and out of the site (Wohl and Goode, 2008), similar to the steady-state tropical end-member. An unpublished study

Table 2
Wood loads reported for diverse old-growth forest streams.

Location	Forest type(s)	Drainage area (km^2)	S_c		Primary wood recruitment process	Hydrological regime	References
			V/L[a] (m^3/100 m)	V/A[b] (m^3/ha)			
Michigan, USA	Hardwood-hemlock	40	25 (7–62)	291 (75–622)	Not reported	Snowmelt/ rainfall	Morris et al. (2007)
s. Appalachian Mtns., USA	Hardwood-hemlock	3.5–11	21.7 (21.2–22.3)		Not reported	Rainfall	Hedman et al. (1996)
New Zealand	Nothofagus sub-antarctic rainforest and conifer/ mixed hardwood subtropical rainforest	0.6–5.8	18 (4–49)	206 (85–470)	Not reported	Not reported	Meleason et al. (2005)
s.e. Australia	*Tristaniopsis laurina* (water gum) and *Eucalyptus* ssp.	187	27.8	576	I_f (wind), I_m, I_{be}	Rainfall	Webb and Erskine (2003)
w. Oregon, USA	Temperate rainforest	0.1–60.5		478 (230–750)	I_m, I_f (wind), I_{be}	Snowmelt/ rainfall	Lienkaemper and Swanson (1987)
s.e. Alaska, USA	Temperate rainforest	0.7–55	24 (7–62)	196 (140–250)		Snowmelt/ rainfall	Robison and Beschta (1990)
Chilean Andes	Temperate Nothofagus and Araucaria	5.5–11	39 (3.8–236)	495 (4.8–4000)	I_m, I_s (landslides)	Rainfall/ snowmelt	Andreoli et al. (2007); Comiti et al. (2008a,b)
Tierra del Fuego, Argentina	Sub-antarctic Nothofagus	5–12.9	7 (1–24)	121 (20–395)	I_f (wind)	Glacionival	Mao et al. (2008)
Colorado, USA	Subalpine conifer	2.4–29	(6.6–27.1)	182 (92–254)	I_m	Snowmelt	Richmond and Fausch (1995)
La Selva, Costa Rica	Tropical wet	0.1–8.5	12.3 (3–35)	189 (41–612)	I_m	Rainfall	Cadol et al. (2009)

[a] V/L is volume of instream wood per length of channel; average value, followed by range in parentheses.
[b] V/A is volume of instream wood per area of channel surface; average value, followed by range in parentheses.

in the Front Range begun in 2008 indicates that individual logjams create large spatial variability in wood load and sediment storage and persist for perhaps a decade (Wohl, unpub. data), similar to the episodic end-member of the tropical sites. An important difference between the tropical and Front Range sites is that logjams form in the laterally confined Front Range channels in the absence of mass wood recruitment through landslides or blowdowns. We interpret this to reflect limited transport capacity at the temperate-zone site; individual pieces of wood can be fluvially transported, but any local decrease in transport capacity initiates jam formation.

Given similar recruitment mechanisms, the end-member model facilitates evaluation of how regional differences in hydrology and decay lead to differences in S_c and ΔS_c. Among the differences are that values of transport (Q_i/Q_o) and decay (D) are typically lower in temperate zones (Wohl and Jaeger, 2009; Cadol and Wohl, 2010), whereas wood loads (S_c) are higher, at least in temperate rainforest zones (Table 2). The limited available documentation suggests that logjams tend to be smaller and more closely spaced in temperate-zone headwater streams, whether or not the streams are subject to landslides (Gregory et al., 1993; May and Gresswell, 2003; Mao et al., 2008) and that individual jams persist longer than 1–2 years (Gregory et al., 1985; Gurnell and Sweet, 1998; Hyatt and Naiman, 2001; Martin and Benda, 2001; Abbe and Montgomery, 2003; Jeffries et al., 2003; Andreoli et al., 2007; Sear et al., 2010). Large jams have been documented for mountainous streams in sites such as Switzerland and Slovenia immediately following major floods (>100 year recurrence interval; Comiti et al., 2008b), but it remains unclear how long these jams persist. The longer permanence of logjams in temperate basins implies a greater capacity of wood to influence stream morphology by interacting with sediment transport and thus bar formation, floodplains and terraces, and secondary channels. These types of morphological effects seem to be less common in neotropical settings (Cadol et al., 2009).

Both the typically smaller size and closer spacing of logjams in temperate-zone streams may reflect lower wood transport capacity and slower decay rates in temperate streams compared to streams in the tropics. Episodic mass wood recruitment in temperate streams creates localized jams rather than jams that incorporate pieces transported from multiple mass movements upstream and, once incorporated in a jam, the flows needed to mobilize the mass of more solid wood occur less frequently, probably ~10 years or longer based on published studies. Jams in tropical environments may also promote faster decay rates for instream wood by elevating some pieces above the base flow, which presumably facilitates breakdown and transport of the wood composing the jam during higher flows. As with some of the interpretations discussed above, further documentation of characteristics such as jam persistence in tropical and temperate headwater streams is necessary to test these inferences.

Recognition of the different watershed characteristics that produce each end-member can facilitate decisions regarding resource management. Maintenance of a healthy riparian corridor that can sustain instream wood recruitment through individual tree fall, for example, is necessary to maintain the geomorphic and ecological functions of wood in the steady-state end-member, whereas maintenance of hillslope forests may be more important as a source of wood recruitment for the episodic end-member. For either end-member, the higher values of wood transport and decay relative to temperate-zone streams suggest that natural or human-induced declines in wood recruitment might cause more immediate and substantial changes in the stream's geomorphic and ecological functioning than in temperate-zone streams, where declining recruitment could be buffered for a longer period of time by previously recruited wood that is retained in the stream.

The model proposed here is based on limited field data from four tropical sites with diverse drainage area, gradient, and wood recruitment processes. The four sites do not, however, fully represent the diversity of tropical environments. All of the sites are laterally confined, single-thread channels in the neotropics. In addition, we have little information on the actual mechanics of wood recruitment and transport within streams; we do not know how the timing of individual treefall, mass recruitment, or jam formation or breakup corresponds to the stream hydrograph. Transitional states likely exist between the two end-members. Data on wood dynamics in tropical rivers are at present very limited, but the model presented here provides a conceptual framework that can help to guide future field work emphasizing channel and valley configurations for which wood dynamics are not yet documented (floodplain rivers, braided rivers) and the details of wood recruitment, transport and longitudinal distribution within streams in the context of variations in the hydrograph and associated hydraulic forces.

Acknowledgements

Field work at La Selva and the Rio Chagres by EW, DC, and JR was funded by National Science Foundation grant EAR-0808255. We thank the staff at La Selva Biological Station for access and support at the station. Weir data for La Selva streams was provided by David Genereux of North Carolina State University. Field work on the Chagres was also facilitated by the US Army Research Office and Environmental Sciences Division program director Russell Harmon. Field work in the Rio Portalon was funded by the EU Project INCO-CT-2004-510735 EPIC FORCE (Evidence-based policy for integrated control of forested river catchments in extreme rainfall and snowmelt). Field work at La Cangreja in 2003 was conducted by volunteer graduate and undergraduate students from the University of Washington with travel support from the Graduate School and the Jackson International School at the University of Washington. Comments by Fred Ogden and two anonymous reviewers helped us to improve this paper.

References

Abbe, T.B., Montgomery, D.R., 2003. Patterns and processes of wood debris accumulation in the Queets River basin, Washington. Geomorphology 51, 81–107.
Andreoli, A., Comiti, F., Lenzi, M.A., 2007. Characteristics, distribution and geomorphic role of large woody debris in a mountain stream of the Chilean Andes. Earth Surface Processes and Landforms 32, 1675–1692.
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.
Beard, K.H., Vogt, K.A., Vogt, D.J., Scatena, F.N., Covich, A.P., Sigurdardottir, R., Siccama, T.G., Crowl, T.A., 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. Ecological Monographs 75, 345–361.
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, 1–16.
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, 1807–1820.
Bilby, R.E., Likens, G.E., 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61, 1107–1113.
Boyce, J.S., 1961. Forest Pathology. McGraw-Hill, New York.
Brooks, A.P., Brierley, G.J., 2002. Mediated equilibrium: the influence of riparian vegetation and wood on the long-term evolution and behaviour of a near-pristine river. Earth Surface Processes and Landforms 27, 343–367.
Bultman, J.D., Southwell, C.R., 1976. Natural resistance of tropical American woods to terrestrial wood-destroying organisms. Biotropica 8, 71–95.
Cadol, D., Wohl, E., 2010. Wood retention and transport in tropical, headwater streams, La Selva Biological Station, Costa Rica. Geomorphology 123, 61–73.
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, 1198–1215.
Clark, D.B., Clark, D.A., Read, J.M., 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. Journal of Ecology 86, 101–112.
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, 237–248.
Collins, B.D., Montgomery, D.R., 2002. Forest development, wood jams and restoration of floodplain rivers in the Puget Lowland, Washington. Restoration Ecology 10, 237–247.
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, 44–63.
Comiti, F., Andreoli, A., Mao, L., Lenzi, M.A., 2008a. Wood storage in three mountain streams of Southern Andes and its hydro-morphological effects. Earth Surface Processes and Landforms 33 (2), 242–262.
Comiti, F., Mao, L., Preciso, E., Picco, L., Marchi, L., Borga, M., 2008b. Large wood and flash floods: evidences from the 2007 event in the Davca basin (Slovenia). In: AA.VV., Monitoring, Simulation, Prevention and Remediation of Dense and Debris Flow II, vol. 60, pp. 173–182.
Covich, A.P., Crowl, T.A., 1990. Effects of hurricane storm flow on transport of woody debris in a rain forest stream (Luquillo Experimental Forest, Puerto Rico). In: Krishna, J.H., Quiñones-Aponte, Gómez-Gómez, F., Morris, G. (Eds.), Tropical Hydrology and Caribbean Water Resources. American Water Resources Association, Bethesda, Maryland, pp. 197–205.
Curran, J.H., Wohl, E.E., 2003. Large woody debris and flow resistance in step-pool channels, Cascade Range, Washington. Geomorphology 51, 141–157.
Dahlström, N., Nilsson, C., 2004. Influence of woody debris on channel structure in old-growth and managed forest streams in central Sweden. Environmental Management 33, 376–384.
Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A., Quintero, N.B., 1998. The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. Biotropica 30, 2–11.
Douglas, I., Guyot, J.L., 2005. Erosion and sediment yield in the humid tropics. In: Bonnell, M., Bruijnzeel, L.A. (Eds.), Forests. Water and People in the Humid Tropics. Cambridge University Press, Cambridge, pp. 407–421.
Downs, P.W., Simon, A., 2001. Fluvial geomorphological analysis of the recruitment of large woody debris in the Yalobusha River network, central Mississippi, USA. Geomorphology 37, 65–91.
Ellis, L.M., Molles, M.C., Crawford, C.S., 1999. Influence of experimental flooding on litter dynamics in a Rio Grande riparian forest, New Mexico. Restoration Ecology 7, 193–204.
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, 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, 187–205.
Frangi, J.L., Richter, L.L., Barrera, M.D., Aloggia, M., 1997. Decomposition of Nothofagus fallen woody debris in forests of Tierra del Fuego, Argentina. Canadian Journal of Forest Research 27, 1095–1102.
Gomi, T., Sidle, R.C., Noguchi, S., Negishi, J.N., Nik, A.R., Sasaki, S., 2006. Sediment and wood accumulations in humid tropical headwater streams: effects of logging and riparian buffers. Forest Ecology and Management 224, 166–175.
Gregory, K.J., Gurnell, A.M., Hill, C.T., 1985. The permanence of debris dams related to river channel processes. Hydrological Sciences Journal 30, 371–381.
Gregory, K.J., Davis, R.J., Tooth, S., 1993. Spatial distribution of coarse woody debris dams in the Lymington Basin, Hampshire, UK. Geomorphology 6, 207–224.
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, 1101–1121.
Gurnell, A.M., Petts, G.E., Hannah, D.M., Smith, B.P.G., Edwards, P.J., Kollmann, J., Ward, J.V., Tockner, K., 2000. Wood storage within the active zone of a large European gravel-bed river. Geomorphology 34, 55–72.
Harmon, M.E., 1982. Decomposition of standing dead trees in the southern Appalachian Mountains. Oecologia 52, 214–215.
Harmon, M.E., Franklin, J.K., 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, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133–302.
Hartshorn, G.S., 1990. An overview of neotropical forest dynamics. In: Gentry, A.H. (Ed.), Four Neotropical Rainforests. Yale University Press, New Haven, CT, pp. 585–599.
Haschenburger, J.K., Rice, S.P., 2004. Changes in woody debris and bed material texture in a gravel-bed channel. Geomorphology 60, 241–267.
Hedman, C.W., Van Lear, D.H., Swank, W.T., 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. Canadian Journal of Forest Research 26, 1218–1227.
Houseal, B., 1999. Plan de manejo y desarrollo del parquet nacional Soberania. In: Ashton, M.S., O'Hara, J.L., Hauff, R. (Eds.), Protecting Watershed Areas – Case of the Panama Canal. Food Products Press, New York, pp. 1–11.
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.
Iroumè, A., Andreoli, A., Comiti, F., Ulloa, H., Huber, A., 2010. Large wood abundance, distribution and mobilization in a third order Coastal mountain range river system, southern Chile. Forest Ecology and Management 260 (4), 480–490.
Jacobson, P.J., Jacobson, K.M., Angermeier, P.L., Cherry, D.S., 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.
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, 61–80.

Keller, E.A., Tally, T., 1979. Effects of large organic debris on channel form and fluvial processes in the coastal redwood environment. In: Rhodes, D.D., Williams, G.P. (Eds.), Adjustments of the Fluvial System. Kendall/Hunt Publishing, Dubuque, Iowa, pp. 169–197.

Kleber, M., Schwendenmann, L., Veldkamp, E., Rösner, 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 183, 1–11.

Lewis, S.L., Phillips, O.L., Sheil, D., Vincenti, B., Baker, T.R., Brown, S., Graham, A.W., Higuchi, N., Hilbert, D.W., Laurance, W.F., Lejoly, J., Malhi, Y., Monteagudo, A., Vargas, P.N., Sonke, B., Supardi, N., Terborgh, J.W., Martinez, R.V., 2004. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. Journal of Ecology 92, 929–944.

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, 150–156.

Linstead, C., 2001. The effects of large woody debris accumulations on river hydraulics and implications for physical habitat. In: Acreman, M.C. (Ed.), Hydro-ecology: Linking Hydrology and Aquatic Ecology. IAHS Publ. No. 266. Wallingford, UK, pp. 91–99.

Lugo, A.E., Scatena, F.N., 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. Biotropica 28, 585–599.

MacFarlane, W.A., Wohl, E., 2003. Influence of step composition on step geometry and flow resistance in step-pool streams of the Washington Cascades. Water Resources Research 39, WR001238.

MacVicar, B., Piegay, H., Henderson, A., Comiti, F., Oberline, C., Pecorari, E., 2009. Quantifying the temporal dynamics of wood in large rivers: field trials of wood surveying, dating, tracking, and monitoring techniques. Earth Surface Processes and Landforms 34 (15), 2031–2046.

Magilligan, F.J., Nislow, K.H., Fisher, G.B., Wright, J., Mackey, G., Laser, M., 2008. The geomorphic function and characteristics of large woody debris in low gradient rivers, coastal Maine, USA. Geomorphology 97, 467–482.

Manners, R.B., Doyle, M.W., Small, M.J., 2007. Structure and hydraulics of natural woody debris jams. Water Resources Research 43, W06432. doi:10.1029/2006WR004910.

Mao, L., Comiti, F., 2010. The effects of large wood elements during an extreme flood in a small tropical basin of Costa Rica. In: De Wrachien, D., Brebbia, C.A. (Eds.), Debris Flow III. WIT Press, UK, pp. 225–236.

Mao, L., Andreoli, A., Comiti, F., Lenzi, M.A., 2008. Geomorphic effects of large wood jams on a sub-Antarctic mountain stream. River Research and Applications 24, 249–266.

Marcus, W.A., Marston, R.A., Colvard, C.R., Gray, R.D., 2002. Mapping the spatial and temporal distributions of woody debris in streams of the Greater Yellowstone Ecosystem, USA. Geomorphology 44, 323–335.

Martin, D.J., Benda, L.E., 2001. Patterns of instream wood recruitment and transport at the watershed scale. Transactions of the American Fisheries Society 130, 940–958.

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, Florida.

May, C.L., Gresswell, R.E., 2003. Processes and rates of sediment and wood accumulation in headwater streams of the Oregon Coast Range, USA. Earth Surface Processes and Landforms 28, 409–424.

Meleason, M.A., Davies-Colley, R., Wright-Stow, A., Horrox, J., Costley, K., 2005. Characteristics and geomorphic effect of wood in New Zealand's native forest streams. Int. Rev. Hydrobiol. 90, 466–485.

Méndez Herrera, J.C., Esquivel, L., 2006. Inundaciones, deslizamientos, flujos de lodo y detritos: Sus efectos sociales y geológicos en las microcuencas de los ríos Guabas y Portalón (Septiembre, 2005). IX Seminario Nacional de Geotecnia, San José, Costa Rica, 14–18 November 2006.

Montgomery, D.R., Buffington, J.M., 1997. Channel-reach morphology in mountain drainage basins. Geological Society of America Bulletin 109, 596–611.

Montgomery, D.R., Buffington, J.M., Smith, R.D., Schmidt, K.M., Pess, G., 1995. Pool spacing in forest channels. Water Resources Research 31 (4), 1097–1105.

Montgomery, D.R., Massong, T.M., Hawley, S.C.S., 2003. Influence of debris flows and log jams on the location of pools and alluvial channel reaches, Oregon Coast Range. Geological Society of America Bulletin 115, 78–88.

Morris, A.E.L., Goebel, P.C., Palik, B.J., 2007. Geomorphic and riparian forest influences on characteristics of large wood and large-wood jams in old-growth and second-growth forests in northern Michigan, USA. Earth Surface Processes and Landforms 32, 1131–1153.

O'Connell, A.M., 1997. Decomposition of slash residues in thinned regrowth eucalypt forest in western Australia. Journal of Applied Ecology 34, 111–122.

O'Connor, J.E., Jones, M.A., Haluska, T.L., 2003. Flood plain and channel dynamics of the Quinault and Queets Rivers, Washington, USA. Geomorphology 51, 31–59.

Organization for Tropical Research, 2007. La Selva daily rainfall, 1963–2006. In: Clark, D.A. (Ed.), Meteorología-OET. <http://www.ots.ac.cr/meteoro/default.php>.

Pettit, N.E., Naiman, R.J., 2006. Flood-deposited wood creates regeneration niches for riparian vegetation on a semi-arid South African river. Journal of Vegetation Science 17, 615–624.

Piégay, H., Gurnell, A.M., 1997. Large woody debris and river geomorphological pattern: examples from S.E. France and S. England. Geomorphology 19, 99–116.

Piégay, H., Thevenet, A., Citterio, A., 1999. Input, storage and distribution of large woody debris along a mountain river continuum, the Drome River, France. Catena 35, 19–39.

Richmond, A.D., Fausch, K.D., 1995. Characteristics and function of large woody debris in subalpine Rocky Mountain streams in northern Colorado. Canadian Journal of Fisheries and Aquatic Sciences 52, 1789–1802.

Robison, E.G., Beschta, R.L., 1990. Coarse woody debris and channel morphology interactions for undisturbed streams in southeast Alaska, USA. Earth Surface Processes and Landforms 15, 149–156.

Scatena, F.N., Planos-Gutierrez, E.O., Schellekens, J., 2005. Natural disturbances and the hydrology of humid tropical forests. In: Bonnell, M., Bruijnzeel, L.A. (Eds.), Forests. Water and People in the Humid Tropics. Cambridge University Press, Cambridge, pp. 489–512.

Sear, D.A., Millington, C.E., Kitts, D.R., Jeffries, R., 2010. Logjam controls on channel:floodplain interactions in wooded catchments and their role in the formation of multi-channel patterns. Geomorphology 116, 305–319.

Seo, J.I., Nakamura, F., 2009. Scale-dependent controls upon the fluvial export of large wood from river catchments. Earth Surface Processes and Landforms 34, 786–800.

Spänhoff, B., Meyer, E.I., 2004. Breakdown rates of wood in streams. Journal of the North American Benthological Society 23 (2), 189–197.

Warren, D.R., Bernhardt, E.S., Hall, R.O., Likens, G.E., 2007. Forest age, wood and nutrient dynamics in headwater streams of the Hubbard Brook Experimental Forest, NH. Earth Surface Processes and Landforms 32, 1154–1163.

Webb, A.A., Erskine, W.D., 2003. Distribution, recruitment, and geomorphic significance of large woody debris in an alluvial forest stream: Tonghi Creek, southeastern Australia. Geomorphology 51, 109–126.

Wohl, E., 2005. Downstream hydraulic geometry along a tropical mountain river. In: Harmon, R.S. (Ed.), The Río Chagres, Panama: A Multidisciplinary Profile of a Tropical Watershed. Springer, Dordrecht, The Netherlands, pp. 169–188.

Wohl, E., Cadol, D., 2011. Neighborhood matters: patterns and controls on wood distribution in old-growth forest streams of the Colorado Front Range, USA. Geomorphology 125, 132–146.

Wohl, E., Goode, J.R., 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. Water Resources Research 44, W09429. doi:10.1029/2007WR006522.

Wohl, E., Jaeger, K.L., 2009. Geomorphic implications of hydroclimatic differences among step-pool channels. Journal of Hydrology 374, 148–161.

Wohl, E., Ogden, F.L., Goode, J., 2009. Episodic wood loading in a mountainous tropical watershed. Geomorphology 111, 149–159.

Wörner, G., Harmon, R.S., Hartmann, G., Simon, K., 2005. Igneous geology and geochemistry of the Upper Rio Chagres basin. In: Harmon, R.S. (Ed.), The Río Chagres, Panama: A Multidisciplinary Profile of a Tropical Watershed. Springer, Dordrecht, The Netherlands, pp. 65–82.

Wyzga, B., Zawiejska, J., 2005. Wood storage in a wide mountain river: case study of the Czarny Dunajec, Polish Carpathians. Earth Surface Processes and Landforms 30 (12), 1475–1494.