DISSERTATION

WOOD IN NEOTROPICAL HEADWATER STREAMS, COSTA RICA

Submitted by

Daniel Cadol

Department of Geosciences

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DANIEL CADOL ENTITLED WOOD IN NEOTROPICAL HEADWATER STREAMS, COSTA RICA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Daniel Cenderelli

Stephanie Kampf

Sara Rathburn

Advisor: Ellen Wohl

Department Head: Sally Sutton

ABSTRACT OF DISSERTATION

WOOD IN NEOTROPICAL HEADWATER STREAMS, COSTA RICA

Wood has been shown to be an integral component of forest streams throughout the temperate climate zone, both in terms of the physical structure of the channel and in terms of aquatic ecosystem function, but the function of wood in undisturbed tropical streams has not been studied. This dissertation represents the first systematic analysis of instream wood in a tropical setting to be published. This study was limited to the headwater streams (drainage area <8.5 km^2) of La Selva Biological Station, on the Atlantic margin of Costa Rica, a wet tropical site with limited landslide activity. Although the results are instructive and enable comparisons with the vast temperate instream wood literature, they should not be construed as representative of debris flow-dominated wet tropical forest streams or of dry or seasonal tropical forest streams.

Wood loads in the thirty 50-m-long study reaches examined ranged from 3.0 to 34.7 m^3 of wood per 100 m of channel length and 41 to 612 m^3 of wood per ha of channel area. Average values are 12.3 m^3/100 m and 189 m^3/ha. These values fall generally in the lower range of wood load reported for temperate streams, with values typically lower than those reported from the Pacific Northwest region and the Great Lakes region and within the range of those reported from the Rocky Mountain region and from Southern Hemisphere study sites. Comparisons to study sites in eastern North America, Europe,

and Japan are problematic because La Selva is a generally undisturbed forest, whereas studies from those regions are conducted in streams with significant human impact and tend to have very small wood loads.

Flow hydraulics appear to be the dominant control on the lateral distribution of wood in the channels of La Selva, but they are only a partial control on the longitudinal distribution of wood, explaining about half of the variation in wood load among the study sites. The remainder of the variation is likely caused by the stochastic nature of large tree fall. In spite of the high temporal variability of lateral input of wood to the channels, spatial variability is small, partially because of the paucity of landslides at La Selva. Therefore, I propose that instream transport has a greater influence on the longitudinal distribution of wood than lateral input variability.

Wood in a representative subset of 10 of the 50-m-long study reaches was monitored for 2.3 years. The wood in the streams of La Selva is more transient than wood in most sites studied in the temperate zone, with piecewise mean residence times ranging from 2 to 12 years and volume-wise mean residence times ranging from 2 to 83 years among the 10 sites monitored. Average values were 5 and 7 years, respectively. These are roughly an order of magnitude shorter than mean residence times reported from the Pacific Northwest, but similar to times reported from the Colorado Rocky Mountains. The short residence times may be a result of more frequent large floods caused by the wet tropical climate, higher decay rates caused by the warm tropical climate, or both.

Perhaps because of this transience, wood was found to have minimal influence on flow resistance in a subset of 6 of the 50-m-long study reaches. In contrast, wood has been shown to be a major control on flow resistance in temperate mountain streams. It is possible that the channel geometry and bed material size are adjusted to the frequent high discharges, which also mobilize and rework the wood, causing grain and form resistance to overwhelm any resistance contribution from wood.

Instream wood at La Selva also appears to have a minimal influence on sediment transport. Jams in sand-bed channels and jams in boulder-bed channels had no associated residual elevation drop. Jams in gravel-bed channels did alter bed elevation by trapping sediment wedges behind them, but analysis of tracer clast movement at one gravel-bed jam resulted in no observable difference in transport distances or mobility between clasts placed upstream of the jam and those placed downstream.

An additional forest-stream interaction that was documented is diel cycles in stream discharge associated with groundwater withdrawal by the forest for evapotranspiration. Analysis of the cycles indicates a strong correlation with vapor pressure differential, which previous researchers have found to correlate with sap flow. Further analysis of the cycles suggests that at low-stage conditions transmissivity dominates groundwater flow into the channel, while at high-stage conditions hydraulic gradient is dominant.

Daniel Douglas Cadol
Department of Geosciences
Colorado State University
Fort Collins, CO 80523
Summer 2010

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1 INTRODUCTION

1.1 Geomorphic and ecologic role of wood

Wood is an important, but commonly overlooked, component of fluvial systems in forested environments. Like sediment, wood can be incorporated into the boundaries of channels and transported by flow. Unlike sediment, the specific weight of wood tends to be less than that of water, enabling transport of relatively larger pieces of wood than sediment. As a result, wood jamming is more common than sediment jamming, because of its larger size relative to channel dimensions (Braudrick et al., 1997). Related to its lesser density, wood is more easily broken and abraded in transport than sediment, leading to more rapid removal down the stream network. Microbes and decay fungi are also able to break down wood, speeding the disintegration process (Anderson et al., 1978). Thus instream wood can be thought of as a more mobile, transient analogue to sediment.

As wood is incorporated into the channel boundaries of a forested stream, it has great potential for altering channel morphology, hydraulic characteristics, and sediment transport. Channels with higher wood loads tend to have more pool area (Montgomery et al., 1995; Richmond and Fausch, 1995; Beechie and Sibley, 1997; Gurnell and Sweet, 1998) and higher steps (Curran and Wohl, 2003). In cases where wood forms steps and causes plunging flow, localized pool scour is common. Wood pieces and jams have the potential to redirect flow, causing either localized scour or shielding, depending on their orientation relative to the flow and to the bank or bed. The increase in flow resistance caused by instream wood can lead to increased overbank flow (Jeffries et al., 2003). In some cases wood jams may block the channel to such a degree that an avulsion is initiated, potentially leading to the development of an anastamosing channel pattern (Makaske et al., 2002). Jams may disrupt the helical flow pattern around bends, reducing bank erosion and bend migration rates (Daniels and Rhoads, 2003; Daniels and Rhoads, 2004).

The tendency to form jams is an important characteristic of instream wood. Many natural jams are initiated by a large, “key”, piece which traps other wood pieces in transport (Hyatt and Naiman, 2001; Abbe and Montgomery, 2003) and in cases where jamming is dependent on key pieces, they control the spatial distribution of jams. Because jamming is promoted by a combination of key pieces and an abundance of other mobile pieces to be racked against them, jams are maximized in medium-sized streams (Wohl and Jaeger, 2009). Jamming in small streams is limited by piece mobility, and jamming in large streams is limited by the lack of stable key pieces. When considering instream wood, stream size is most effectively described relative to wood size, so that a small stream will be one in which most wood pieces are longer than the channel width, and a large stream will be one in which channel width is wider than the longest wood piece (Piegay and Gurnell, 1997; Gurnell et al., 2002).

The primary hydraulic effect of wood is an increase of flow resistance (Shields and Gippel, 1995; Curran and Wohl, 2003; Hygelund and Manga, 2003; Mutz, 2003; Wilcox and Wohl, 2006), dissipating energy that would otherwise be available for sediment transport or channel margin erosion (Assani and Petit, 1995; Buffington and Montgomery, 1999). The increased resistance also lowers velocity and increases flood stage. In some rivers, high wood loads promote sediment deposition and floodplain building, and when the wood is removed dramatic incision ensues (Brooks et al., 2003). At a more local scale, wood jams may impound flow and cause deposition of sediment wedges in their backwater (Smith et al., 1993a; Montgomery et al., 2003b).

Wood has been entering streams for over 400 million years, when the first evidence of trees is observed in the stratigraphic record (Montgomery et al., 2003a). It is no surprise, then, that aquatic organisms are adapted to its presence, and in some cases rely on it for habitat. Because wood pieces are large relative to most instream sediment, they tend to create distinct features that increase habitat complexity and diversity. As wood alters the physical character of a stream, it impacts the biota that use these physical features as habitat (Angermeier and Karr, 1984; Zalewski et al., 2003). A single log across a small stream may trap a sediment wedge behind it, create a hydraulic step where water flows over it, and cause the flow to scour a plunge pool below. Each of these features has an important ecological function. Gravel wedges formed behind wood jams have been observed to be preferred sites for salmon to build their redds (Grette, 1985; Buffington et al., 2003). Hydraulic steps help aerate flow and maintain adequate dissolved oxygen levels for fish in streams (Bisson et al., 1987). And pools can serve as low-flow refugia for aquatic organisms, enabling them to survive extreme droughts (Bisson et al., 1987; Dolloff and Warren, 2003). In addition to creating low-flow refuges for aquatic organisms, wood can create high-flow refuges in the form of low velocity zones behind logs and jams (Dolloff and Warren, 2003). Whereas some species use jam-trapped gravel for nesting, other species rely on the wood itself for nesting, such as armored catfish in Panama that nest within hollow logs (Power, 2003). Wood can serve as substrate for macroinvertebrates, algae, fungi, and microbes (Maser and Sedell, 1994), especially in fine-bedded streams with no other stable substrate (Benke and Wallace, 2003), and the carbon derived from the wood contributes to the nutrient resources available in the stream (Chen et al., 2005). In general, by increasing channel complexity, wood increases the availability of microhabitats and increases the faunal diversity of a stream (Bisson et al., 1987; Kail, 2003; Wondzell and Bisson, 2003).

1.2 Anthropogenic influences on instream wood

Human activity has driven a drastic reduction in the amount of instream wood. Forest cover has been reduced by about half of its peak extent, from nearly two thirds of Earth's land surface area to less than one third today (Atjay et al., 1979; Montgomery et al., 2003a), reducing the number of streams wherein wood delivery is possible. Large quantities of woody material were historically delivered to coastal and marine environments, but the rate is much reduced today (Maser et al., 1988). Wood has also been actively removed from streams, for example to facilitate navigation and to improve flood conveyance. Log jams were common on major rivers in North America and Australia at the time of European settlement, and were generally viewed as an impediment to transportation (Hill, 1957, in Montgomery et al., 2003a). For example, a jam on the Red River in Louisiana called the 'great raft', near Shreveport, jammed the river for 300 km and enabled crossing of the river by foot (Triska, 1984; Keller and MacDonald, 1995). This jam was cleared between 1832-1839 by Captain Henry Shreve, opening the way for riverboat traffic and the establishment of the port (Lobeck, 1939, in Keller and MacDonald, 1995). Dynamiting of snags and jams has been a common practice on rivers in regions settled by people of European descent since the 17th century.

As a result, channel complexity has been reduced in most rivers of the world. In some cases wood removal was carried out with the intent of improving fish passage (Maser et al., 1988). These misguided efforts in fact led to channels that were devoid of resting places for fish, thereby reducing the spawning success rate. Additionally, wood is often removed from streams in order to protect downstream structures, such as bridges and irrigation diversion structures. Wood that is mobilized in a flood can become pinned against these structures, increasing the force applied to the structure as more wood accumulates, with the potential to eventually cause failure. For this reason wood is typically removed from streams along transportation corridors by road maintenance crews.

Efforts have been made in recent years to reintroduce wood into some wood-depleted streams (Cederholm et al., 1997; Brooks et al., 2001; Abbe et al., 2003; Borg et al., 2007; Kail et al., 2007). Success has been mixed, in part because wood is a highly mobile component of fluvial systems. Anchoring pieces in place increases the longevity of the wood feature, but prevents it from evolving with changes in channel location or morphology. Even if the channel does not migrate away from the anchored jam, the wood will eventually decay and the feature will cease to function as designed. The success of these installed features commonly depends on the ability of a large, “key” piece to trap other wood pieces in transport, forming a jam that has the potential to evolve.

1.3 Tropical streams and wood

The research on wood outlined above was conducted in temperate climate zone streams, primarily in the Pacific Northwest of Canada and the United States. The earliest research on instream wood was conducted in the Pacific Northwest in the 1970s and

1980s (Anderson et al., 1978; Beschta, 1979; Keller and Swanson, 1979; Keller and Tally, 1979b; Bilby and Likens, 1980; Triska and Cromac, 1980; Marston, 1982; Megahan, 1982; Melillo et al., 1983; Grette, 1985; Harmon et al., 1986; Bisson et al., 1987), and over the two decades since then, researchers have expanded the scope of inquiry to the Appalachian Mountains (Golladay and Webster, 1988; Hart, 2002; Valett et al., 2002), Rocky Mountains (Richmond and Fausch, 1995; Wohl and Goode, 2008; Powell et al., 2009; Wohl and Jaeger, 2009), Sierra Nevada (Berg et al., 1998), Upper Midwest (Morris et al., 2007), and New England (Thompson, 1995; Magilligan et al., 2008; Fisher et al., 2010) of North America, as well as Australia (Brooks and Brierley, 2002; Brooks et al., 2003; Webb and Erskine, 2003), New Zealand (Evans et al., 1993; Baillie and Davies, 2002; Meleason et al., 2005; Meleason and Hall, 2005), Europe (Piegay and Gurnell, 1997; Gurnell and Sweet, 1998; Gurnell et al., 2000b; Díez et al., 2002; Dahlström et al., 2005; Comiti et al., 2006), southern South America (Andreoli et al., 2007; Comiti et al., 2008; Mao et al., 2008), Japan (Haga et al., 2002; Seo and Nakamura, 2009), China (Harmon and Hua, 1991; Deng et al., 2002), and southern Africa (Jacobson et al., 1999). Yet all of these sites are in temperate regions, meaning very few studies have taken place in high latitudes (polar regions) or low latitudes (tropical regions). The only exception I have found to date, other than the research presented herein and a companion study of the Rìo Chagres in Panama (Wohl et al., 2009), is a study of wood accumulation in logged forests of Malaysia by Gomi and his colleagues (2006). This dissertation thus represents one of the first efforts to extend the investigation of instream wood into the tropics.

In this effort to expand our understanding of instream wood into the tropical climate zone, it is valuable to first consider the differences between temperate and tropical streams which may impact wood loads and dynamics. The tropics are characterized by year-round warm temperatures and high precipitation. These climatic characteristics lead in turn to high biological productivity (Clark et al., 2001), the prominence of large tree species, high decay rates, high weathering rates and deeply weathered soils (Kleber et al., 2007), and flashy flow regimes. Each of these factors may influence the size and amount of wood entering streams, the spatial and temporal distribution of its entry, or the rates at which downstream transport and decay remove the wood.

Many tropical trees grow to heights over 50 m and have trunk diameters above their buttresses that exceed 2 m (Lieberman et al., 1985; Hartshorn and Hammel, 1994). Additionally, many species have decay-resistant compounds in their wood, and the specific gravity of the wood can exceed 1 (i.e., wood more dense than water) (Chave et al., 2006). It is very difficult to make generalizations about tropical trees because of the extremely high species diversity relative to the temperate zone. In a study from Costa Rica, foresters documented over 100 species in one hectare, 80% of which had fewer than 2 individuals with diameter at breast height (dbh) ≥10 cm in the sample (Lieberman and Lieberman, 1994). Therefore, the wood entering tropical streams has the potential for very wide size and density distributions. If large, dense, decay-resistant pieces are dominant, one would expect wood retention to be relatively high, if all other factors were unchanged.

Not all other factors remain unchanged, however, between typical temperate and tropical streams. Hydraulic geometry and variation in sinuosity may have different trends in the tropics relative to the temperate zone, with lower width-to-depth ratios as a result of the dense bank vegetation (Holz et al., 1979). This would lead to deeper flows and more frequent floatation of wood. Floods are expected to be more frequent, larger, and flashier in the tropics, because of the higher precipitation, greater runoff production, and occurrence of intense tropical storms (Gupta, 1988). Runoff production will be increased by the relatively high clay content of the highly weathered tropical soils, which can promote overland flow (Calvo-Gobbett et al., 2005). At the same time, fractures from wetting and drying of the clay soils and macropores from decayed roots and animal and insect burrows can quickly route water through the subsurface into the channel (Niedzialek and Ogden, 2005). Tropical storms and hurricanes, in regions where they occur, will deliver precipitation in rates and volumes that are unmatched in the intervals between these events (Gupta, 1988; Garcin et al., 2005). The deep flows generated by large, flashy floods will have enhanced wood transport capacity, especially for floating pieces. Yet these same storms that increase transport may also increase wood delivery by triggering landslides that have the potential to deliver vast quantities of wood into the stream (Wohl et al., 2009).

Decay rates are expected to be relatively high in the tropics, but direct measurements of instream decay are rare in the temperate zone (Bilby et al., 1999; Díez et al., 2002), and unreported for the tropics. Wood decay on the forest floor has been measured, yielding mean residence times of 9 years in a tropical forest in Costa Rica (Clark et al., 2002), 30-100 years in humid temperate forests (Graham and Cromack, 1982; Harmon et al., 1986; Harmon and Hua, 1991), and >100 years in semiarid environments (O'Connell, 1997; Ellis et al., 1999). These variations in decay may not transfer directly to instream wood because of the anaerobic conditions that occur around submerged pieces and because of the abrasion of wood by transported sediments. Nonetheless, I expect the warmer temperatures, the lack of freezing, and the higher microbial diversity of the tropics to lead to higher decay rates for instream wood. Additionally, wood in tropical streams may experience greater rates of abrasion because of the relatively high unit discharges and frequent sediment mobilization.

Some of the differences outlined above would promote greater wood delivery in the tropics (e.g., larger trees), while others would promote lesser wood delivery (e.g., faster decay rates on the forest floor). Likewise, some promote greater wood transport (e.g., greater unit discharges), while others promote greater wood retention (e.g., higher wood density). The purpose of the work conducted for this dissertation was to determine how these various factors balance one another in a particular old-growth tropical forest environment at La Selva Biological Station, Costa Rica.

1.4 Study Site

La Selva Biological Station (10º 26’ N, 84º 01’ W), of the Atlantic margin of Costa Rica, is a 16 km^2 research reserve operated by the Organization for Tropical Studies (Figure 1.1). The forest is classified as Tropical Wet Forest in the Holdridge system (Hartshorn and Peralta, 1988). About half the reserve, 730 ha, is old-growth forest, and the remainder is primarily composed of second-growth forest that is at least 30 years old. This wet tropical study site is not expected to be representative of seasonal or dry tropical environments.

1.4.1 *Cimate*

Strong microgeographic and orographic effects over the area help to create a mean annual precipitation of over 4 m. There is a short dry season, usually occurring sometime between February-May, but condensation drip occurs most nights, even during the dry season. Mean annual precipitation from 1963-2008 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 online data, 2009). Standard deviation of annual precipitation from 1963-2008 was 700 mm. Mean annual temperature is 26 ºC. Monthly average temperature fluctuates by less than 5 ºC, whereas daily temperature typically fluctuates by at least 10 ºC. Hurricanes seldom reach the area, with the only recorded occurrence in the early 1960s, but intense rains are generated from November to January by the establishment of a cold front that penetrates the air mass over the Caribbean Sea to as low as 10 ºN (Janzen, 1983).

1.4.2 *Geology*

The bedrock at La Selva consists of a sequence of andesitic lava flows originating from the volcanoes of the Central Cordillera (Alvarado, 1990, in Kleber et al., 2007). The wet climate results in intense weathering of these underlying andesitic lava flows, producing oxisols enriched in kaolinite-group minerals (Kleber et al., 2007). Clay-rich saprolite is several meters thick on most ridges, with soils typically about 1 m thick above the saprolite (Sollins et al., 1994). Bedrock outcrops are primarily limited to stream beds and banks. The clasts that compose the bedload are also weakened by weathering. In coarse-bed streams, the bed clasts could not be used to drive rebar into gravel; even 20 cm diameter cobbles broke in half after a few strikes.

1.4.3 *Topography and hill slopes*

Elevation at the station ranges from 34 m to 110 m and reflects the transition from the low, steep foothills of the Central Volcanic Cordillera to the Sarapiquí coastal plain. Although hill slopes are frequently steep, typically about 20° but up to 45°, no evidence of landslides was observed during field work, and landslides have not been observed at La Selva in over four decades of extensive field work (D.A. Clark and D.B. Clark, personal communication, 2007). This may be because hill slope length is rarely greater than 50 m, or possibly because rapid subsurface routing of rainfall to the streams through macropores prevents pore pressure increases adequate to trigger landslides.

La Selva is bordered to the south by Braulio Carillo National Park, a 476 km^2 preserve that extends to the high volcanic peaks of the Central Cordillera. It protects a large area of intact primary forest that includes the volcanoes Poaz (2704 m), Barva (2906 m) and Irazu (3423 m). The land to the north and east is a flat coastal plain. With the national park, La Selva forms a peninsula of preserved rainforest that extends to the edge of the Caribbean lowlands and is surrounded by land that has been cleared for pastures and plantations.

1.4.4 *Streams*

The northern border of La Selva is formed by the Rìo Sarapiquì, flowing east and draining 432 km^2, and the Rìo Puerto Viejo, flowing west and draining 370 km^2. These two rivers join at La Selva and flow north to the Rìo San Juan and the Nicaraguan border. The primary drainages of La Selva are El Surà, El Salto, and Quebrada Esquina, with respective drainage areas of 4.8 km^2, 8.5 km^2, and 2.3 km^2; all flow north into the Rìo Puerto Viejo. 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.

These three smaller streams and their tributaries have segmented longitudinal profiles, reflecting the underlying topography of low-gradient valley bottoms atop the lava flows, steep segments where the streams cross the fronts of the lava flows onto the alluvial terraces of the Rìo Puerto Viejo, and low-gradient segments on the terraces. Lower gradient reaches tend to have beds of silty fine sand and dune-ripple or pool-riffle morphology (Montgomery and Buffington, 1997), whereas steeper segments have gravel- and boulder-size sediments and pool-riffle or step-pool morphology. The floodplains of the Rìo Sarapiquì and Rìo Puerto Viejo coincide with the portion of La Selva that is below 51 m elevation. The portions of the smaller rivers that cross this floodplain are subject to backflooding when the larger rivers flood.

Floods occur frequently at La Selva, and the streams are very responsive to rainfall, resulting in a flashy hydrograph. Baseflow periods are rare because of the frequency of rainfall events. Stream water temperature at a gage placed at the final bedrock step on El Surà ranged from 22-26 °C, with baseflow generally warmer, and storm flow generally cooler. Inter-basin groundwater flow is a major source of water in some low-elevation watersheds at La Selva, although its influence is spatially heterogeneous (Genereux et al., 2002).

1.4.5 Forest

All stream corridors used in this study are densely vegetated, with smaller woody vegetation immediately adjacent to the active channel. Trees at La Selva can reach 60 m in height. There are over 300 identified hardwood species at La Selva (Hartshorn and Hammel, 1994) and over 80% of these have ≤2 individuals 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 portion of La Selva have a mean dbh of approximately 20 cm, and the mean number of stems per hectare is approximately 450 (Clark and Clark, 2000). Stem turnover is approximately 2% per year 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 greater than 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 0.35-0.98 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.

Although forest ecologists recognize four geomorphic surfaces at La Selva and associated differences in forest composition (Clark et al., 1998; Clark et al., 1999), mean diameters of trees have a small range (21.5-24.6 cm) among the different surfaces. Similarly, the number of stems per hectare varies only from 312.5 to 477.6 (Clark and Clark, 2000). No significant differences in volume or mass of standing or fallen CWD occur among the different geomorphic surfaces.

1.5 Objectives of the research

This dissertation represents an effort to expand our understanding of instream wood to the wet tropics. The primary objectives were to document wood loads in a tropical setting, and to observe the retention rate of wood within reach-scale sites. From these data the goal was to explore potential controls on wood distribution (i.e., to evaluate the relative importance of transport, recruitment, and decay on wood) and to identify differences or similarities between wood in tropical and temperate streams. These objectives are addressed in chapters 2 and 3 of this dissertation. Several secondary objectives arose during the course of the research: analysis of the flow resistance contribution from wood in the study sites, analysis of the effect of jams on sediment transport, and analysis of diel cycles in flow related to forest evapotranspiration. These objectives gave rise to the smaller projects that form chapters 4-6 of this dissertation. A final effort to synthesize the findings into a wood budget is presented in the concluding chapter, 7, along with suggested lines of future inquiry.

1.6 Figures

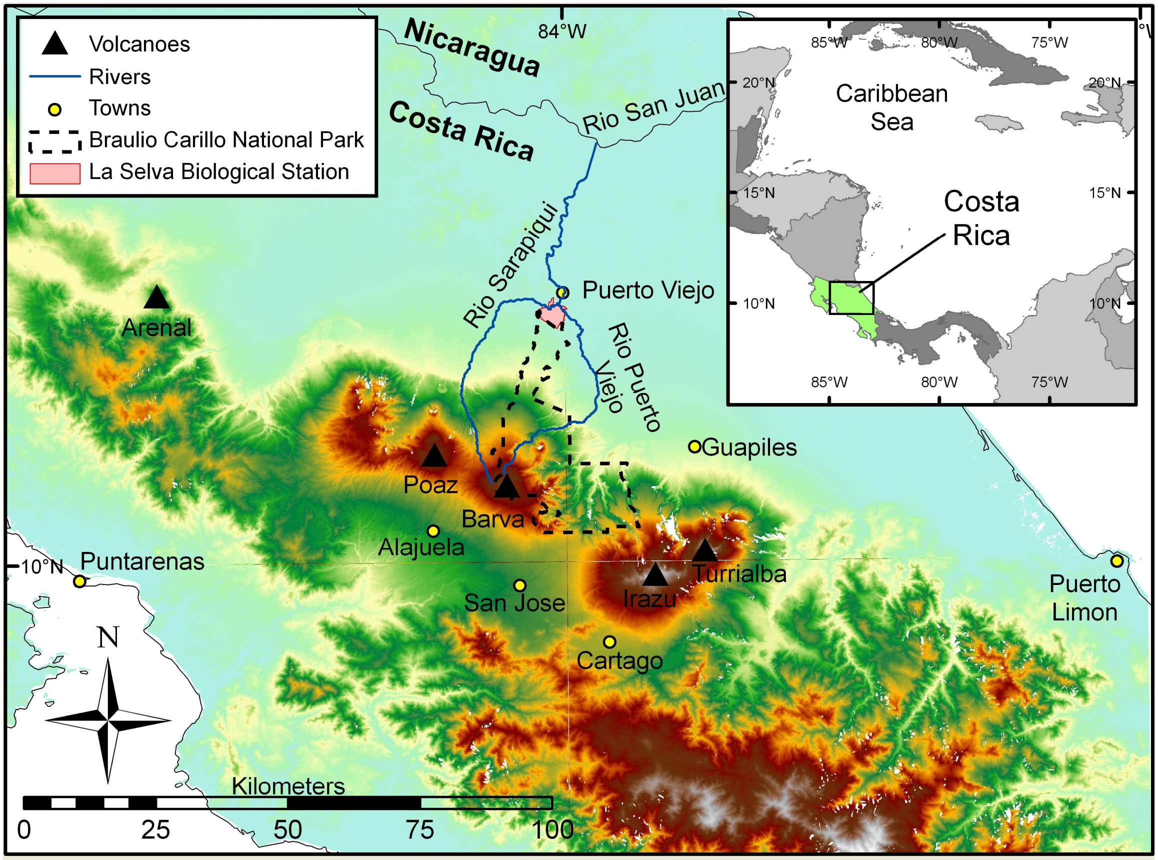

Figure 1.1. Location of Sa Selva Biological Station, Costa Rica

2 WOOD DISTRIBUTION

2.1 Introduction

Headwater streams are the low-order channels that form a large proportion of a drainage network and strongly influence processes in downstream portions of the network (Freeman et al., 2007). Headwater streams are or were historically forested in many parts of the world, and extensive research along such streams in temperate zones indicates the geomorphic and ecological importance of wood in these streams. Geomorphic effects of wood include increased hydraulic roughness of channel boundaries (Keller and Tally, 1979b; Curran and Wohl, 2003; MacFarlane and Wohl, 2003; Daniels and Rhoads, 2004; Wilcox and Wohl, 2006), greater storage of sediment and organic matter on the streambed (Faustini and Jones, 2003), enhanced localized bed and bank scour (Daniels and Rhoads, 2003), and altered local streambed gradient and channel morphology (Keller and Swanson, 1979; Baillie and Davies, 2002; Curran and Wohl, 2003; Montgomery et al., 2003a). Ecological effects of wood include increased retention of organic matter and nutrients (Bilby and Likens, 1980; Erman and Lamberti, 1992; Raikow et al., 1995), greater habitat diversity associated with diversity of substrate and hydraulic variables (Bisson et al., 1987; Maser and Sedell, 1994; Kail, 2003), and food and habitat for many species of microbes and invertebrates (Maser and Sedell, 1994; Wright and Flecker, 2004).

Until very recently, the great majority of existing studies on the effects of wood in stream channels came from the northwestern portion of the United States. Within the past decade, investigators have extended this work to streams in other parts of North America (Richmond and Fausch, 1995; Thompson, 1995; Marcus et al., 2002; Magilligan et al., 2008), as well as Europe (Piegay et al., 1999; Gurnell et al., 2000b; Dahlström and Nilsson, 2004; Wyzga and Zawiejska, 2005; Comiti et al., 2006), Australia (Brooks et al., 2003), New Zealand (Baillie and Davies, 2002; Meleason et al., 2005), South America (Andreoli et al., 2007; Comiti et al., 2008; Mao et al., 2008), and Asia (Haga et al., 2002). Together, these studies clearly indicate that wood is of fundamental geomorphic and ecological importance in forested streams around the world, and that systematic removal of both forests and instream wood has dramatically decreased the abundance of wood in streams.

These studies also indicate that, although the basic functions of wood can be similar in streams across a broad range of environments, important differences also occur between environments. In particular, environmental controls that create variation in the size and abundance of wood introduced to a stream, combined with the rate of wood decay and the magnitude, frequency, and duration of hydraulic forces exerted on the wood, create differences in the residence time and function of wood in streams (Benda et al., 2003; Gurnell, 2003; May and Gresswell, 2003b). Conceptual models of wood dynamics developed for temperate-zone streams provide a starting point, however, from which to examine how wood dynamics differ in other environments. The intent here is to use data on wood loads from headwater streams in Costa Rica to examine potential differences in wood dynamics between temperate and tropical headwater streams.

2.1.1 Wood dynamics in headwater streams

At any stream site, wood load reflects some combination of wood recruitment into the channel from the riparian zone and adjacent valley side slopes; hydraulic transport of wood into and out of the site; and decay of wood in the stream, as expressed in Benda and Sias (2003)

$$\Delta S_c = [L_i - L_o + Q_i/\Delta x - Q_o/\Delta x - D]\Delta t \qquad (2.1)$$

where ΔS_c is change in wood load (measured as a volume per unit length of channel) within a reach of length Δx over time interval Δt. Lateral wood recruitment rate per unit length of channel (L_i) depends on chronic forest mortality, toppling of trees following wildfire and windstorms, wood inputs from bank erosion, wood delivered by mass movements on the valley side slopes, and buried wood exhumed from the channel and floodplain. Wood is also recruited via transport from upstream into the reach (Q_i). Wood is removed from a stream via overbank deposition and channel avulsion (L_o) and *in situ* decay (D), as well as downstream transport out of the reach (Q_o).

The relative importance of these different processes varies among rivers, and with time and space at a river (Keller and Swanson, 1979; Gurnell et al., 2002; Benda and Sias, 2003; Gurnell, 2003; Swanson, 2003), as do the characteristics of instream wood. Lateral recruitment via mass movements from adjacent hillslopes can be particularly important along confined headwater streams (Bilby and Ward, 1989; Bilby and Bisson, 1998). Recruitment via bank erosion and transport from upstream become more important as channel lateral mobility, channel width, and transport capacity increase downstream (Martin and Benda, 2001). Transport within the stream also becomes progressively more important downstream because mobile pieces are commonly shorter than bankfull channel width (Swanson et al., 1984; Lienkaemper and Swanson, 1987).

Changes in wood mobility with stream size also influence the relative volume and spatial distribution of wood. Volume of wood tends to decrease with increasing drainage area (Bisson et al., 1987). Volume of wood correlates with time since the last mass movement in some headwater streams (May and Gresswell, 2003a), and autochthonous jams are most common in headwater channels, whereas transport jams increase in frequency downstream (Abbe and Montgomery, 2003; Mao et al., 2008). Spatial distribution of wood is more likely to reflect recruitment processes in headwater streams, and transport processes in larger rivers. Wood along large rivers is preferentially stored in zones of flow separation or high elevations (e.g., bar crests) within the channel where flow depth is less than buoyant depth (Gurnell et al., 2000a; Braudrick and Grant, 2001).

Less is known about wood decay in rivers than about recruitment or transport. Decomposition is more rapid in larger rivers during high discharges because abrasion removes softened tissue and exposes fresh wood to decay processes (Maser and Sedell, 1994). Nutrient content, density, tree species and age, submergence, and size also influence decay rates (Triska and Cromac, 1980; Maser and Sedell, 1994; Hyatt and Naiman, 2001; Grudd et al., 2002).

Given the limited information on wood decay in rivers, the more numerous studies of wood decay in terrestrial environments provide some insight into relative rates of wood decay in different climatic settings. Wood in tropical environments might be expected to decay more rapidly because the warm, moist conditions that favor biochemical decomposition are present throughout the year (Panshin et al., 1964; Zabel and Morrell, 1992). Studies of the decay of fallen wood in forests are difficult to directly compare, however, because they cite different measures of wood decay (e.g., percent rates, half-life, turnover time). As a first-order approximation, decay rates for logs on a forest floor are on the order of 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). Instream wood that is waterlogged probably decays more slowly.

In temperate-zone streams where many types of wood decay relatively slowly, the relative rates of introduction and transport of wood are primary controls on instream wood load and can create self-enhancing feedbacks such that stream segments with abundant wood have reduced transport of wood and greater bank instability or lateral channel movement that facilitate further recruitment of wood (Braudrick and Grant, 2000; Montgomery and Abbe, 2006).

Studies from diverse temperate environments indicate that the greatest wood loads within a channel network occur in small headwater streams because of limited transport and decay (Bisson et al., 1987; Marcus et al., 2002; Wohl and Jaeger, 2009). Equation 2.1 can thus be expressed for temperate headwater streams as

$$\Delta S_c = [\boldsymbol{L_i} - L_o + Q_i/\Delta x - Q_o/\Delta x - D]\Delta t \qquad (2.2)$$

where bold font indicates processes exerting a greater influence on dynamics and volume of wood load. As studies of wood in stream channels of the temperate zone continue, however, there remains a significant gap in our understanding of instream wood because of the dearth of studies conducted in tropical environments.

2.1.2 Wood in tropical streams

Research on instream wood in tropical environments has thus far focused on the ecological effects of wood. Wood alters local flow velocities in a manner important to filter-feeding shrimp at the microhabitat scale in Puerto Rico (Pyron et al., 1999), and provides critical nesting habitat for armored catfish in Panama (Power, 2003). Greater numbers of individuals and more species of fish occur in pools with wood than in pools without wood in a Venezuelan piedmont stream (Wright and Flecker, 2004). These limited studies suggest that wood plays an important role in structuring aquatic communities in tropical streams.

Research demonstrating the distribution and geomorphic influences of wood has not been published for forested headwater streams in the tropics. The physical patterns and processes of instream wood might be expected to differ in the tropics for at least two reasons. First, decay rates of many species of wood are much higher in tropical environments than in temperate environments (Panshin et al., 1964; Zabel and Morrell, 1992), and decay might therefore exert a stronger control on instream residence time of wood in tropical than in temperate streams. Second, tropical streams commonly have a hydrologic regime characterized by frequent, short duration, high magnitude flows (Arenas, 1983; Lewis et al., 1995; Niedzialek and Ogden, 2005; Wohl and Springer, 2005). This characteristically flashy hydrograph could generate greater flow depths, higher values of stream power per unit area, and greater transport capacity for wood.

Personal observations along unmanaged, old-growth forest streams in Panama and Puerto Rico indicate a dearth of wood relative to analogous streams in temperate zones, despite the huge trees growing densely along the stream banks. However, rivers in other regions, such as Papua New Guinea (W.E. Dietrich pers. comm. 2005) or eastern Peru (D.J. Cooper pers. comm. 2005), do not seem to lack wood. These differences, and the lack of systematic studies in tropical environments, strongly suggest that the first step in better understanding the geomorphic and ecological functions of wood in tropical rivers is to inventory wood load and residence time for different tropical regions and different stream types.

2.1.3 Objectives and hypotheses

This paper presents results from an inventory of wood distribution in forested headwater streams (drainage area < 10 km^2) of La Selva Biological Station in northeastern Costa Rica. The basic objectives of the research were to (i) evaluate how wood loads in tropical headwater streams compare to those reported for temperate headwater streams, (ii) assess the best predictor variables for reach-scale wood loads as a means of examining the relative importance of recruitment and transport in controlling wood load, and (iii) analyze the within-reach spatial distribution of wood, especially the lateral distribution of wood and the frequency of jams. In this context, I define wood load as the volume of wood per unit length or unit area of active channel, where active channel is the area flooded multiple times each year during the wet season.

The objectives contribute to the evaluation of three hypotheses with respect to influences on wood load and geomorphic effects of wood. I do not directly measure recruitment, transport, or decay in this assessment of wood loads along multiple stream reaches at a point in time. Instead, I infer the mechanisms and relative importance of these factors by examining correlations among wood characteristics, valley and channel geometry, and hydraulics. My approach follows that of Comiti *et al*. (2006), who interpreted the lack of correlation between reach-scale channel characteristics and wood load along streams in the Italian Dolomites as reflecting the greater importance of recruitment relative to transport. The first objective, by comparing total wood storage in channels of different regions, enables comparison of the integrated effects of recruitment, transport, and decay. The second objective enables evaluation of the possibility that wood load in the studied tropical headwater streams might correlate most strongly with variables reflecting transport capacity, or might correlate better with variables reflecting recruitment potential. Previous work suggests that wood in temperate-zone streams with small drainage areas should be more strongly controlled by recruitment than transport (equation 2.2). The high discharges per unit drainage area of the tropics, however, might produce sufficient transport capacity to make this process a dominant influence on wood load even for small (< 10 km^2) drainage areas. Consequently, the analyses in this chapter focus on the inferred relative importance of transport in producing wood loads observed in headwater tropical streams. Subsequent chapters will discuss resurveys of study sites at La Selva to evaluate decay versus transport in the study area.

The initial data set allows testing of three hypotheses regarding the relative importance of recruitment versus transport: H_1 and H_{1a} if transport dominates and H_2 if recruitment dominates. H_1: If transport dominates wood load, then loads would be highest in channels with lowest stream power. Also, wood in channels with high stream power would be concentrated in zones of flow separation or low velocity. The reasoning behind this hypothesis is that where transport capacity is relatively high, wood will be rapidly removed from a reach and wood loads at any point in time will be proportionately low. Conversely, wood will be stored in reaches of lower transport capacity. Any wood stored in reaches with high transport capacity will only be found in localized zones of reduced transport and relatively high elevation (Gurnell et al., 2000a).

Stream power is a simple metric of the ability of water to move material and perform work against the channel boundaries, and has been used to quantify differences in sediment transport and channel change (O'Connor, 1993) among streams, as well as wood mobility (Gurnell et al., 2000b). Stream power might not be the best predictor of wood transport, however, because 1) streams with high transport capacity can also have very rough boundaries that trap wood (Faustini and Jones, 2003; Bocchiola et al., 2006), 2) exceptionally high wood recruitment such as from a landslide can at least temporarily overwhelm transport capacity, and 3) wood can float (although some tropical trees have wood as dense as water). Consequently, the ratios of wood length to channel width and wood diameter to flow depth are used to infer relative transportability (Braudrick and Grant, 2000; Braudrick and Grant, 2001; Haga et al., 2002). Numerous investigators note that logs are more readily transported as the ratio of piece length to channel width decreases, and Abbe et al. (1993) found that logs are stored where flow depth is less than approximately half of the log diameter. These considerations lead to H_{1a}: If transport dominates wood load, then loads of transported pieces are highest in channels with the largest ratio of wood length to channel width and/or wood diameter to flow depth, both of which indicate lower transport capacity.

An assumption implicit in the first hypothesis set is that recruitment is similar at all sites, so that differences in wood load reflect primarily differences in transport. An alternative scenario is reflected in H_2: If recruitment dominates, then load correlates with valley geometry, such that steep side slopes increase tree fall into streams and create high loads. Many other processes can influence recruitment, as summarized previously, but variability in recruitment caused by hillslope mass movements, mass blowdown, land-use history, wildfires, substantial lateral channel mobility, and differences in forest type were able to be discounted because these are not present in the study area. The reasoning behind H_2 is that, all else being equal, a falling tree is more likely to fall toward the stream channel where valley side slopes are steep (Jackson and Sturm, 2002; Nowakowski and Wohl, 2008).

The final hypothesis focused on geomorphic effectiveness of wood, as evidenced by localized scour or deposition associated with individual pieces and jams. H_3: Geomorphic effectiveness is greatest in channels with predominantly fine (pebble and finer) substrate. This hypothesis reflects H_1 and the expectation of greater wood loads in reaches of low transport capacity and thus lower gradient and finer substrate, as well as greater substrate mobility and preferential deposition around obstacles such as jams in finer-grained reaches (Gurnell et al., 2000a).

I examine the relative importance of recruitment versus transport as a means of understanding the observed distributions of wood load in the study area. Such understanding is also important in managing headwater streams. In locations where land use has reduced forest cover and wood recruitment, or altered rainfall-runoff relations, flow regime and wood transport, it becomes particularly important to understand the factors limiting wood loads and how to mitigate the effect of changes in these factors.

It is important to recognize the limitations of these hypotheses and this study area. First, there is no *a priori* reason that the relative importance of recruitment, transport, and decay is consistent throughout a channel network. Transport might dominate in reaches with high transport capacity, for example, and decay in reaches with low transport capacity. I developed hypotheses based on simple, linear assumptions partly because the data come from streams with limited variability in recruitment processes, forest type, and hydrology, and partly because I wanted to test the simplest scenarios first before inferring more complex patterns. Second, existing studies of wood loads in temperate-zone streams support the idea of a spectrum from streams with large temporal variability in wood loads as a result of point sources of wood recruitment, such as hillslope mass movements, to streams with much less temporal variability because wood is predominantly recruited through individual tree fall (May and Gresswell, 2003a; Wohl and Goode, 2008). The streams discussed in this dissertation fall into the latter category and thus do not fully represent the range of conditions present in tropical forested headwater streams.

2.2 Study Area

The study reaches analyzed in this study are located within La Selva Biological Station (Figure 2.1). The morphology is variable, from step-pool to pool-riffle, and boulder-bed to sand-bed (Figure 2.2). Floods occur frequently at La Selva, and the streams are very responsive to rainfall, resulting in a flashy hydrograph. In the three months prior to data collection (January to March 2007), a weir operated by David Genereux on the Taconazo (Figure 2.2d, drainage area 0.28 km^2) recorded 19 floods that more than doubled the base flow (unpublished data, 2007), approximately corresponding to 18 days with recorded rainfall greater than 10 mm. The rising limb of these events occurred on average in 1 hour, whereas the falling limb averaged 10 hours and ranged from 6 to 30 hours, depending on the peak discharge. This three-month period (January to March 2007) included most of the dry season, and the highest recorded daily rainfall was

121 mm. Extended records for La Selva Biological Station show that from 2002 to 2006 there were 181 days (36 per year) when over 40 mm of rainfall was recorded. In November 2007, a stage gage was installed on El Surá (near Figure 2.2a, drainage area 3.36 km^2) and a stage-discharge relationship was estimated from 8 salt-slug method discharge measurements (Waldon, 2004). Discharge was monitored until the gage was destroyed by a flood in July 2009 (Figure 2.3). This flood had an estimated peak of about 10 m^3/s, equivalent to runoff production of 3.0 $m^3/s/km^2$.

2.3 Methods

2.3.1 Data collection

Wood and stream data were collected for 30 study reaches, each approximately 50 m long, located throughout La Selva Biological Station in old-growth forest (Figure 2.4). Although study reaches were selected near maintained trails to enable access, selected reaches represent the range of drainage area, stream gradient, valley geometry, and wood loads present at La Selva. The surveys were conducted in March, during the driest time of the year at La Selva. Channels that had no flow were excluded, as were stagnant reaches.

A piece of wood was included in the study if its length was at least 1 m and its diameter was at least 10 cm, or if its length was at least 2 m and its diameter was at least 5 cm. If a piece of wood extended beyond the active channel, two lengths were measured, the total length and the length within the active channel. The level of active flow was evaluated in the field using changes in riparian vegetation (presence of woody stems) and channel morphology (top of stream banks). In this study, the active level represents the maximum stage of flows that occur repeatedly each year during the wet season, and is probably best approximated statistically as the mean annual peak flow. The locations of the endpoints of each wood piece were surveyed using a total station and its length and mid-point diameter were measured with a tape. The in-channel volume (V) of each wood piece was approximated using the formula for the volume of a cylinder,

$$V=\pi(d/2)^2L, \tag{2.3}$$

where d is the midpoint diameter of the log, and L is the length of the log in the active channel. In cases of logs with branches, the larger branch was used and the smaller branch was ignored. Wood load for each reach was calculated both as a volume per channel length (total cubic meters of wood divided by the reach length in meters, multiplied by 100, resulting in wood volume per 100 m length of stream, $W_{v/l}$) and as a volume per channel area (total cubic meters of wood divided by hectares of active channel area, resulting in wood volume per hectare, $W_{v/a}$), in order to follow metrics of wood load already established in the literature. Additionally, each piece was classified as bridge, ramp, unattached, or buried. A bridge spans the channel, resting on both banks. A ramp has one end resting on the channel bank above the level of active flow and the other end in the channel. An unattached piece is contained within the active channel and is not buried in the streambed. A buried piece is contained within the active channel and partially buried in bed sediment or pinned beneath another log. I categorized bridges and ramps as *in situ* wood that reflects primarily recruitment, and unattached and buried pieces as transported wood. Although this might misclassify the status of a few pieces (e.g., a buried piece might be buried without transport), it provides a straightforward and consistent means of differentiating *in situ* and transported wood in the absence of direct observations of the history of each piece.

Numerous channel characteristics were measured for each reach. Using a total station, the thalweg of the channel through the study reach was surveyed with intervals of 1-5 m between points, as were two detailed cross sections and at least four additional active width measurements. Valley side slopes were characterized over lengths of 200-300 m using an inclinometer and tape. The intermediate diameters of 100 clasts, selected by random walk, were measured to determine grain size distribution in stream reaches with substrate predominantly of pebble size or larger. I assigned qualitative values of clast size and sorting to reaches with finer substrate based on visual estimates of the predominance of sand and silt. The contributing drainage area at each site was found using a GIS and a LIDAR-derived 1m DEM of La Selva and the adjacent Braulio Carillo National Park.

2.3.2 Data analysis

Statistical analyses used the following metrics, which were calculated for each study site from the measurements described above: contributing drainage area (A), stream gradient (S), bedform roughness as quantified by the variance (mean square error) of the thalweg elevation (BF_{var}), grain size of the 84th percentile bed material (D_{84}), grain sorting measured with the sediment inclusive graphic standard deviation in phi units (s_{sd}) (Folk, 1980), average active width (w), width to depth ratio (w/d), average valley side slope (VS_{avg}), maximum valley side slope (VS_{max}), thalweg sinuosity (P), the product of drainage area and stream gradient as an indirect measure of total stream power (Ω), the product of drainage area and stream gradient divided by width as an indirect measure of unit stream power (ω), the ratio of average wood length to active channel width (L/w), and the ratio of average wood diameter to active flow depth ($diam/d$). I also used a categorical variable for backflooding (*B*). Backflooding from the main channels (the Sarapiquí and Puerto Viejo rivers) to which the study streams are tributary can extend for as much as 3 km upstream along low gradient portions of the study streams. Because some of the study reaches are located within this zone where backflooding can reduce hydraulic forces during floods and thus facilitate deposition of wood in transport, I categorically assigned the study reaches as being subject or not subject to backflooding. I chose the variables listed above as commonly used metrics of valley geometry, channel geometry, hydraulics, and wood dimensions.

Multiple regression models were created and evaluated using a combination of the R statistical package (version 2.6.2) and SAS statistical software (SAS Institute, 2003). I created three models, for total wood load per hectare of channel ($W_{v/a}$), transported wood load per hectare ($tW_{v/a}$), and *in situ* wood load per hectare ($iW_{v/a}$). For each model, all possible subsets of the stream variables were compared. The best subset of variables to use in each model was selected based primarily on the model corrected Akaike Information Criterion (AIC_C) (Akaika, 1973; Hurvich and Tsai, 1989) because of the small sample size, although the R-square and adjusted R-square values were also considered. More weight was given to the AIC_C because it penalizes models for excessive parameterization, selecting the most parsimonious model. Models that were adversely affected by multi-collinearity, as indicated by parameters with high variance inflation factors, were excluded. The models using the best variable subsets were analyzed for the p-value significance of each parameter estimate and retained if all p-values (excluding the intercept) were less than 0.1.

In order to test the portion of H_1 that posits that wood stored in reaches of high transport capacity will only be found in zones of reduced transport and high elevation relative to the channel thalweg, I divided channels into lateral zones based on distance from the thalweg. The study reaches all had relatively simple cross sections lacking the prominent bars or islands and divided flow common in larger rivers. Consequently, zones of reduced transport and high elevation occurred predominantly along the channel margins. The lateral distribution of the wood within each channel segment was determined by calculating the volume of wood within each of 7 concentric zones around the thalweg using GIS software. Most logs spanned multiple zones, so the volume of wood was distributed among the zones according to the distribution of the center line of the log. The volume of wood within one-fourth of the reach-average width of the thalweg was considered the central channel wood. This central wood value was divided by the volume of wood outside the central channel to determine the ratio of wood within the central 50% of the channel to wood outside this zone in each reach.

2.4 Results and Discussion

The channel and basin data are summarized for each study reach in Table 2.1, and the instream wood data are summarized in Table 2.2. Figure 2.5 and Figure 2.6 illustrate the dimensions of wood at the 30 study reaches. Mean piece length and diameter vary by less than a factor of two among the study reaches. Frequency declines rapidly as piece length and diameter increase, whereas relative volume is more uniformly distributed among size classes, as documented for other streams (Gurnell et al., 2002; Meleason et al., 2005; Comiti et al., 2006). The percentage of pieces shorter than active channel width varies from 56-98% among the 30 reaches. This is much higher than values of 23-39%

(Lienkaemper and Swanson, 1987) and 38% (May and Gresswell, 2003a) reported from temperate headwater streams.

Two field observations are important to understanding the results and discussion: (1) forest type in terms of height, diameter, and density of trees is consistent among the study sites (Clark and Clark, 2000), and (2) mass movements such as landslides and debris flows have not been observed at the study site either during field work or by other researchers continuously active at La Selva since the 1970s (D. Clark, pers. comm., 3/2007). Lateral mobility is also limited along many of the channels, limiting individual tree fall as a result of bank erosion. Because of these observations, much of the analysis and interpretation is based on the assumption of constant wood input and relatively low variability in wood load through time. I also tested the spatial representativeness of a 50-m-long study reach by measuring wood abundance between the four study reaches along the Quebrada Esquina. Wood counts within 23 successive 50-m-long reaches produced a mean abundance of 34.2 pieces/50 m, with standard deviation of 10.6 and values varying between reaches by a factor of 3 or less (Figure 2.7). This does not indicate large spatial variability in wood; Comiti et al. (2006), for example, found 1-2 orders of magnitude variation in wood volume between adjacent stream reaches in the Dolomite region, Italy.

2.4.1 Values of wood load

Wood loads at La Selva range from 3 to 34.7 m^3/100 m (Figure 2.8) and from 41 to 612 m^3/ha, with mean values of 12.3 m^3/100 m and 189 m^3/ha. Abundance ranges from 35 to 130 pieces/100m, with a mean of 77.1 pieces/100m.

Values of wood loads at La Selva fall within the range of wood loads reported elsewhere in the world (Figure 2.8), but it is important to note some of the sources of variation among these data sets (Table 2.3). Sites chosen for comparison here are in relatively small, steep streams flowing through old-growth and unmanaged forests, but differences in minimum size of wood pieces counted and length of channel characterized can create differences in measured wood load. Many of the sites have substantially larger drainage areas, which implies that these streams may have larger floodplains, more lateral mobility, and thus potentially different mechanisms of wood recruitment. Similarly, many of the sites have wood recruitment through hillslope mass movements, unlike La Selva.

Given these caveats, wood load values reported for the Pacific Northwest, Michigan, Chile, and Australia tend to be higher than La Selva. All of these regions have high biological productivity, with large native tree species. Mean temperatures and/or humidity are higher in Costa Rica than in the temperate regions, and microbial diversity also is likely higher, both of which lead to higher decay rates (Harmon, 1982; Lewis et al., 2004), potentially accounting for the lower tropical wood loads. Wood load values reported from the Rocky Mountain region tend to be lower, although northwest Wyoming (WY2 in Figure 2.8) appears to be an exception. I expect decay rates to be higher at La Selva than in the Rocky Mountains for the same reasons mentioned above, which alone would tend to lead to lower wood loads, although the dry climate of the Rockies leads to lower productivity and smaller tree sizes, potentially offsetting the decay rate differences. Whatever the combination of mechanisms involved, wood loads in the headwater streams of La Selva are not substantially greater or less than the range of wood loads documented in headwater streams of the temperate zones.

2.4.2 Correlation of channel, basin, and hydraulic variables with wood load

Simple regression of wood load ($W_{v/a}$) on relative unit stream power (ω), average piece length/channel width (L/w), and average piece diameter/channel depth ($diam/d$) give a preliminary basis on which to evaluate H_1 and H_{1a} (Figure 2.9). Distinguishing between transported ($tW_{v/a}$) and *in situ* ($iW_{v/a}$) wood loads reveals that $tW_{v/a}$ has no correlation with ω, L/w, or $diam/d$. However, $iW_{v/a}$ correlates negatively with ω and positively with L/w, and $diam/d$, leading to similar correlations for $W_{v/a}$, although the relationships are generally weak.

Statistical models for total wood load allow for a more complete analysis, and suggest that transport parameters have a strong influence on wood load, but cannot explain the full range of variability observed. Table 2.4 describes the multiple regression selected as the most parsimonious model for $W_{v/a}$. This model, which has a coefficient of determination (R^2) of 0.64, includes $diam/d$, BF_{var}, B, w/d, and ω as predictors. This model is a mix of transport variables ($diam/d$, B, ω) and channel geometry variables (BF_{var}, w/d). The estimated $diam/d$ parameter ($\beta_{diam/d}$ = 453.6) indicates that, all else being equal, wood load increases as the $diam/d$ ratio increases, which presumably reflects the progressive loss of ability to move wood as $diam/d$ increases. The BF_{var} parameter (β_{BFvar} = 2836.6) indicates that wood load is greater in channels with greater variation in thalweg elevation. The B parameter (β_B = 138.2) indicates that reaches that experience backflooding have higher wood loads, a trend that is expected because the stagnant, or even upstream flowing, water during floods will prevent wood being flushed through the reach. The w/d parameter ($\beta_{w/d}$ = -8.3) indicates that less entrenched channels have lower wood load per unit area. This may be an artifact of wider channels having more channel area for an equal length of banks from which to recruit wood. Or it may simply reflect a spurious statistical result produced by interactions among variables that are calculated using width or depth. The ω parameter (β_{ω} = -86.5) suggests that higher ω leads to lower wood loads, which presumably reflects the ability of flows to mobilize or mechanically break down wood.

Table 2.5 describes the multiple regression selected as the best model for transported wood volume ($tW_{v/a}$). The model (R^2 = 0.39) selected ω, A, and w/d as predictor variables. The most influential of these (ω, A) are transport variables. In a separate model for $tW_{v/l}$, as opposed to $tW_{v/a}$, these two variables alone also explain 59% of the variability in transported wood volume measured as m^3/100m. The negative parameter estimate for ω again indicates an inverse relationship between wood load and unit stream power. The positive parameter estimate for A indicates that larger drainage areas will result in higher wood loads, presumably because the larger contributing area from which wood may be collected and delivered increases wood load. The negative parameter estimate for w/d again indicates that less entrenched channels have lower wood load per unit area.

Table 2.6 describes the multiple regression selected as the best model for *in situ* wood volume ($iW_{v/a}$). The model (R^2 = 0.63) selected $diam/d$, w/d, B, and S as predictor variables. These predictors are also predominantly transport variables ($diam/d$, B, S). It is particularly noteworthy that no valley geometry variables are predictors in this model, and that the only channel geometry variable that is significant is w/d; the parameter estimate ($\beta_{w/d}$ = -9.4) suggests that *in situ* wood load is higher in channels with smaller w/d ratios, as seen in the previous models.

The residuals of each model support the underlying assumptions necessary for application of linear regression. The variance inflation factors do not indicate major multicollinearity problems. Most of the variables, such as BF_{var} and *ω*, are not normally distributed, but instead have a right skew, and it could be argued that they are lognormal. I chose not to transform these variables to allow for straight-forward interpretation of the models. To test the validity of this choice, I log-transformed the potentially lognormal variables and conducted the model selection procedure on the modified dataset. In the $W_{\mathrm{v/a}}$ model, *S* replaced *ω* in the list of selected variables, while the selected variables remained identical in the $tW_{\mathrm{v/a}}$ and $iW_{\mathrm{v/a}}$ models. The signs of the parameters were the same, and the R^2 values increased slightly.

In summary, the transport-related variables *diam/d* and *ω*, and the channel geometry variable *w/d*, were consistently selected as predictors in statistical models of wood load. The parameter estimates for the transport variables indicate greater wood loads where transport capacity declines. The negative parameter estimates for *w/d* indicate greater wood loads in channels with lower *w/d* ratio, suggesting that relatively narrow channels better trap wood in transport. This final parameter estimate is counterintuitive, and may simply reflect a spurious statistical result produced by interactions among variables that are calculated using width or depth.

Other, simple comparisons also provide some insight into the relative importance of recruitment and transport. Variability in recruitment rates among the study reaches appears to be relatively small. Using the frequency of ramps and bridges as a surrogate for local wood introduction (range 3.7-59.7 pieces/100m, but most < 35 pieces/100m; Table 2.2), the recruitment rate appears to be relatively constant throughout the drainage network. Changes in *A* or *w* vary systematically through the drainage network, but have no correlation with ramp and bridge frequency. The mean *L*/*w* ratio for most study reaches is < 1 and the mean *diam*/*d* is < 0.5 (Table 2.2), indicating a high transport potential for the majority of wood pieces. The relatively minor importance of recruitment variables on measured wood loads at the study sites may reflect the consistency of forest characteristics and the absence of hill slope mass movements.

The first two hypotheses posed in the introduction deal with the relative importance of transport versus recruitment in controlling wood loads in the study area. Results support H_1 (transport dominates) in that ω is inversely correlated with $W_{v/a}$ and $iW_{v/a}$ (Figure 2.9), and was selected in the best models for $W_{v/a}$ and $tW_{v/a}$, indicating that wood loads are highest in stream segments with the lowest stream power. Results of the statistical analyses were more mixed with respect to H_{1a} (transport dominates); *diam/d* is positively correlated with $W_{v/a}$ and $iW_{v/a}$, indicating that wood loads are highest in channels with the largest ratio of wood diameter/flow depth. The variable *L/w* has a positive correlation with both $W_{v/a}$ and $iW_{v/a}$ (Figure 2.9), but it was not selected for the wood load models, suggesting that piece length may also be correlated to a combination of other variables. The results do not support H_2 (recruitment dominates) because no measure of valley geometry correlates with any measure of wood load. I thus infer that transport dominates wood distribution in the channels of La Selva.

Although previous studies have not explicitly used statistical analyses to infer the relative importance of recruitment and transport in determining wood loads at specific study reaches, the consensus from earlier work is that transport capacity increases downstream and the relative importance of tree fall from individual tree mortality decreases in importance downstream (Martin and Benda, 2001; Swanson, 2003). In examining headwater channels with very small drainage areas, one might therefore expect to see limited transport and a strong influence exerted by individual tree fall. My inferences regarding the relative importance of recruitment and transport suggest that the very high unit discharges of these tropical streams, and the associated transport capacity, increase the importance of transport relative to recruitment in comparison to temperate-zone streams of similar drainage area, which have been interpreted as being transport-limited with respect to wood (Marcus et al., 2002; Wohl and Jaeger, 2009), effectively decreasing the drainage area necessary for wood transport in tropical basins.

2.4.3 Lateral distribution of wood

If transport dominates wood loads, as suggested by the multiple regression analyses, wood in channels with high stream power should be concentrated in low energy zones, such as the channel margins. The lateral distribution of wood volume (Figure 2.10) indicates that the distribution of wood relative to the thalweg varies systematically with channel energy. The results suggest that at La Selva the ratio of wood in the outer portion of the channel to wood in the central portion of the channel (C_R) varies linearly with ω according to the equation

$$C_R = W_{vo}/W_{vc} \approx 1 + 1.7\omega, \qquad (2.4)$$

where W_{vo} is the volume of wood in the outer 50% of the channel and W_{vc} is the volume of wood in the central 50% of the channel (Figure 2.11). An advantage of this empirical equation is that when $\omega = 0$, meaning there is no fluvial redistribution of wood, then C_R = 1, meaning the wood is evenly distributed between the outer 50% and the inner 50% of the channel. The coefficients in this equation are empirical and site-specific. Because ω

was calculated as a surrogate for relative unit stream power ($\omega = AS/w$), the coefficients have no physical meaning. As with the regression analysis of influences on wood load, the analysis of distribution of wood relative to the thalweg supports H_1.

2.4.4 Correlations between jams and bed characteristics

As a surrogate for sediment storage associated with channel-spanning jams, the change in bed elevation associated with each jam was calculated from the thalweg survey. The bed elevation drop caused by the jam was estimated as the difference between the residual of the thalweg survey point immediately upstream from the jam to the residual of the survey point immediately downstream from the jam. Using the residual helped correct for the influence of reach gradient variations on the drop height. Four of the seven jams were observed to trap sediment, all four of which were located on the Quebrada Esquina (sites 17, 18, & 21; two jams in site 18, Figure 2.10). The two jams located in silt-bedded channels (sites 2 & 3) and the one jam located on a steep boulder-bed reach (site 24) did not appear to be geomorphically effective in trapping and storing sediment. The Quebrada Esquina tends to have much higher gravel content than the other streams of La Selva. The transport of this size fraction appears to be most affected by wood jams. I speculate that finer material is transported over jams in turbulent flood flows, and flows that transport boulders also tend to break up jams, leaving only the intermediate grain sizes to be affected by jams. Sediment transport at one of these gravel-bed jams was closely studied (Chapter 5), revealing that although channel morphology can be altered over short time periods, individual clast mobility was not measurably altered by the jam. Production of gravel may be related to the underlying geology. The Quebrada Esquina is incised into the Esquina Andesite, as opposed to the El Salto

Andesitic Basalt or Taconazo Basic Andesite, which dominate the other study basins. Variations in thalweg elevation in the vicinity of jams as a function of predominant grain-size on the streambed thus did not support H_3 (geomorphic effectiveness is greatest in fine-grained channels).

Although numerous investigators have documented large cumulative volumes of sediment storage behind closely spaced logjams or log steps in small, steep channels, I have not found any explicit comparison of volume of sediment stored in relation to substrate type. Most comparisons tend to focus instead on changes in sediment storage along a channel network; Bilby and Ward (1989), for example, noted that stored sediment became more widely spaced longitudinally but also larger in volume as stream size increased.

Jams are relatively rare in the La Selva study reaches, with a total of 7 observed among the 30 study reaches, giving an average of 4.7 jams per km of channel. The Quebrada Esquina considered separately has a jam frequency of 16 jams/km, while the rest of La Selva has 2.4 jams/km. By comparison, Comiti et al. (2006) found 7.1-30.6 jams/km in five managed streams of the Italian Dolomites, and Mao et al. (2008) found 61 jams/km in streams of Tierra del Fuego, Argentina. Thom et al. (2001) found a median of 5.5 jams/km, with a range from 1-20 jams/km, in 46 reference reaches in Oregon. The lack of jams in most channels at La Selva might seem to contradict my inferences about the importance of transport, because other studies have correlated increased potential for jam formation with increased mobility of wood (Abbe and Montgomery, 2003). Three factors might explain the observed rarity of jams. First, transport capacity is so high in all the surveyed reaches that wood is being carried downstream to major changes in channel geometry such as channel junctions, none of which were included in the study reaches. This is supported by the observation of jams present at the junction of each tributary channel with the larger Sarapiquí and Puerto Viejo rivers. Second, decay rates are so high that wood recruited into the channel is abraded, shattered, and decayed into smaller pieces that remain mobile throughout the study reaches, rather than remaining in place and retaining wood transported from upstream reaches. This is supported by the one large tree fall that was observed during the March 2007 field season. Although the tree was several times longer than the active channel width, the trunk shattered when the tree fell, creating smaller, more readily transported and decayed sections that would be less effective in forming jams. The relatively high proportions of pieces shorter than the active channel width also supports the likelihood of the first two factors limiting jam formation. Third, the absence of mass movements and analogous large point sources of wood inputs removes the possibility of jams formed in this manner, which can be an important source of jam formation in temperate headwater rivers (Benda et al., 2003; May and Gresswell, 2003a; Swanson, 2003).

2.5 Conclusions

I interpret the field observations and statistical analyses to indicate that transport exerts a stronger control on wood loads in headwater streams at La Selva than does recruitment. If recruitment from individual tree mortality strongly controlled wood loads, I would expect to see a large percentage of *in situ* wood, some correlation with valley geometry, and a lack of correlation with transport-related variables. I do not intend to downplay the influence of tree fall from individual tree mortality. A single large tree can substantially increase reach-scale wood load, as observed during field work, but wood introduced in this manner appears to be transported and/or decay relatively quickly, especially as stream power increases, facilitating a scenario in which wood load correlates strongly with measures of transport capacity. The differences between headwater streams in the tropical study area and temperate headwater streams can be expressed by reformulating equation (2.2) as

$$\Delta S_c = [L_i - L_o + \boldsymbol{Q_i}/\Delta x - \boldsymbol{Q_o}/\Delta x - D]\Delta t \qquad (2.5)$$

with the caveat that D likely also deserves bold font. As in equation (2.1), ΔS_c is change in wood load within a reach of length Δx over time interval Δt, L_i is lateral wood input, L_o is lateral wood output, Q_i is fluvial wood input from upstream, Q_o is fluvial wood output, and D is decay. The relative importance of transport and decay is considered in subsequent chapters.

Values of wood load at La Selva are intermediate between higher values reported from humid temperate zones and lower values from semiarid temperate zones. This presumably reflects interactions among recruitment, inferred high decay rates of wood, and frequent runoff-generating precipitation and large unit discharges. The expected effect of high decay and transport is a rapid turnover rate for in-channel wood. In a dynamic system with high turnover rates, wood is less likely to create long-lived features that affect channel morphology. Jams are relatively rare and are only effective at trapping sediment in moderate energy, gravel-bed channels. Field observations suggest that buried logs tend to persist only in low energy stream reaches with sand or finer substrate. This suggests that in channel reaches with high stream power, logs are removed by the flow before they can be incorporated into the bed. Wood entering a high energy reach is either flushed through or broken into pieces against the coarse bed material. Buried pieces in the low energy reaches rarely form steps or significantly alter channel morphology. This suggests that they are mobile during major floods and then drop out of transport during the falling limb of the flood hydrograph. This may explain how wood concentrates near the thalweg (more than 50% of the wood in the central 50% of the channel) in some of the low gradient reaches.

Modeling wood load with 3 to 5 mostly transport-related parameters explains 39-64% of the variability in wood load. The lateral distribution of wood correlates well with ω, which also suggests the importance of post-recruitment transport in controlling wood distribution. Variables that were measured to reflect recruitment (VS_{ave} and VS_{max}) were not useful in modeling wood loads. The forest type was consistent among the study reaches, and evidence of mass wasting has not been observed at La Selva, thus differences in recruitment are expected to be linked to hill slope steepness. The frequency of ramps and bridges is expected to correlate to local wood recruitment rates, and is constant across sites. Thus, transport parameters appear to be more influential than recruitment parameters, although there remains unexplained variability in wood load values that may be related to stochastic tree fall recruitment. The inferred dominance of transport on wood loads represents a substantial difference between temperate and tropical headwater streams. It may be that the threshold for wood transport is crossed at smaller drainage areas in tropical watersheds because of the higher rainfall or potentially higher decay rates. One of the management implications of these observations and inferences is that, in a system with high rates of wood transport, it is particularly important to maintain recruitment sources via forested stream corridors.

2.6 Tables

Table 2.1. Basin, channel form, and hydraulic parameters

Site number	A (km^2)	S (%)	P	BF_{var}	w (m)	w/d	VS_{avg} (°)	VS_{max} (°)	D_{84} (mm)	S_{sd} (φ)	Ω ($A \cdot S$)	ω ($A \cdot S/w$)	Back-flooding	Channel type
1	0.28	0.32	1.12	0.012	6.3	8.3	17	21	2	0.60	0.09	0.014	yes	sandy run[a]
2	0.40	0.22	1.04	0.012	7.3	8.4	16	30	0.01	0.40	0.09	0.012	yes	dune-ripple
3	4.79	0.24	1.16	0.016	8.1	7.5	16	52	1	0.70	1.15	0.142	yes	dune-ripple
4	0.08	0.22	1.12	0.012	5.4	11.6	10	14	0.01	0.35	0.02	0.003	yes	silt bed[a]
5	3.36	1.22	1.05	0.012	10.3	12.2	14	31	630	1.45	4.10	0.397	no	step-pool
6	0.61	0.24	1.22	0.017	5.9	5.6	16	31	0.5	0.55	0.15	0.025	yes	silt bed[a]
7	0.83	0.51	1.15	0.007	3.8	5.8	11	28	220	1.38	0.42	0.112	no	pool-riffle
8	0.10	6.28	1.10	0.083	3.8	7.6	15	39	630	1.08	0.63	0.163	no	step-pool
9	1.64	0.74	1.09	0.040	5.2	7.9	12	32	550	1.73	1.21	0.235	no	pool-riffle
10	0.12	7.91	1.14	0.036	5.1	8.8	15	35	620	0.99	0.95	0.187	no	step-pool
11	3.26	5.91	1.08	0.045	13.4	12.7	27	39	730	1.09	19.27	1.438	no	step-pool
12	4.24	0.17	1.08	0.007	8.1	7.7	10	27	0.01	0.55	0.72	0.089	yes	dune-ripple
13	0.18	0.32	1.39	0.004	4.5	14.3	11	25	0.01	0.40	0.06	0.013	yes	silt bed[a]
14	6.77	0.97	1.10	0.058	7.8	7.7	8	15	0.5	1.50	6.57	0.837	no	dune-ripple
15	8.48	4.81	1.07	0.121	13.8	11.3	19	38	940	0.80	40.79	2.951	no	step-pool
16	1.74	2.09	1.07	0.006	7.5	9.4	19	30	410	1.79	3.64	0.483	no	pool-riffle
17	1.64	3.17	1.05	0.031	8.3	9.6	10	40	350	1.57	5.20	0.625	no	step-pool
18	1.09	1.11	1.04	0.044	8.1	8.4	19	45	300	1.54	1.21	0.150	no	pool-riffle
19	5.27	0.28	1.10	0.061	7.8	6.0	17	27	40	1.29	1.48	0.189	no	pool-riffle
20	2.18	0.79	1.24	0.044	7.7	12.2	12	30	110	1.31	1.72	0.225	no	pool-riffle
21	2.27	0.75	1.03	0.006	8.2	15.1	29	37	220	1.52	1.70	0.209	no	pool-riffle
22	0.10	1.42	1.26	0.004	3.1	12.9	16	28	0.01	0.80	0.14	0.047	no	silt bed[a]
23	1.40	2.42	1.07	0.019	6.9	13.9	22	44	270	1.36	3.39	0.494	no	step-pool
24	5.55	2.11	1.13	0.017	15.0	14.5	21	30	640	2.13	11.71	0.781	no	pool-riffle
25	0.51	0.20	1.03	0.006	4.2	11.4	7	23	0.5	0.80	0.10	0.024	no	sandy run[a]
26	0.56	1.78	1.18	0.009	5.7	14.6	8	11	480	1.34	1.00	0.175	no	step-pool
27	6.52	3.14	1.10	0.040	13.4	26.5	10	13	610	1.45	20.47	1.530	no	step-pool
28	0.09	3.44	1.24	0.017	7.8	52.7	21	24	270	2.18	0.31	0.040	no	step-pool
29	0.32	8.01	1.18	0.044	5.7	25.3	26	30	340	1.43	2.56	0.446	no	step-pool
30	1.20	0.49	1.16	0.007	4.9	6.8	9	17	20	1.43	0.59	0.120	no	sandy run[a]

Symbols: area (A), slope (S), sinuosity (P), bed elevation variance (BF_{var}), width (w), width to depth ratio (w/d), average valley side slope (VS_{ave}), maximum valley side slope (VS_{max}), 84th percentile bed material size (D_{84}), bed material sorting (S_{sd}), stream power (Ω), and unit stream power (ω).

[a] Some small, low gradient, fine grained reaches do not fit well into the Montgomery-Buffington classification system.

Table 2.2. Wood parameters

Site number	Wood abundance (# pieces/ 100m)	Wood volume: W_{vt} (m^3)	Wood load		*In situ* piece frequency (#/100m)	Average diam. / channel depth	Average piece diameter (m)		Average length / channel width	Average piece length (m)	
			$W_{v/l}$ (m^3/100m)	$W_{v/a}$ (m^3/ha)			mean (st.dev.)	range		mean (st.dev.)	range
1	73.6	13.3	26.4	420	23.9	0.34	0.26 (0.24)	0.07 - 1.50	0.75	4.7 (7.9)	1 - 43.4
2	70.8	1.5	3.0	41	6.1	0.14	0.12 (0.08)	0.05 - 0.32	0.44	3.2 (2.4)	1 - 11.7
3	116.2	18.8	34.7	428	24.0	0.19	0.21 (0.18)	0.06 - 0.85	0.50	4.1 (3.7)	1 - 20.4
4	61.6	5.3	10.4	192	13.8	0.39	0.18 (0.15)	0.07 - 0.74	0.72	3.9 (5.7)	1 - 26.3
5	115.7	7.5	15.0	146	33.9	0.27	0.23 (0.09)	0.12 - 0.56	0.28	2.9 (2.1)	1 - 11.0
6	46.2	2.3	4.2	71	3.7	0.13	0.14 (0.06)	0.06 - 0.33	0.52	3.0 (3.4)	1 - 17.8
7	50.8	1.1	3.2	84	8.5	0.21	0.14 (0.05)	0.08 - 0.23	0.91	3.4 (3.3)	1 - 14.1
8	110.8	11.0	23.5	612	59.7	0.51	0.26 (0.16)	0.07 - 0.70	0.90	3.5 (3.1)	1 - 14.1
9	48.9	1.9	3.2	61	8.4	0.23	0.15 (0.07)	0.06 - 0.32	0.69	3.6 (3.9)	1 - 16.2
10	69.2	9.1	17.9	354	31.6	0.38	0.22 (0.16)	0.07 - 0.68	0.96	4.9 (5.3)	1 - 21.1
11	105.1	4.3	7.4	55	24.1	0.15	0.16 (0.07)	0.06 - 0.37	0.23	3.1 (2.8)	1 - 16.0
12	103.6	15.1	24.1	296	11.2	0.19	0.20 (0.15)	0.06 - 0.90	0.46	3.8 (4.4)	1 - 27.1
13	51.6	11.5	19.2	424	13.3	0.76	0.24 (0.14)	0.07 - 0.65	1.20	5.4 (6.8)	1 - 25.6
14	90.2	4.4	7.8	99	14.1	0.16	0.16 (0.07)	0.08 - 0.37	0.41	3.2 (2.4)	1 - 11.0
15	63.5	5.7	9.0	65	14.3	0.15	0.18 (0.10)	0.07 - 0.42	0.29	4.0 (3.3)	1 - 16.8
16	44.6	2.1	4.1	55	11.6	0.21	0.17 (0.08)	0.07 - 0.34	0.48	3.6 (4.2)	1 - 18.9
17	52.0	3.8	7.3	87	17.3	0.23	0.20 (0.10)	0.07 - 0.43	0.51	4.3 (4.3)	1 - 21.0
18	112.9	7.2	13.1	163	9.1	0.17	0.16 (0.10)	0.07 - 0.55	0.39	3.1 (3.4)	1 - 21.2
19	130.2	13.9	25.1	322	23.5	0.17	0.22 (0.13)	0.07 - 0.80	0.47	3.7 (3.5)	1 - 18.0
20	66.1	3.3	6.2	81	15.1	0.24	0.15 (0.08)	0.07 - 0.54	0.52	4.0 (3.6)	1 - 17.0
21	78.4	7.0	12.2	150	20.9	0.33	0.18 (0.11)	0.08 - 0.75	0.57	4.6 (4.2)	1 - 25.0
22	43.6	6.9	12.0	392	22.7	1.02	0.24 (0.16)	0.09 - 0.70	1.85	5.6 (5.8)	1 - 20.5
23	35.0	5.4	9.9	144	18.4	0.53	0.26 (0.21)	0.07 - 0.86	0.88	6.0 (5.1)	1 - 15.2
24	118.7	10.4	18.1	121	21.0	0.17	0.18 (0.10)	0.06 - 0.55	0.25	3.8 (4.2)	1 - 20.0
25	88.2	1.8	3.9	92	8.6	0.38	0.14 (0.05)	0.05 - 0.30	0.58	2.4 (1.9)	1 - 9.9
26	99.9	3.8	8.2	144	58.6	0.41	0.16 (0.08)	0.07 - 0.48	0.83	4.7 (3.9)	1 - 15.6
27	74.7	6.0	10.2	76	13.6	0.36	0.18 (0.08)	0.07 - 0.40	0.37	4.9 (4.5)	1 - 17.5
28	63.1	9.0	15.8	202	29.8	1.13	0.17 (0.14)	0.07 - 0.75	0.63	4.9 (5.8)	1 - 23.0
29	48.6	2.3	4.7	82	22.3	0.59	0.16 (0.12)	0.06 - 0.50	0.62	3.6 (3.6)	1 - 16.3
30	78.3	4.4	10.1	207	6.9	0.29	0.21 (0.14)	0.07 - 0.67	0.52	2.5 (1.6)	1 - 7.1

Table 2.3. Wood loads from selected unmanaged streams

Location	Abr.	n	*A* (km^2)	*S* (%)	Wood load m^3/100 m	Minimum size: diam / length (m)	Forest type	Source
La Selva, Costa Rica	CR	30	0.1-8.5	0.2-8	3-34.7	0.10 / 1	tropical wet	this study
Western, WA	WA1	46	0-4	n/r	0-87	0.10 / 2	various	Fox & Bolton, 2007
Western, WA	WA2	45	4-20	n/r	3-142	0.10 / 2	various	Fox & Bolton, 2007
Cascade Range, WA	WA3	28	2.3-119	< 4	1.6-60.7	0.10 / 2	western hemlock	Beechie & Sibley, 1997
Western, OR	OR1	46	n/r [a]	0.5-27.4	2-100	0.15 / 3	various	Thom *et al*., 2001
Coast Range, OR	OR2	9	~5-21.5	1.2-3.6	81-262	0.30 / 3	spruce-hemlock-fir	Reeves *et al*., 2003
Southeast Alaska	AK	5	0.7-55.4	0.8-2.5	7-62	0.20 / 1.5	Sitka spruce-hemlock	Robison & Beschta, 1990
SW British Columbia	BC	4	7.3	1.2-0.5	16.6-85	0.10 / 1	Douglas fir	Fausch & Northcote, 1995
Northern Michigan	MI	12	n/r [b]	0.9-5	7-62.3	0.10 / 1	hardwood-hemlock	Morris *et al*., 2007
Front Range, CO	CO1	12	8-270	3-19	0.1-9.7	0.10 / 1	mixed conifer	Wohl, unpublished data
Front Range, CO	CO2	11	2.4-29.1	0.4-6.4	9.1-27.1	0.10 / 1	mixed conifer	Richmond & Fausch, 1995
Bighorn Range, WY	WY1	9	5.7-85	0.7-5.6	0.4-9.5	0.05 / 1	pine-spruce-fir	Nowakowski, 2007
Absaroka Range, WY	WY2	10	17-40	2.2	15.3-28.9	0.10 / 2	pine-spruce-fir	Zelt & Wohl, 2004
Bridger Teton NF, WY	WY3	13	4.2-100	1.5-10	4.8-54.5	0.10 / 1[c]	pine-spruce-fir	Bragg *et al*., 2000
Southern Andes, Chile	SA	33	9-11	5-8	14.2-64.4	0.10 / 1	southern beech	Comiti *et al*. 2008
Tierra del Fuego, Arg.	TF	32	12.9	6.5	7.2	0.10 / 1	southern beech	Comiti *et al*. 2008
SE Australia	AU	14	187	0.2	27.8	0.10 / 1	gum-eucalyptus	Webb & Erskine, 2003
South Island, New Zealand	NZ	5	0.8-1.4	3.2-5.7	0.2-7.4	0.10 / 1	southern beech	Baillie & Davies, 2002

n/r - data not reported in source
[a] Active channel width ranged from 1.2-24.6 m
[b] Bankfull channel width ranged from 2.4-18.6 m
[c] Study included the entire volume of any wood piece that extended at least 1 m into the bankfull channel

Table 2.4. Wood load (m^3/ha) model parameters

Parameter	Estimate	Std. Error	p-value	VIF
Intercept	62.8	45.6	0.18	
$\beta_{diam/d}$	453.6	110.9	<0.001	2.3
β_{BFvar}	2836.6	952.3	0.007	2.0
β_B	138.2	48.0	0.008	1.2
$\beta_{w/d}$	-8.3	3.0	0.011	2.3
β_ω	-86.5	43.9	0.060	2.3
Multiple R^2: 0.637			Adjusted R^2: 0.562	

Table 2.5. Transported wood model parameters

Parameter	Estimate	Std. Error	p-value	VIF
Intercept	67.5	11.9	<0.001	
β_ω	-44.0	14.2	0.005	2.2
β_A	10.8	3.7	0.007	2.2
$\beta_{w/d}$	-1.2	0.67	0.091	1.1
Multiple R^2: 0.392			Adjusted R^2: 0.322	

Table 2.6. *In situ* wood model parameters

Parameter	Estimate	Std. Error	p-value	VIF
Intercept	26.2	32.4	0.43	
$\beta_{diam/d}$	466.4	86.3	<0.001	1.9
$\beta_{w/d}$	-9.4	2.4	0.001	2.0
β_B	116.4	42.0	0.010	1.2
β_S	17.8	7.6	0.027	1.3
Multiple R^2: 0.632			Adjusted R^2: 0.574	

2.7 Figures

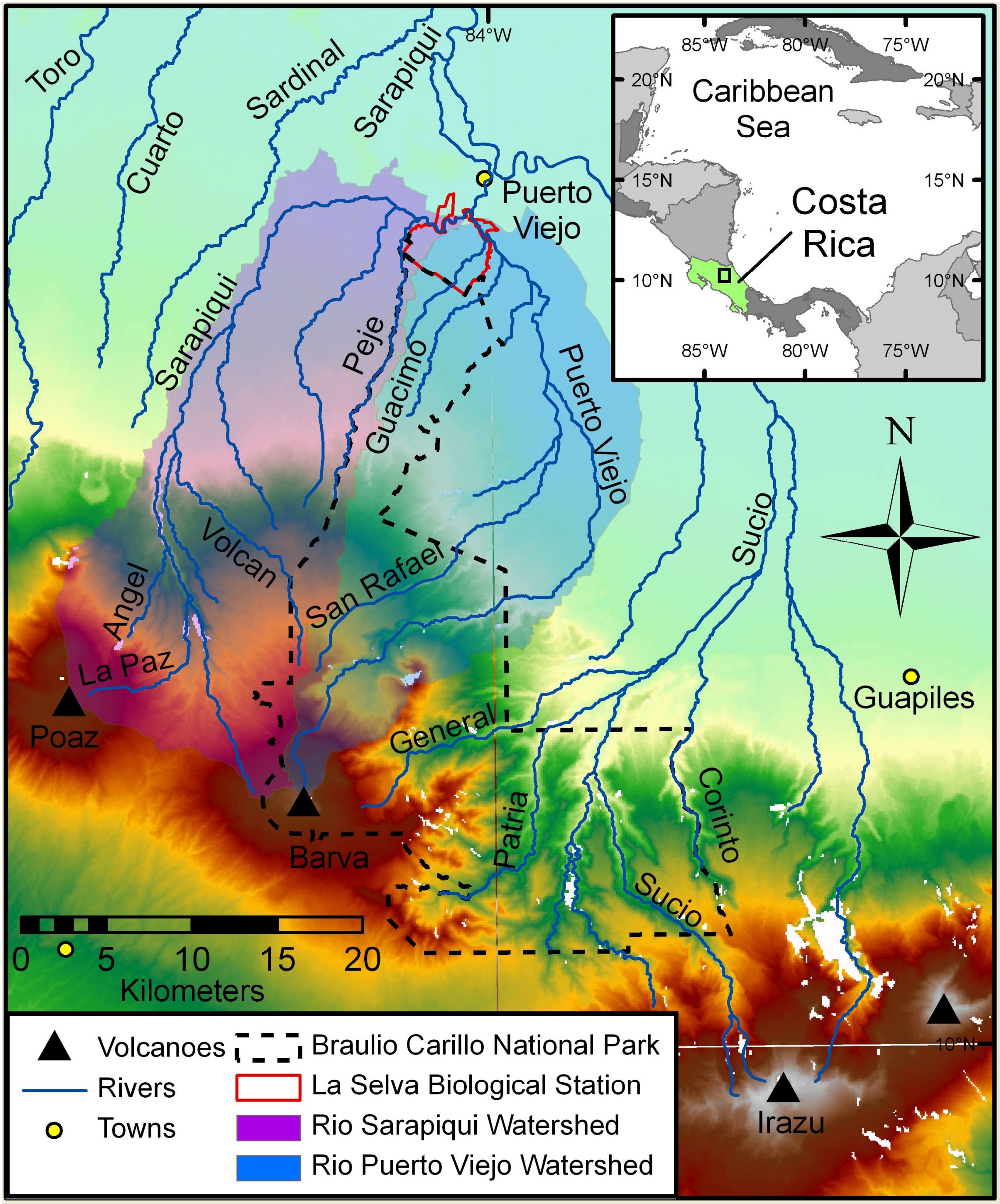

Figure 2.1. Location map of La Selva Biological Station in Costa Rica, showing the primary drainages in the region.

Figure 2.2. Views of (A) site 11, El Surá, with slope of 5.91%, and drainage area of 3.26 km^2; (B) site 17, Quebrada Esquina, with slope of 3.17%, and drainage area of 1.64 km^2; (C) site 3, El Surá, with slope of 0.24%, and drainage area of 4.76 km^2; and (D) site 1, Taconazo, with a slope of 0.32%, and drainage area of 0.28 km^2.

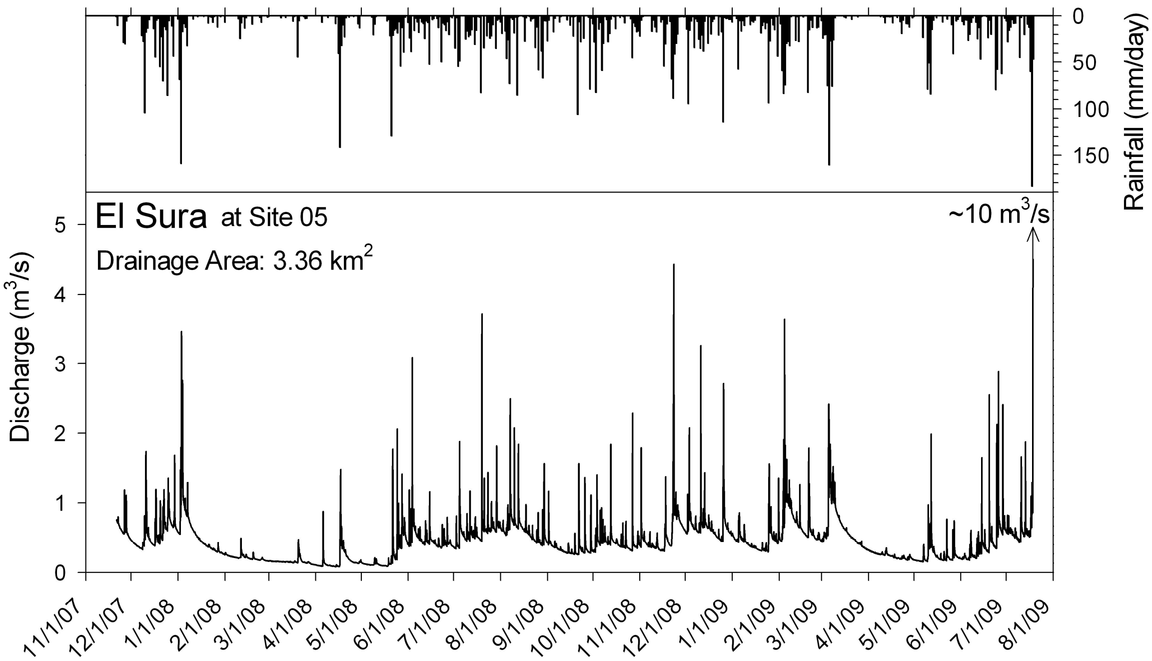

Figure 2.3. Hydrograph at El Surá site 05, 11/21/2007 - 7/18/2008. Rainfall data collected by the Organization for Tropical Studies at the La Selva visitor center, 2 km east of site 05.

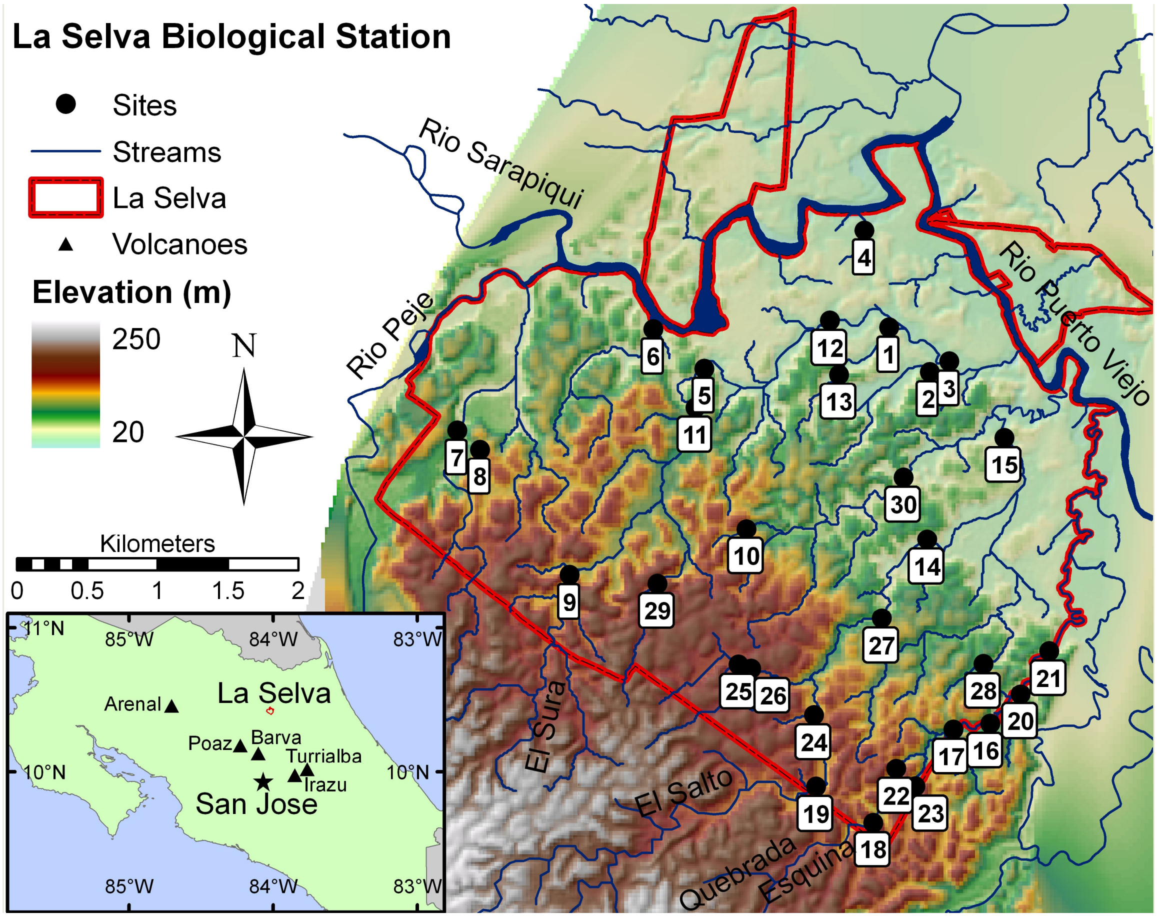

Figure 2.4. Location map of study reaches within La Selva.

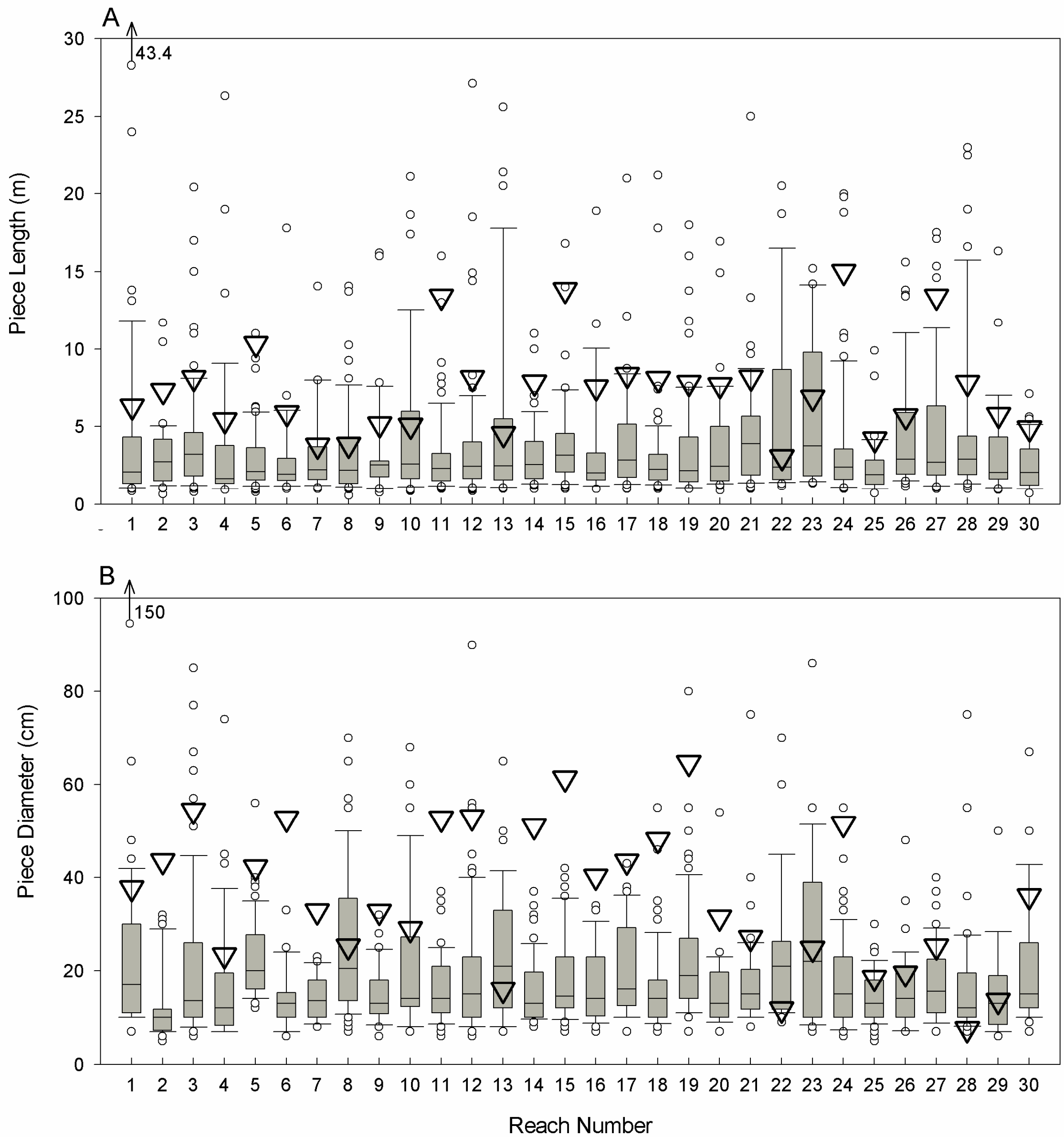

Figure 2.5. Box plots of wood length (A) and wood diameter (B) measured at the La Selva study reaches. The line within each box indicates the median value, box ends are the upper and lower quartile, whiskers are the 10th and 90th percentiles, and solid dots are outliers. Dark triangles indicate the active channel width in diagram A, and half the active channel depth in diagram B. The largest piece, located in site 01, was 43.4 m long and 150 cm in diameter (all other values fit in the plotted range).

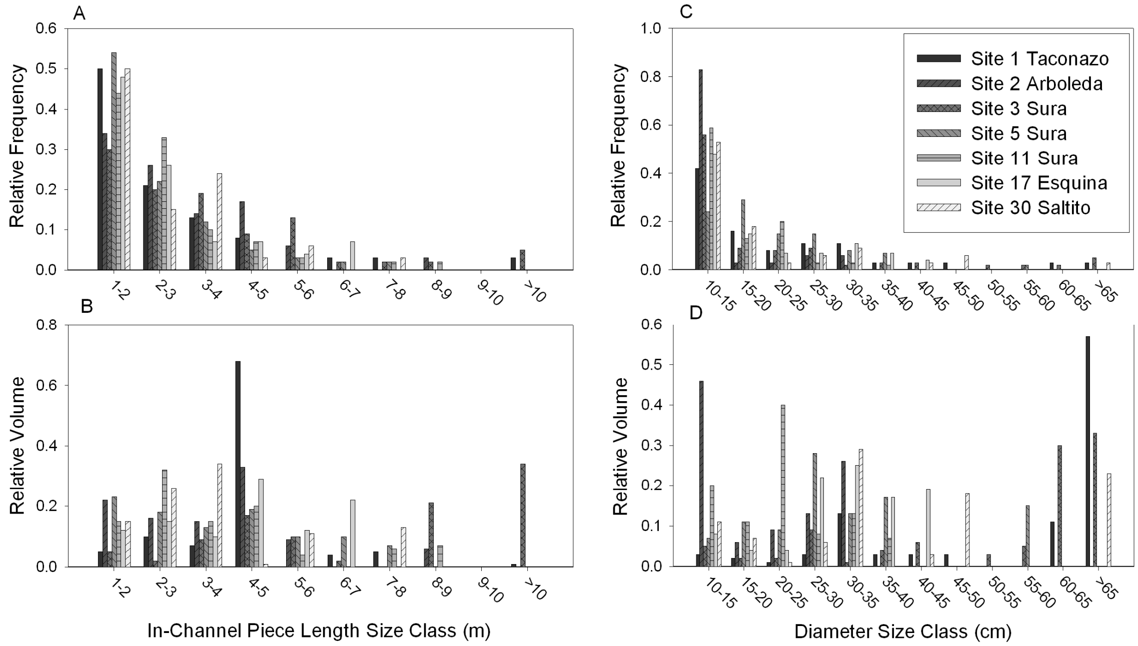

Figure 2.6. Diagrams of (A) frequency of size classes for wood length measured within the active channel, (B) relative volume of size classes for wood length measured within the active channel, (C) frequency of size classes for wood diameter, and (D) relative volume of size classes for wood diameter. In order to keep individual graphed bars legible, 7 reaches are selected to illustrate the range of values present among all 30 study reaches.

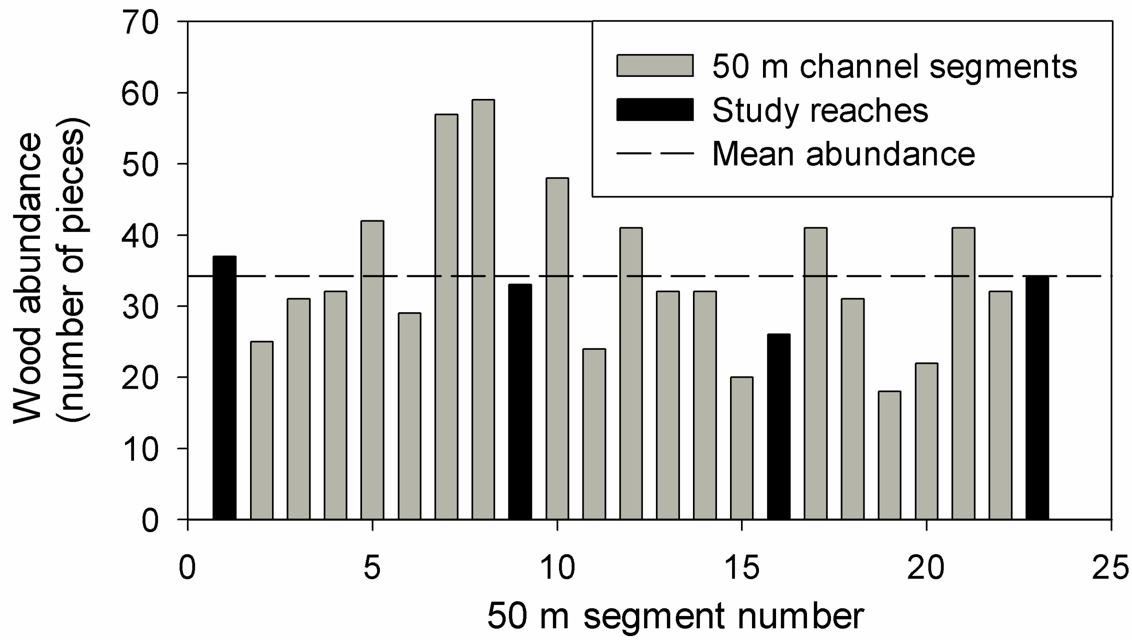

Figure 2.7. Wood abundance along 23 successive 50-m-long reaches of Quebrada Esquina. Horizontal dashed line indicates mean abundance for all reaches (mean = 34.2, standard deviation = 10.6).

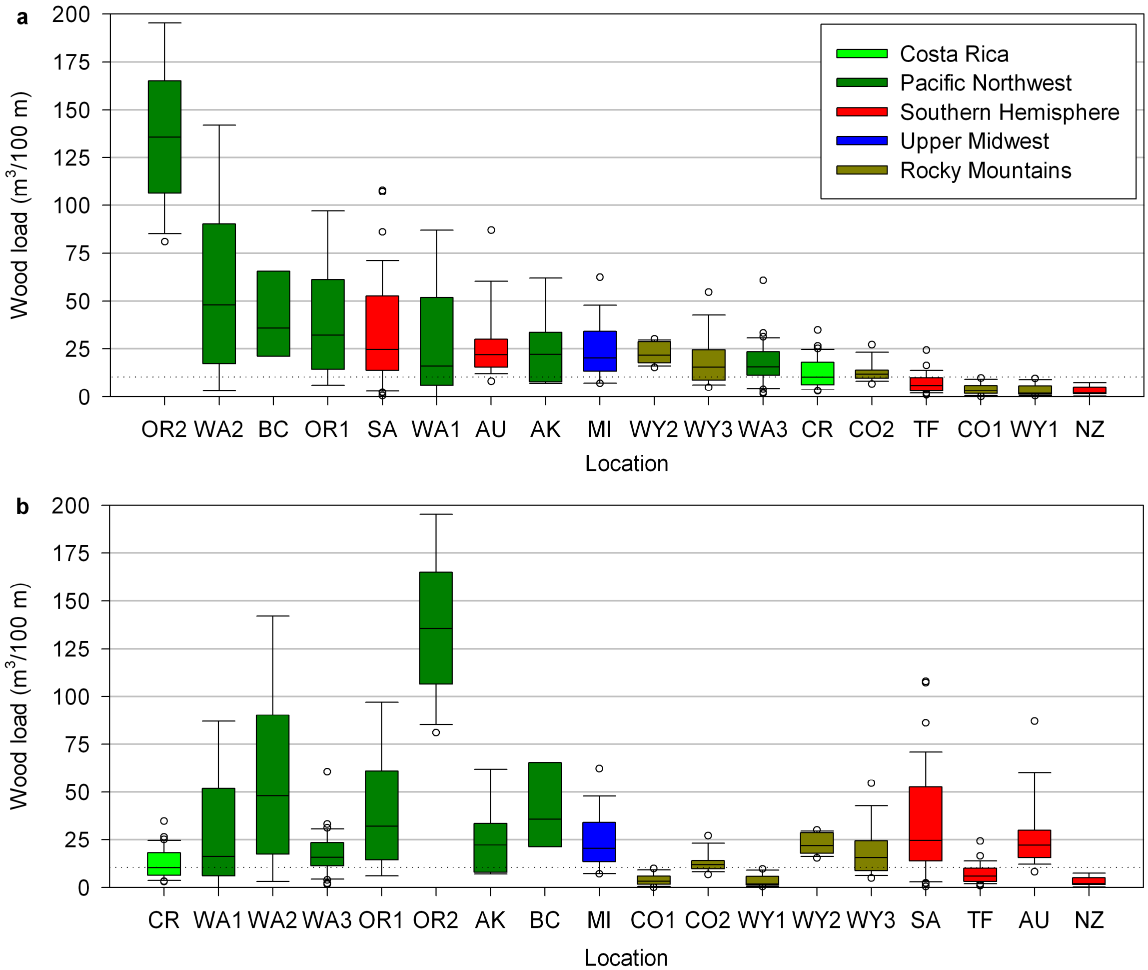

Figure 2.8. Box plots of wood load at La Selva & a selection of other studied sites, using m^3 of wood per 100 m of channel, sorted a) by load, and b) by region. CR = La Selva, Costa Rica; WA1, WA2 = western Washington; WA3 = Cascade Range, Washington; OR1 = western Oregon; OR2 = Coast Range, Oregon; AK = southeastern Alaska; BC = southwestern British Columbia; MI = northern Michigan; CO1, CO2 = Colorado Front Range; WY1 = Bighorn Range, Wyoming; WY2 = Absaroka Range, Wyoming; WY3 = Bridger Teton National Forest, Wyoming; SA = southern Andes, Chile; TF = Tierra del Fuego, Argentina; AU = southeastern Australia; NZ = South Island, New Zealand; see Table 2 for more description of these sites.

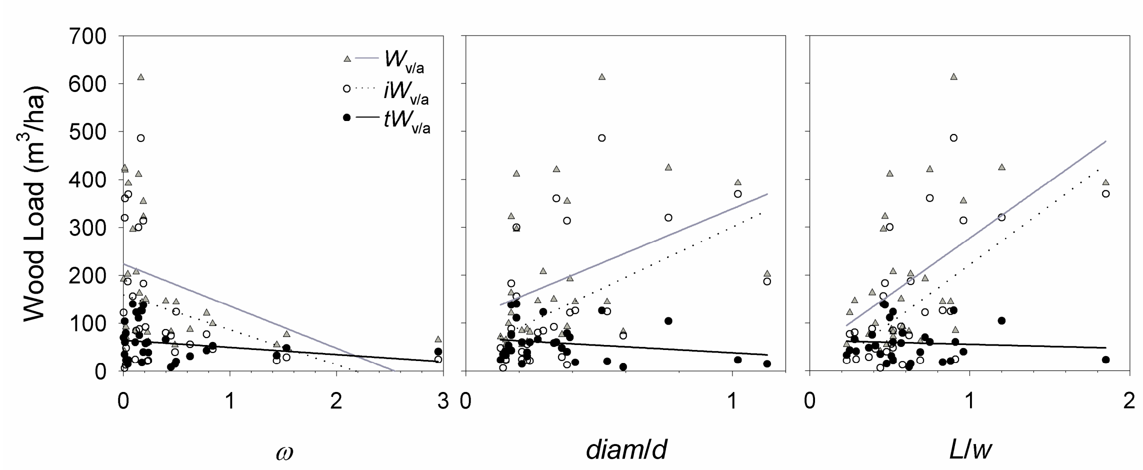

Figure 2.9. Total wood load ($W_{v/a}$), and the transported ($tW_{v/a}$) and *in situ* ($iW_{v/a}$) portions of the wood load, plotted against a unit stream power surrogate ($\omega = AS/w$), average wood length/channel width (L/w), and average wood diameter/channel depth ($diam/d$).

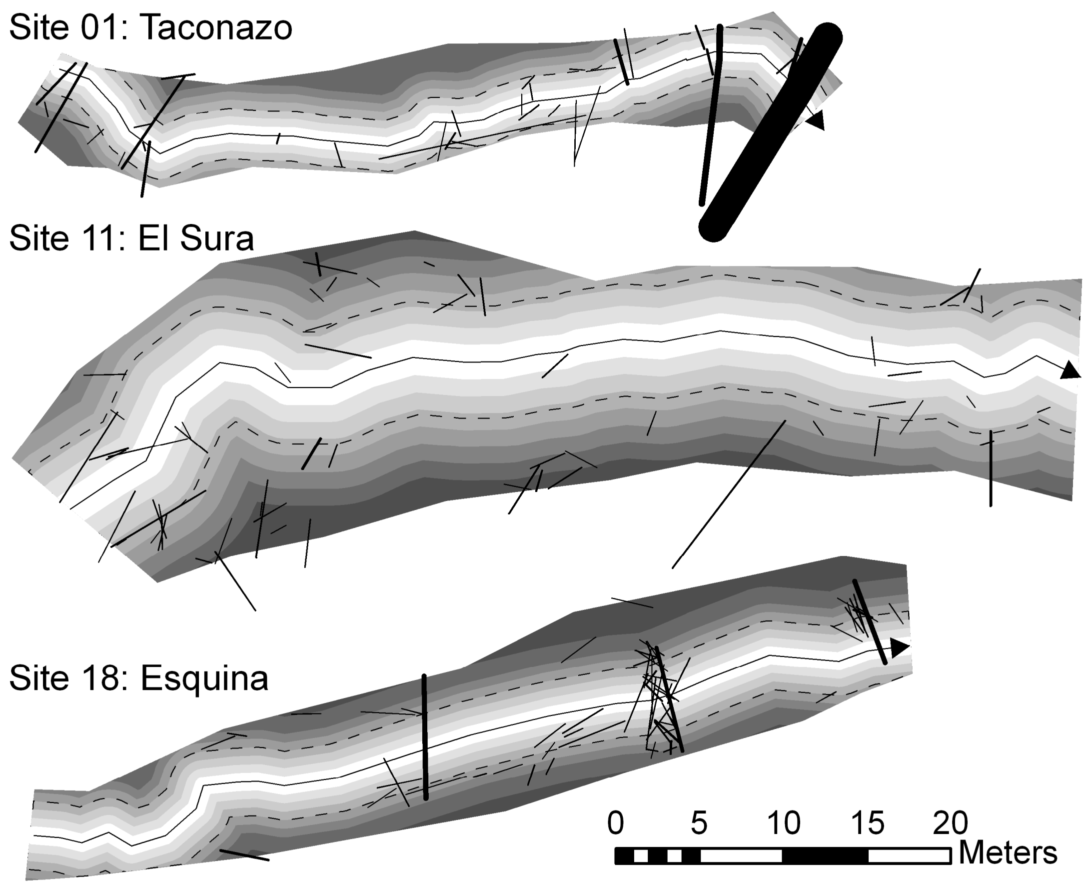

Figure 2.10. Spatial distribution of wood volume in three study reaches. The edge of the shading is the approximate edge of the active channel. The thin solid line is the thalweg, with the arrow showing flow direction. Shading represents relative distance from the thalweg. The dotted line delineates the edge of the central channel (i.e. the area within one-fourth of the average channel width of the thalweg). The black lines of variable thickness are logs, where the line width is proportional to the cross sectional area of the piece. These three reaches were selected to show the full range of conditions. All long-term monitoring reaches are shown in Appendix B.

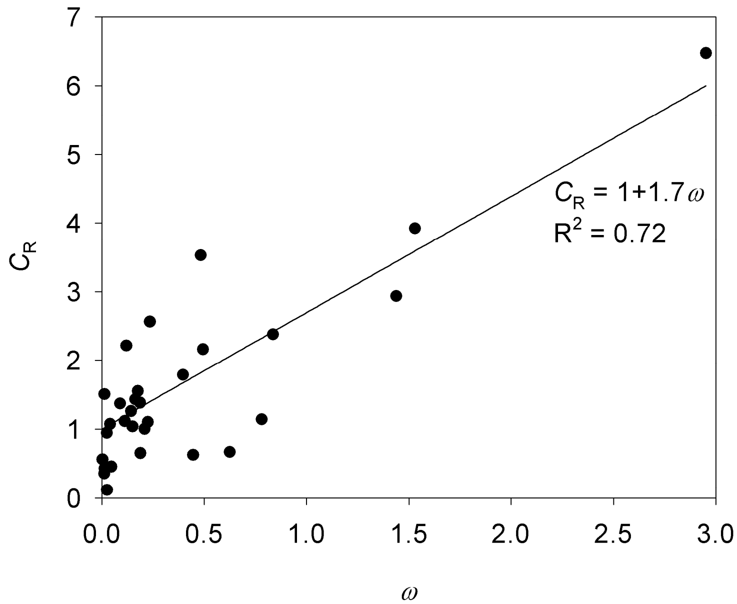

Figure 2.11. Plot of a surrogate for unit stream power ($\omega = AS/w$) versus ratio of wood in the outer 50% of the channel to wood in the inner 50% of the channel (C_R) for the study reaches at La Selva.

3 WOOD TRANSPORT AND RETENTION

3.1 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 which deflect or impound flow. Such pieces may do any or all of the following: 1) increase resistance to flow (Curran and Wohl, 2003; Wilcox and Wohl, 2006), 2) deflect flow toward channel margins (Daniels and Rhoads, 2003), 3) shield channel margins (Brooks et al., 2003) 4) form steps and pools (Richmond and Fausch, 1995; Beechie and Sibley, 1997; Gurnell and Sweet, 1998), 5) induce pool scour (Fausch and Northcote, 1992; Baillie and Davies, 2002), 6) trap sediment or nutrients (Smith et al., 1993b; Hart, 2002; Faustini and Jones, 2003), 7) force avulsions (Maser and Sedell, 1994), and 8) 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 coarse particulate organic matter (CPOM) (Bilby and Likens, 1980; Webster et al., 1994), which is a major source of energy and nutrients in many streams. The wood hosts macro-invertebrates (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, I expect to see a correlation between wood residence time and geomorphic effectiveness. For example, a frequently moving piece of wood is less likely to affect CPOM flux or induce deep scour. And, although jams may be persistent even if the individual pieces turn over quickly, thereby maintaining flow deflection characteristics, a jam that frequently loses wood will likely pass sediment and CPOM as well. 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 when balancing the needs of natural stream function and infrastructure protection and maintenance. For these reasons, quantification of wood mobility either 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 dendrochronology (Keller and Tally, 1979a; Murphy and Koski, 1989; Dahlstrom 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. As discussed in the preceding chapter, wood loads in La Selva Biological Station, Costa Rica, a tropical rainforest, are lower than in the temperate rainforests of the Pacific Northwest. I infer that the lower wood loads reflect increased mobility of in-stream wood because both regions have equally large trees and primary productivity is expected to be as high or higher in the tropical rainforest as in the temperate rainforest, although there are potentially large errors in these estimates of productivity (Clark et al., 2001). Here I 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. 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. Although it is possible that the reduction in decay rates caused by submergence in anoxic conditions (Triska and Cromac, 1980) or the decay-resistant compounds present in the wood of many tropical trees reduce the influence of decay, tropical forest-floor decay rates several times higher than those from temperate zones make it unlikely that wood in tropical streams does not decay faster than wood in temperate streams. Runoff production is higher 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 low hydraulic conductivity of the soils at depth (Godsey et al., 2004) as well as by high infiltration rates resulting from the presence of fractures and abundant macropores which 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 I 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.

Dendrochronology 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 I established a regimen of flagging and monitoring of in-stream wood in old-growth rainforest catchments in La Selva Biological Station. The 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. I hypothesize that the study streams will exhibit shorter retention times for in-stream wood than temperate headwater streams with similar characteristics.

3.2 Methods

3.2.1 Wood monitoring

All stream reaches in this study were located in old-growth forest within La Selva Biological Station (Figure 3.1). 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 (Figure 3.2) were selected for monitoring from an initial group of 30 reaches surveyed in March 2007. 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 approximately 50 m long, with gradients ranging from 0.2% to 6.2%, bankfull widths ranging from 4.9 m to 13.4 m, and drainage areas ranging from 0.3 km^2 to 6.8 km^2 (Table 3.1).

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). I delineated the active channel at the edge of dense vegetation where there was a break in slope, a level that is probably flooded once or twice each year. Attached pieces included pieces that were buried in streambed sediment, pinned under rocks, and pinned in log 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. 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, surface slightly rotted; 6- surface extensively rotted, center solid; 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 re-flagged and described, but not re-measured unless they had broken since the previous survey. All pieces were re-surveyed with a total station. Some low gradient sites had very deep silt deposits which 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.

3.2.2 *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 (Jimenez, 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 sub-canopy 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). I was 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 approximately 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.

3.2.3 Stream discharge gaging and flow characterization

A vented pressure sensor stage gage was installed at one of the sites (Site 5, Surà) that recorded stage every 15 minutes 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 flows available during field work. On 18 July 2009 the installation was destroyed by a flood, although a non-vented 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 between 3-6 $m^3/s/km^2$. The second largest flood recorded was estimated to be 4.4 m^3/s, on 23 November 2008.

I 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). I considered the cumulative distributions of discharge, maximum depth at the gage site, and estimated cross section average depth at a riffle for El Surà at La Selva and Mack Creek at HJ Andrews. I estimated riffle depth at these sites from discharge records using surveyed cross sections 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 Surà (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. I 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.

3.2.4 Retention rates and mean residence times

The percentage of logs retained within each study reach was calculated for every time interval, from ~4 months (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 3-5 months. Retention rates weighted by piece volume (v) were also calculated for all time intervals, calculating piece volume as $v = l_{bf}\pi(d_w/2)^2$. I 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, 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, cdf's, and mean residence times can be calculated in terms of the number of wood pieces, wood volume, wood mass, and carbon content, among others. I calculated residence times in terms of wood pieces and wood volume.

3.2.5 Logistic regressions

A logistic regression analysis was performed using R 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. I 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), channel width (w), average 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). I 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 'glm' general linear modeling command in R, which helps choose the most parsimonious model by balancing predictive power with the number of variables included in the model. 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, I 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.

I analyzed two data sets: the full data set of all pieces observed during the study, and the set of all pieces excluding those first observed in November 2009. The second data set is expected to have better predictive power because the pieces that were first observed in November 2009 never had an opportunity to be transported. Thus, 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 I was unable to re-survey the reaches subsequent to its emplacement.

3.3 Results

3.3.1 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 (Figure 3.3), although the wood piece depletion rate during each interval between surveys correlated very well with peak discharge at the stream gage site (Figure 3.4). I 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 one may extrapolate the observations of wood retention rates over the 28-month period 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 3.2). Averaging the yearly retention rates calculated from the various time intervals within each site gives a range of 0.55-0.91

among the sites. In terms of wood volume, the average retention rates ranged from 0.67 to 0.99 among the sites (Table 3.3). 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 3.0-83.2 years, which includes one high outlier, Taconazo01 (Table 3.3). It 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. It should be noted 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 Taconazo01) with ±0.01 uncertainty will lead to mean residence times that could range from 45-500 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, I do not think a simple average of the 10 residence times will necessarily represent mean residence time in the study area. Therefore, I 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.

There is only very limited data with which to constrain the uncertainty involved in scaling up the observed depletion rates either spatially or temporally. I 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 1963-2008 was 4365 mm, with a standard deviation of 700 mm. Precipitation during the three 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 three years of the study, the maximum monthly precipitation of each year was 619 mm in November 2007, 550 mm in August 2008, and 658 in July 2009, all less than the record average. It is thus possible that the study 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 ten 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 (Figure 3.5). There were no multivariate models for mean residence time using the stream variables listed above 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.

3.3.2 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 not be differentiated using a bank penetrometer since they were both more resistant than the maximum pressure I 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 3.4). 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 (Figure 3.6), 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 I had been able to fully dry each piece, the trends might have been more consistent.

3.3.3 Statistical modeling of wood retention

As a precursor to modeling, I 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). I 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 (Figure 3.7) and the natural logarithm of l_w (Figure 3.8). It does not correlate well with c_d (Figure 3.9). The four type classes have distinct wood loss rates, with unattached pieces being removed at the highest rate, followed by attached, ramp, and bridge (Figure 3.10).

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). This model correctly predicted the status, either retained or transported, of 72% of the pieces (Figure 3.11a, b). 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 (Figure 3.11c). 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 (Figure 3.11d). Interpreting the estimated parameters of the model ($\beta_{\ln lr}$ =0.920, $\beta_{\ln s}$ =0.493, β_{tu}=0.964), one finds 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 $o = p(1-p)^{-1}$.

3.3.4 Comparison of flow characteristics

I 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 (Figure 3.12). Floods that exceeded 0.4 $m^3/s/km^2$ were 4-10 times more common at La Selva than at HJ Andrews (Table 3.5). Flows of a given frequency were deeper in El Surà, La Selva, than in Mack Creek, Oregon (Figure 3.13). This is in part because of the lower width to depth ratio in El Surà, 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 days per year on average at Mack Creek, but 150.6 days per year at El Surà, while d_{ave} at the surveyed riffles never exceeded 0.5 m at Mack Creek over 30 years of records, but exceeded 0.5 m 6 times at El Surà in 1.66 years (Table 3.6). 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 greater than 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.

3.4 Discussion

3.4.1 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 (Figure 3.5), 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. Trans-basin 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.

Increased gradient led to increased mobility for the full range of slopes included in the study sites. This contrasts with the increased retention observed in cascade and step-pool channels by Montgomery and Buffington (year). This apparent contradiction is likely the result of the absence in my study sites of transport limited reaches analogous to the headwater reaches studied by Montgomery and Buffington. The high precipitation and runoff production of the tropics will tend to cause transport limited reaches to occur higher in the drainage network than they would in the temperate zone.

Decay class was not correlated with the likelihood of a piece being retained within the study reaches. However, I 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 (Figure 3.4), a finding similar to that of Wohl and Goode (2008). I 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. There is relatively little annual variation in precipitation at La Selva, either in total rainfall (4375 ± 700 mm, mean ± standard deviation) or distribution (minimum monthly precipitation is 103 ± 61 mm, and falls between Feb-Apr 93% of years; maximum monthly precipitation is 734 ± 196 mm, and falls between May-Aug 60% of years and between Nov-Dec 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 because of the lack of long-term gage records. 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 (see section 1.4.2 Study Site). 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 I 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.

I found a variation of up to 0.25 in wood retention rates depending on of the length of time interval analyzed (Table 3.2). Part of this variation is because pieces that both enter and exit the study reach in the interval between surveys are not recorded, although more frequent sampling increases the chances of including these pieces. This effect will lead to lower retention rates for shorter sample intervals. However, in the study I 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 inter-sample 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 my methods, and the need for long-term monitoring to capture the range of inter-annual and seasonal variation in retention rates.

3.4.2 Comparison of tropical and temperate zone residence times

The estimated mean residence time of wood across all the study reaches of 4.9 years for a piece of wood and 6.9 years for a unit volume of wood is shorter than most estimates from the temperate zone, particularly estimates from old-growth forests (Table 3.7), although not all studies to which I compare my data were conducted on similar sized streams or used similar methods. In a fire-influenced landscape in western Alberta, Canada, Powell and others (2009) used dendrochronologic techniques to find the age distribution of in-stream wood pieces, using the same minimum size criteria as in this study (1 m length, 0.1 m diameter). Their resultant distribution curves for pine- and spruce-dominated areas have approximate mean ages since death of 45 and 55 years, respectively. Their methodology cannot be replicated at La Selva because most tropical trees do not form annual rings. Even longer residence times were found for wood from a meandering stream reach in Missouri, USA, which was dated using dendrochronology and radiocarbon dating (Table 3.7). The maximum residence time found was 9485 years, and the mean carbon residence time (similar to wood residence time by mass) was 350 years (Guyette et al., 2002). The oldest residence times are likely the result of wood burial and exhumation as the channel migrates across its floodplain. Mean residence times of wood may not meaningfully reflect stream processes if disturbances prevent the attainment of steady state. The channels of the heavily exploited forests of northern Sweden, for example, have experienced wide variation in input rates and species composition over the time period integrated by the in-stream wood, so researchers who have analyzed the age distribution of the wood in these streams have refrained from presenting a mean residence time (Dahlstrom et al., 2005). In the Rocky Mountains of Colorado, Wohl and Goode (2008) found a mean residence time of 3.4 years. Only pieces that both entered and exited the study reaches during the 10 years of the study were included in this calculation, possibly contributing to the relatively short residence time. Wohl and Goode observed average annual depletion rates of 16-23%, which translate to mean residence times of 4.3-6.3 years, assuming steady-state. The Colorado study streams were in forests that had not been logged for 100 years, but were not old-growth, which likely contributed to the relatively small piece sizes and the short residence times.

Most temperate zone mean residence time estimates in old-growth forests come from the Pacific Northwest region, USA, and are summarized by Hassan and others (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 3.7). Keller and Tally (1979a), working in Redwoods National Park, California, dated 33 pieces of in-stream wood that had also served as nurse logs for subsequent trees by coring the trees growing on the logs. This method limited their analysis to stationary large pieces, for which they found a mean residence time of 100 years. Murphy and Koski (1989) modified this method by weighting the age distribution by piece diameter class, but the method is still limited by the need for pieces to be nurse logs. In their southeast Alaska field site, Murphy and Koski estimated mean residence time to be 54 years. Lienkaemper and Swanson (1987), working in HJ Andrews Experimental Forest, Oregon, used a method similar to this study, but rather than measuring depletion rate they measured input rate (by volume) for 11 years and reasoned that, since the wood load was fairly constant, depletion rate must be similar. They found input rates ranging from 0.012-0.087 yr^{-1}, which is equivalent to mean residence times of 12-83 years. Hyatt and Naiman (2001) used a combination of dendrochronology and radiocarbon dating to find the age of key wood pieces (≥60 cm diameter, ≥5 m length) in the Queets River, Washington. The mean residence time of these large pieces in this large river was ~30 years. These four studies were conducted in old-growth forests, but logging will influence wood retention, both short and long term. 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 >50 m and diameters >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 conifers of the Pacific

Northwest. Tropical trees may contribute more small pieces to streams by dropping branches which are then more mobile than the main boles, or by breaking at the more numerous branching sites upon falling.

The presumed higher tropical decay rate 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 $\geq$ 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 and others (1986) and generally range from 30-90 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 emplaced pieces, and may reduce the influence of the temperature and microbe factors that lead to higher decay 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.

3.5 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. I found annual piece retention rates from 0.55-0.91, and annual volume retention rates from 0.67-0.99. 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 I believe 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 the 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. The shorter residence time of wood in tropical streams implies that maintaining wood recruitment into the streams is particularly important in this region in order to preserve the geomorphic and ecological function of in-stream wood.

3.6 Acknowledgements

Temperate zone flow data were provided by the HJ Andrews Experimental Forest research program, funded by the National Science Foundation's Long-Term Ecological Research Program (DEB 08-23380), US Forest Service Pacific Northwest Research Station, and Oregon State University.

3.7 Tables

Table 3.1. 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	Surà	0.24	4.79	8.1	Sand
5	Surà	1.22	3.36	10.3	Boulder
11	Surà	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

Table 3.2. Average retention rates for wood pieces

Site #	Stream name	Retention rates (average rate for interval length, equivalent annual rate) 4 month	8 month	12 month	16 month	20 month	24 month	28 month	Average annual retention rate	Equivalent mean residence time (yrs)
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	Surà	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	Surà	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	Surà	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 3.3. Average retention rates for a unit wood volume

Site #	Stream name	Retention rates (average rate for interval length, equivalent annual rate) 4 month	8 month	12 month	16 month	20 month	24 month	28 month	Average annual retention rate	Equivalent mean residence time (yrs)
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	Surà	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	Surà	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	Surà	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

Table 3.4. Decay results

Piece #	Stream	Species	Vertical Location	Wet Density (g/cm^2)	Dry Density (g/cm^2)
1	Surà	Cec.	Top	0.910	0.239
2	Surà	Cec.	Mid	0.984	0.329
3	Surà	Cec.	Low	1.028	0.291
4	Surà	Dip.	Top	1.273	0.896
5	Surà	Dip.	Mid	1.227	0.861
6	Surà	Dip.	Low	1.334	0.937
7	Surà	Pent.	Top	1.089	0.373
8	Surà	Pent.	Mid	1.167	0.523
9	Surà	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

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

Table 3.5. Comparison of La Selva and H.J. Andrews study sites

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

Table 3.6. Frequency of flow depths at Mack Creek and El Surà, relative to wood size

	Mack Creek, OR	El Surà, CR
length of record (yrs)	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 w/ 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 w/ 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 w/ 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 w/ ave. d at riffle > max. wood diam	0	1
average # of events/year	0	0.6

Table 3.7. 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 (yr)	Methods	Reference
		Diam. (cm)	Len. (m)				
Redwoods National Park, Calif.	redwood, old-growth	10		6-19	~100	age of trees germinated on piece	Keller & Tally, 1979
Southeast Alaska	hemlock-spruce, old-growth	10	3	8-31	~54	age of trees germinated on piece	Murphy & Koski 1989
HJ Andrews Experimental Forest, Ore.	Douglas fir-hemlock, old-growth	10	1.5	3-24	12-83	observation of wood input	Lienkaemper & Swanson, 1987
Olympic Peninsula, Washington	hemlock-spruce-Douglas fir, old-growth	60	5	165	30	dendro-chronology, radiocarbon	Hyatt & Naiman, 2001
Medicine Creek, Missouri	*Quercus–Carya–Acer*, gallery forest	25		not reported est. ~2	350 (carbon)	dendro-chronology, radiocarbon	Guyette , Cole, Dey, & Muzika, 2002
Rocky Mtn. foothills, Alberta	pine- or spruce-dominated, ~100 yr. fire recur. int.	10	1	0.8-3.5	45-55	dendro-chronology	Powell, Daniels, & Jones, 2009
Rocky Mtns., Colorado	sub-alpine, logged ~100 yrs ago	5	1	4.3-6.5	4.3-6.3	observation of wood export	Wohl & Goode, 2008
La Selva, Costa Rica	tropical, old-growth	10	1	5-13	5 (piece); 7 (volume)	observation of wood export	this study

3.8 Figures

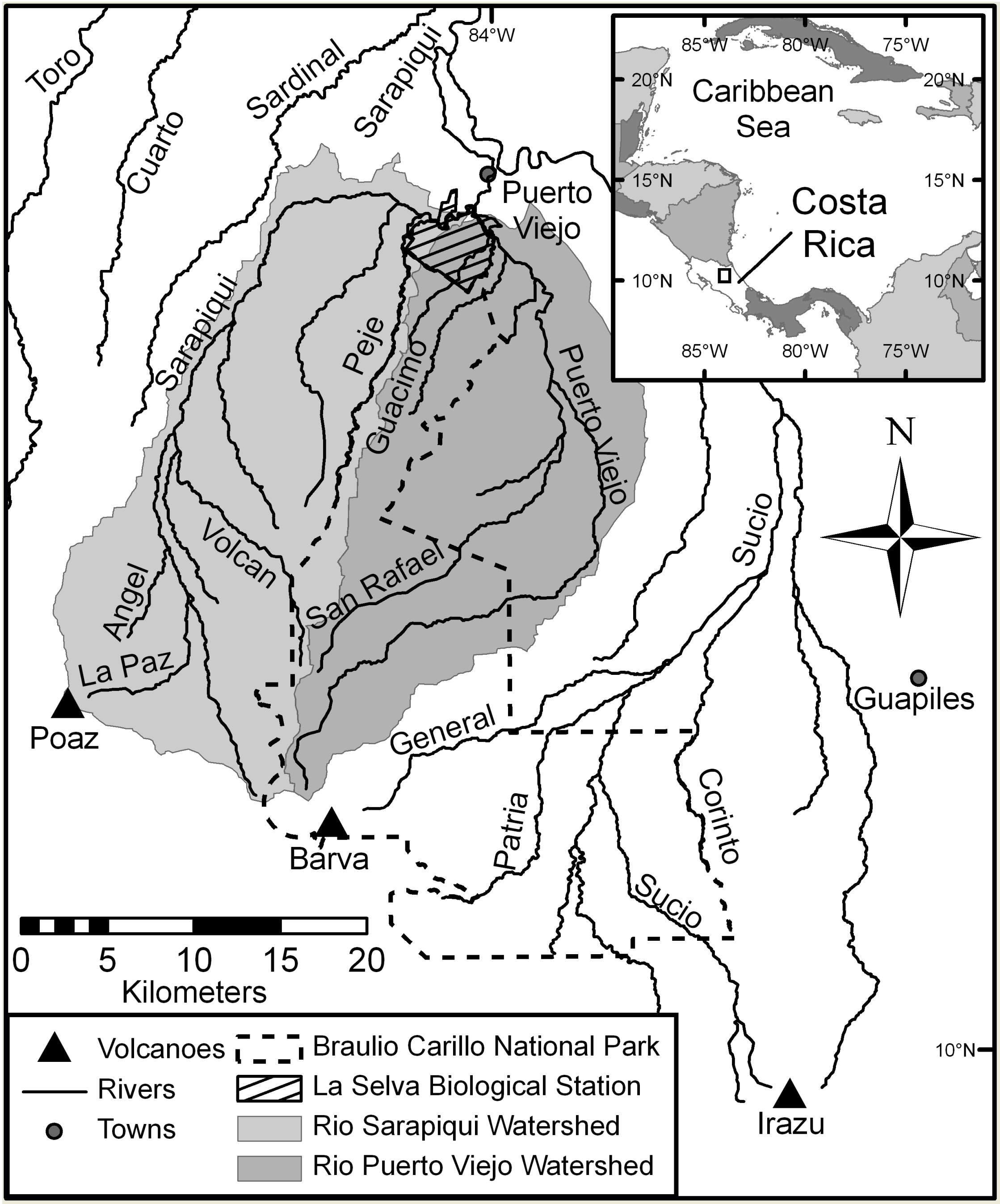

Figure 3.1. Map showing the location of La Selva Biological Station within the upper Rìo Sarapiquì drainage basin.

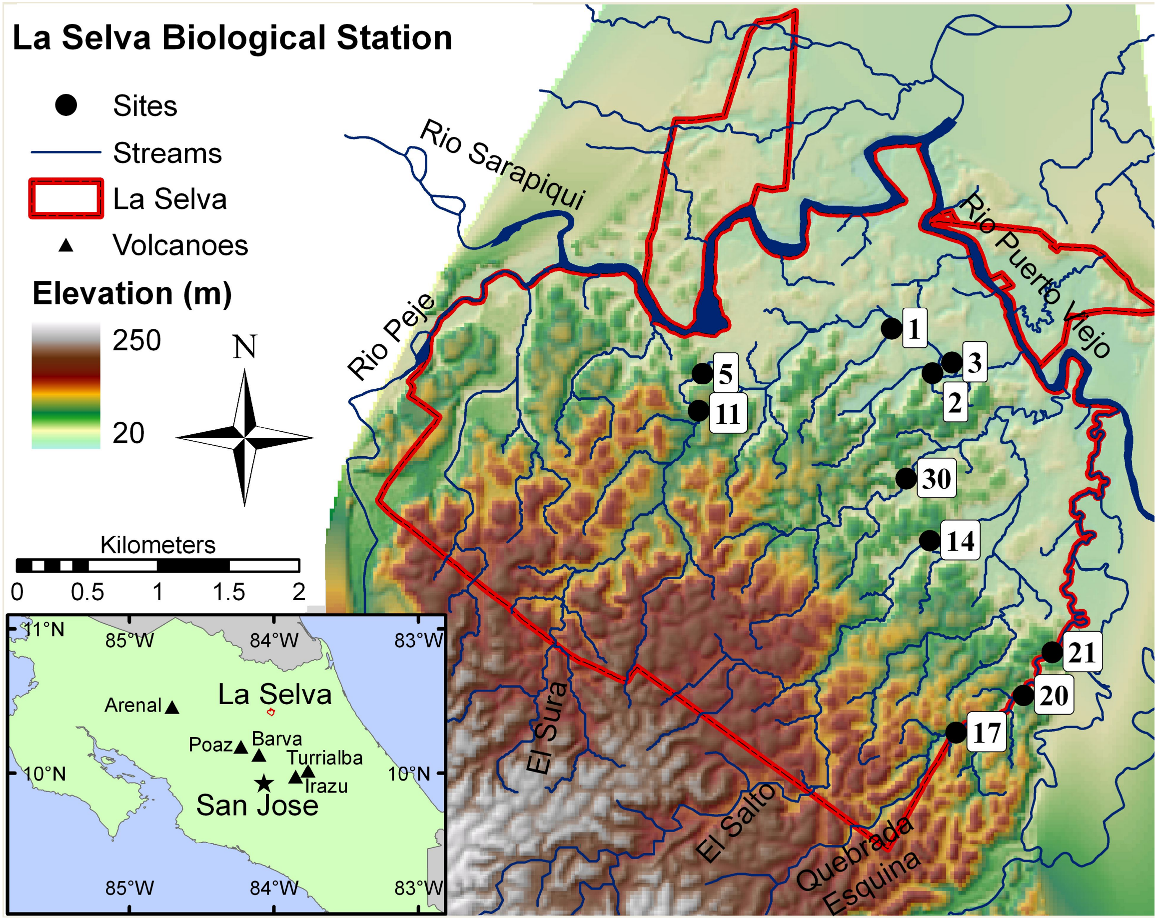

Figure 3.2. Map of the primary drainages of La Selva, showing the locations of the 10 study reaches in which wood was monitored.

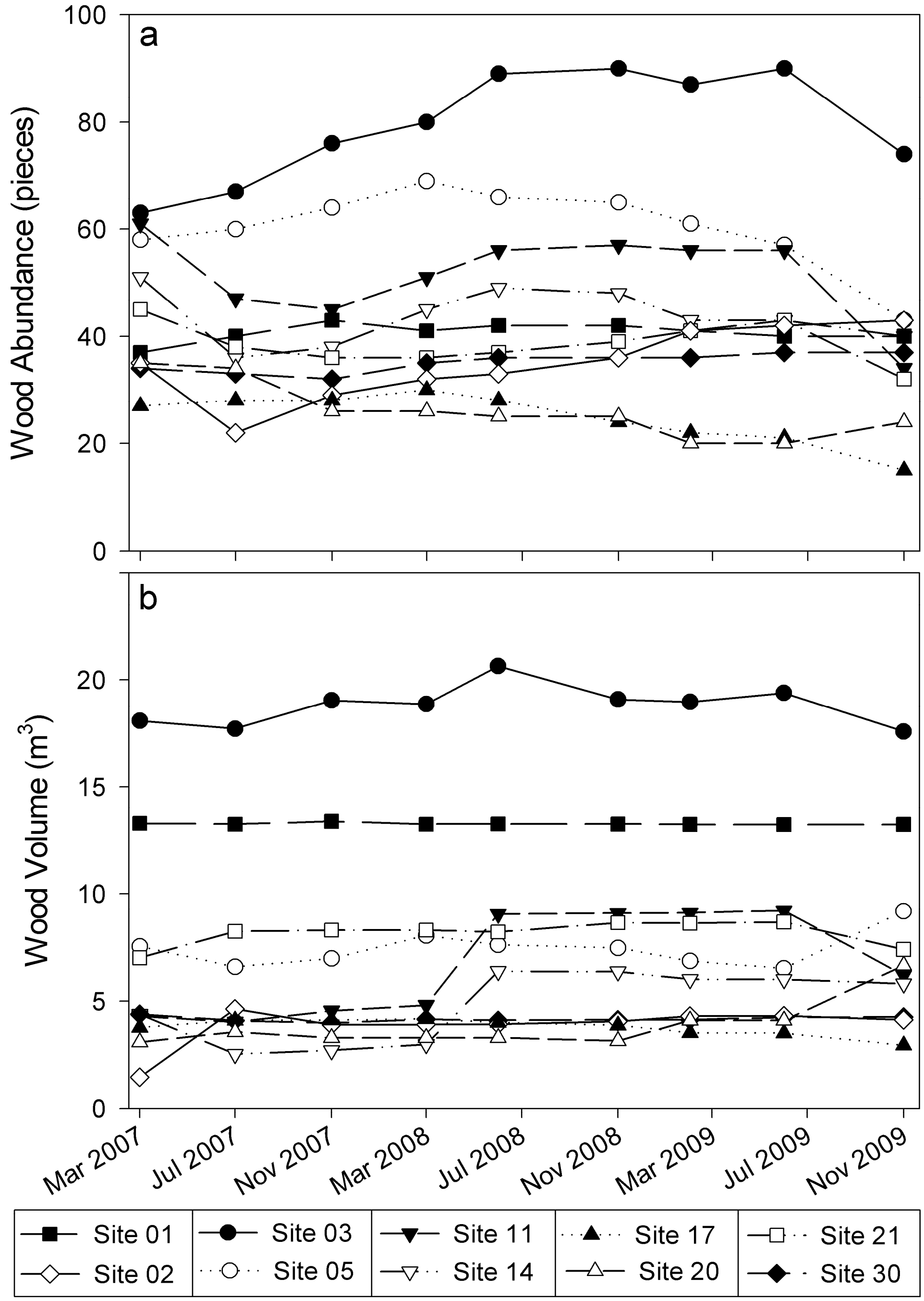

Figure 3.3. Variation in wood load in the 10 study reaches during the study period, in terms of a) piece abundance and b) total in-stream wood volume. No consistent trends through time were observed.

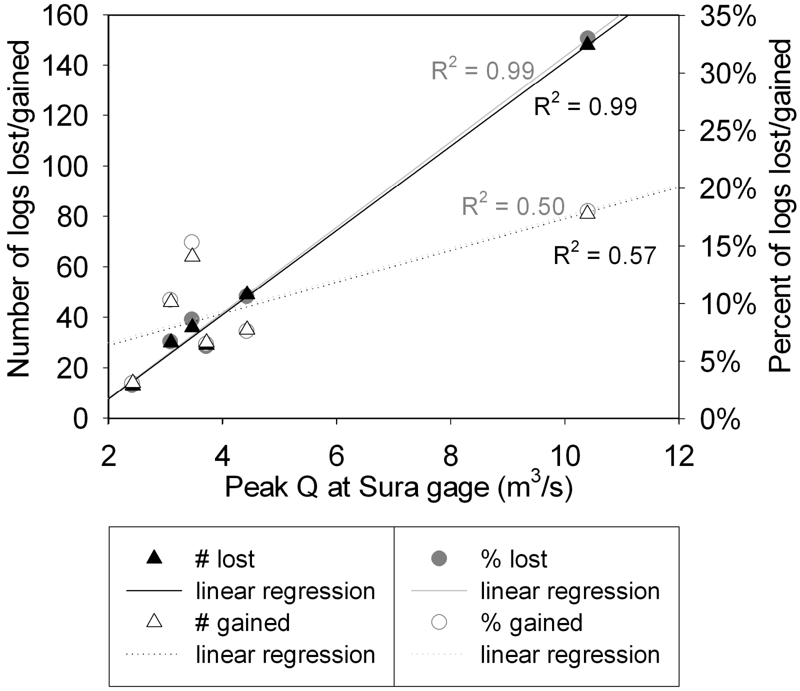

Figure 3.4. Wood piece loss and gain relative to peak discharge at the gage on El Surà at Site 05. Stage at El Surà was recorded at 10 minute intervals. The highest discharge measurement used to establish a stage-discharge relationship was 1.25 m^3/s, so all peaks reported here are estimates based on extrapolation using a power function.

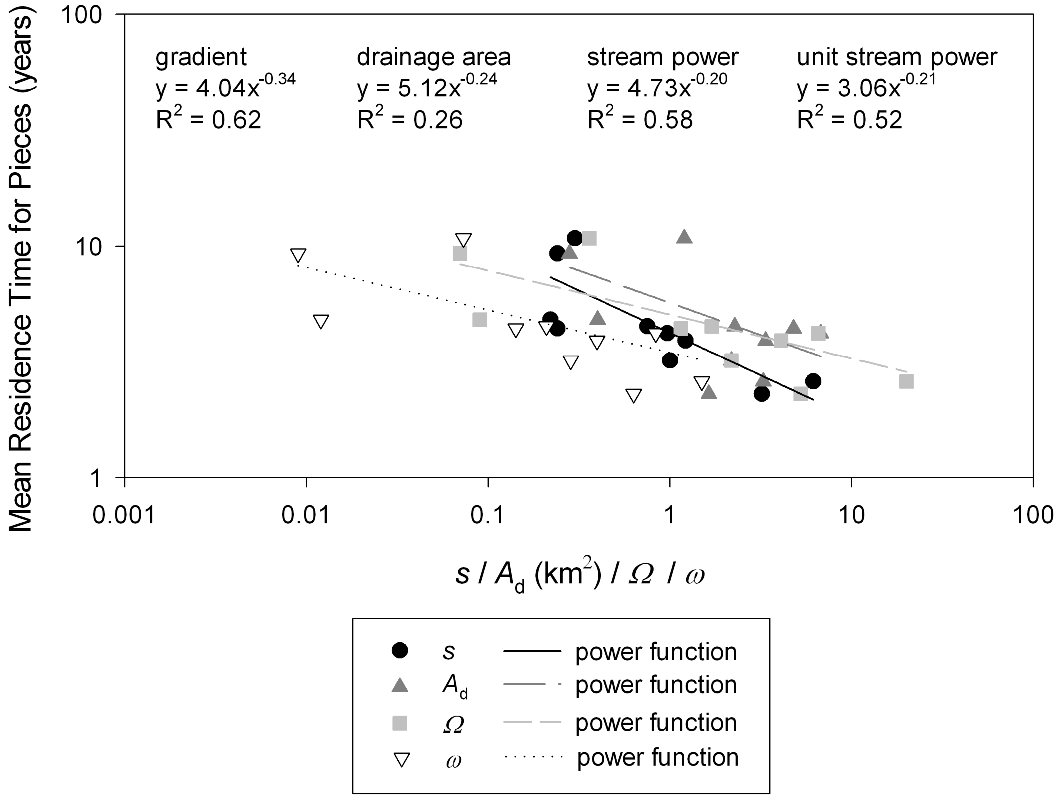

Figure 3.5. Mean residence time for in-stream wood pieces in the 10 study reaches plotted against gradient (*s*), drainage area, (A_d), relative stream power (Ω, calculated as the product of s and A_d, using A_d as a surrogate for discharge), and relative unit stream power (ω, calculated as Ω divided by the reach average active channel width). Gradient has the highest coefficient of determination (R^2).

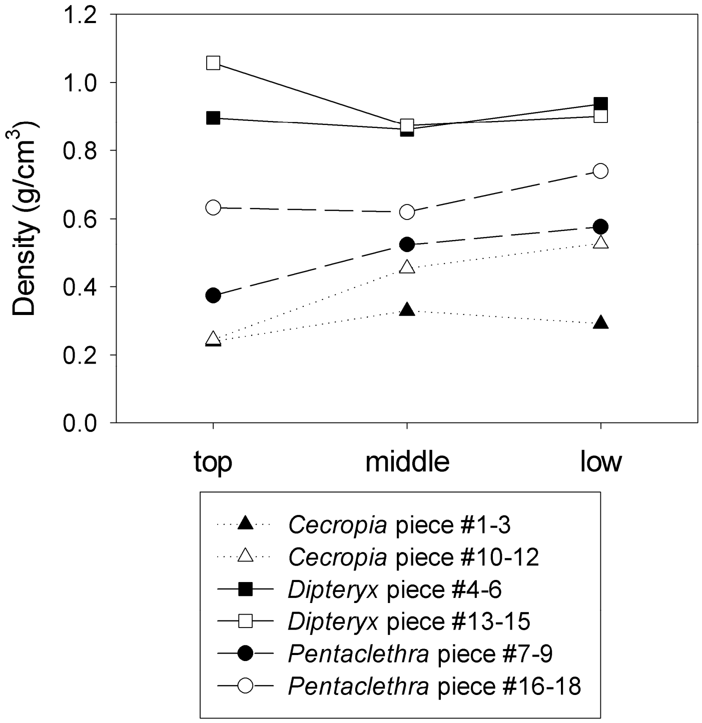

Figure 3.6. Density of wood after 2.3 years affixed to bridge piers in El Surà and El Salto. The 1-m-long pieces were oriented vertically such that the low portion was sunken in sediment, the middle portion was nearly always submerged, and the top was above the water surface at base flows but submerged 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.

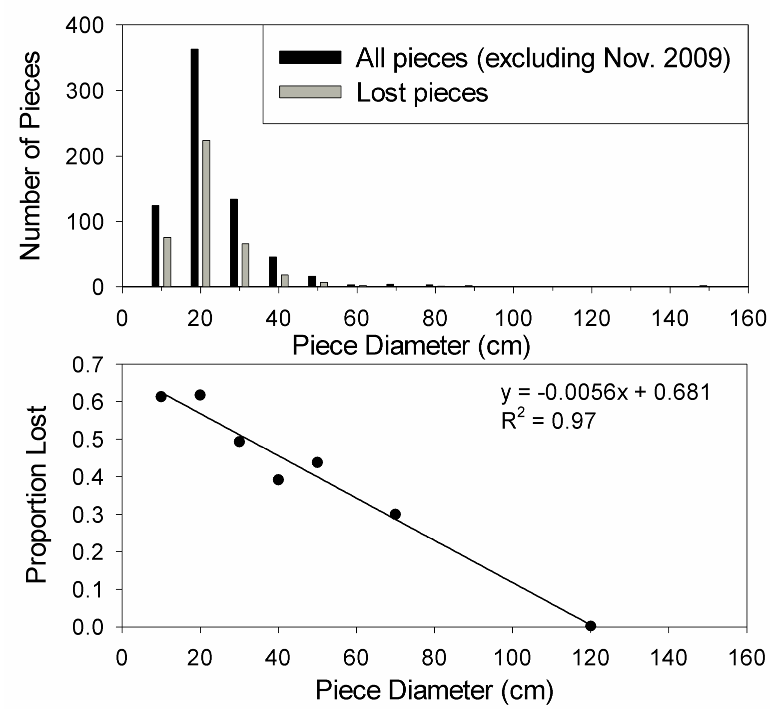

Figure 3.7. Diameter distribution of all measured pieces (excluding those first observed in November 2009) and pieces that were transported out of the study reaches, and the proportion of pieces lost by diameter class. November 2009 pieces were excluded because there was no opportunity to observe transport of these pieces.

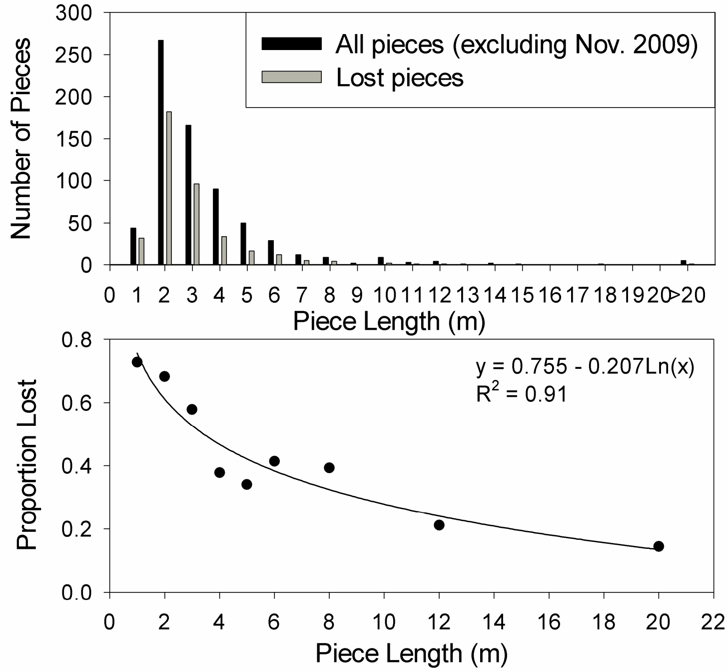

Figure 3.8. Length distribution of all measured pieces (excluding those first observed in November 2009) and pieces that were transported out of the study reaches, and the proportion of pieces lost by length class. November 2009 pieces were excluded because there was no opportunity to observe transport of these pieces.

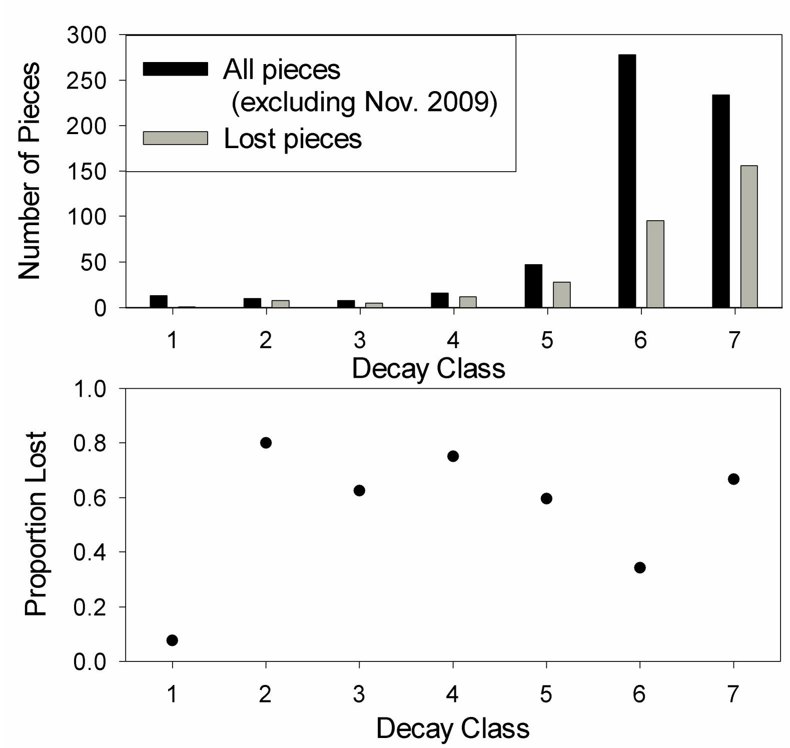

Figure 3.9. Decay class distribution of all measured pieces (excluding those first observed in November 2009) and pieces that were transported out of the study reaches, and the proportion of pieces lost by decay class. November 2009 pieces were excluded because there was no opportunity to observe transport of these pieces.

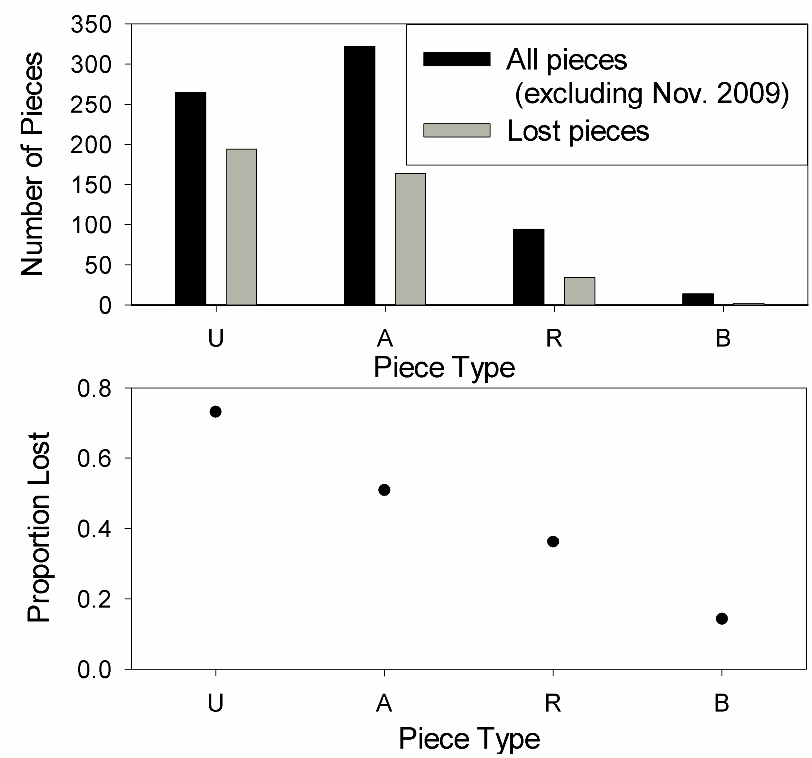

Figure 3.10. Piece type distribution of all measured pieces (excluding those first observed in November 2009) and pieces that were transported out of the study reaches, and the proportion of pieces lost by type. U=unattached, A=attached, R=ramp, B=bridge (see methods section for type description). November 2009 pieces were excluded because there was no opportunity to observe transport of these pieces.

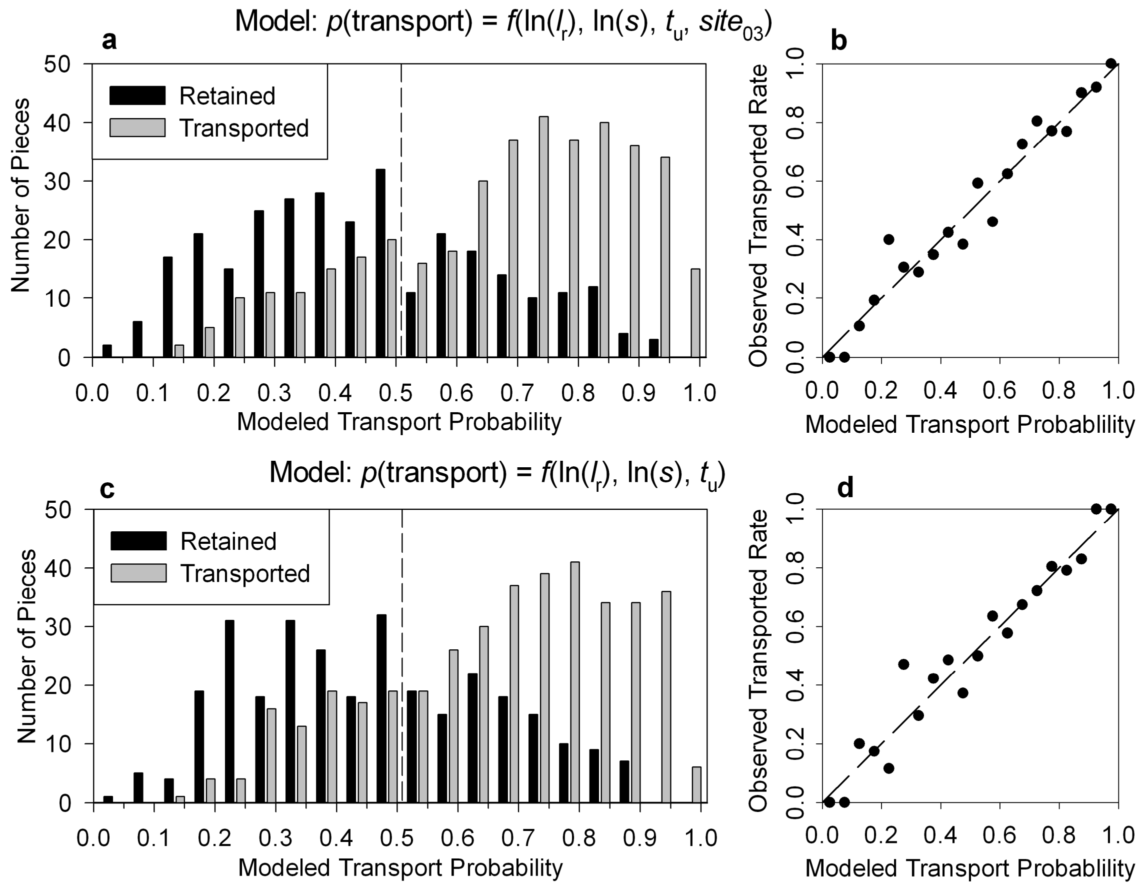

Figure 3.11. a) Results of the best model that includes categorical site variables. The continuous variables in this model are the natural log of relative piece length (l_r, piece length divided by channel width) and the natural log of stream gradient (s), and the categorical variables are whether the 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.

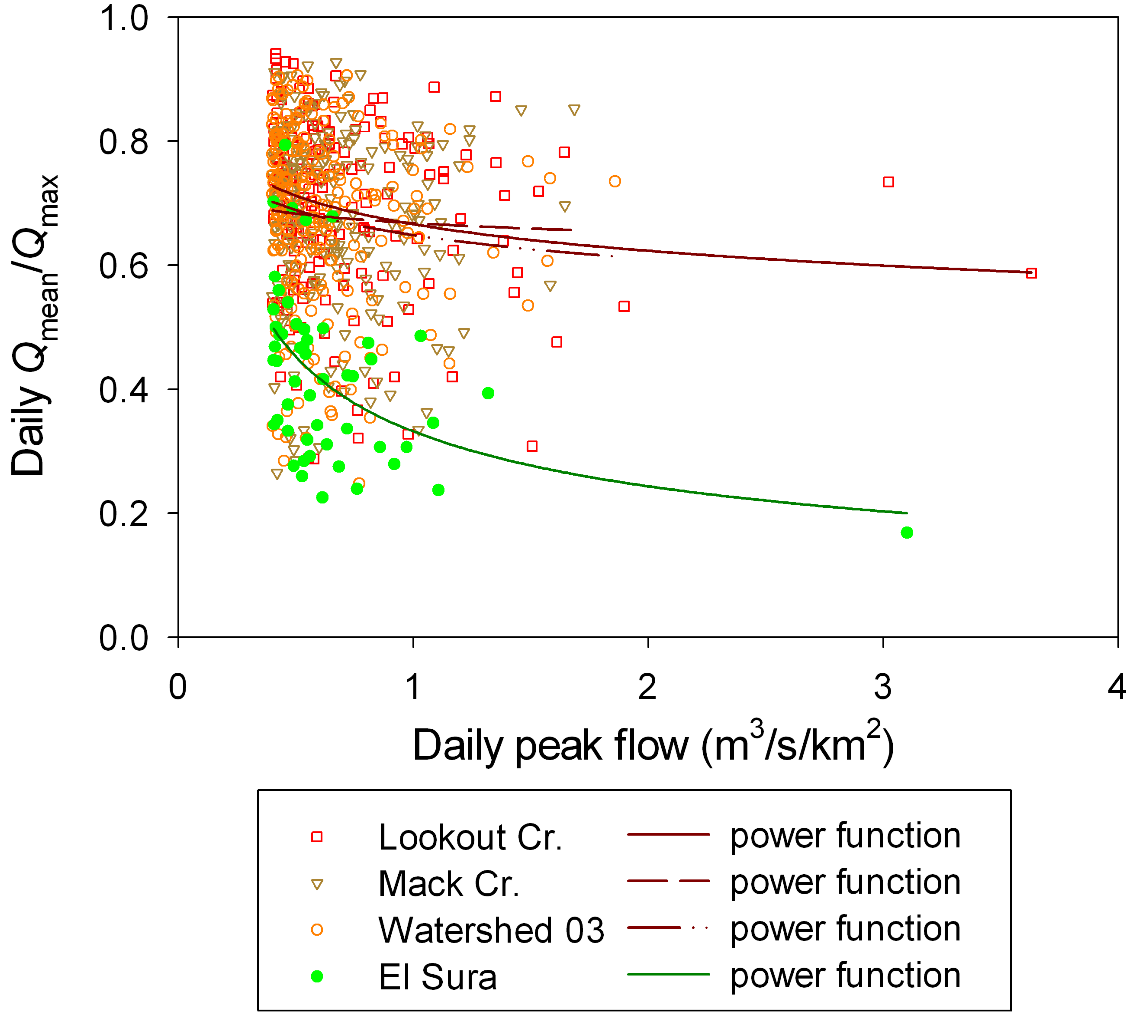

Figure 3.12. Ratio of Q_{mean}/Q_{max} for all days with peak flow > 0.4 $m^3/s/km^2$. Note that all three streams in HJ Andrews Experimental Forest (Lookout Cr., Mack Cr, and Watershed 03) had similar trends in spite of the wide range of drainage areas (62.40 km^2 5.81 km^2 and 1.01 km^2 respectively). In contrast, El Surà 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 that a day and that the flood was flashy. The largest El Surà 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.

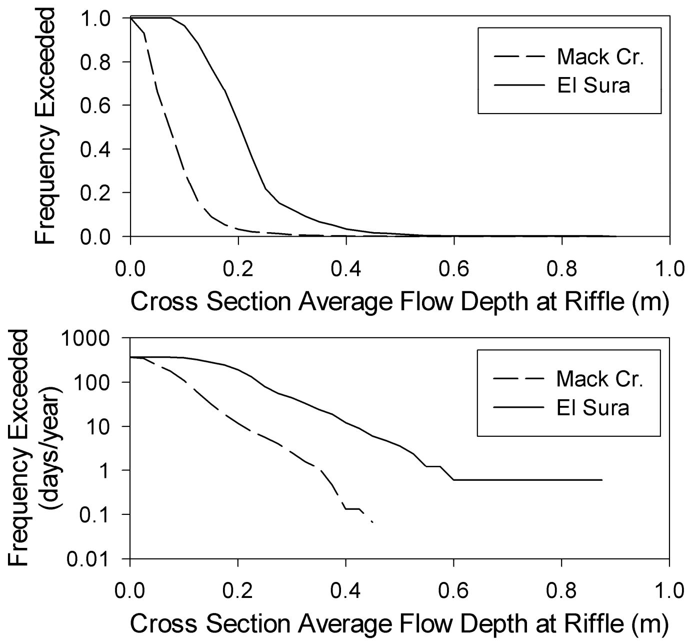

Figure 3.13. Proportion of days for which average depth over a riffle exceeds a given value. Depth was calculated from discharge records using surveyed cross sections and the Mannings equation. The Mannings *n* coefficient was visually estimated at Mack Cr., in HJ Andrews Experimental Forest, Oregon (*n* = 0.07), and calibrated to match measured stage and discharge at El Surà, in La Selva Biological Station, Costa Rica (*n* = 0.08).

4 FLOW RESISTANCE

4.1 Introduction

The quantification and prediction of flow resistance is valuable to our understanding of streams, in large part because of its relationship with sediment transport. If velocity is uniform, the energy generated as water flows downstream is partitioned between friction (i.e., flow resistance) and sediment transport, with gains to one resulting in losses to the other (Knighton, 1998). There are multiple ways to subdivide friction. One possible division is into external resistance, such as bed and bank friction, and internal friction, such as turbulence (Leopold et al., 1964). Another well established partition is into grain resistance and form resistance (e.g., Einstein and Barbarossa, 1952; Millar, 1999), where grain resistance encompasses the skin friction and turbulence caused by individual grains (Parker and Peterson, 1980) and form resistance includes the energy loss caused by pressure drag around large scale bed or bank irregularities (Griffiths, 1989). To these two components may be added spill resistance (Leopold et al., 1960), which is the energy lost in the hydraulic jumps and turbulence associated with plunging flows common in steep channels with step-pool morphology (Comiti et al., 2009).

The components of flow resistance (grain, form, spill, wood) are commonly treated as linearly additive (Einstein and Barbarossa, 1952; Millar, 1999; Comiti et al., 2009), although flume experiments reveal significant interactions between grain, form, and wood resistance that call this assumption into question (Wilcox and Wohl, 2006). Increasing discharge will in many cases reduce the contribution of individual roughness elements to flow resistance as the elements affect a smaller proportion of the total flow (e.g., Comiti et al., 2009). In this way high flows are doubly important in transporting sediment and shaping channel morphology: they have higher energy from the increased discharge and more of the energy is available for sediment transport.

Wood can also be an important component of total channel roughness and flow resistance (Buffington and Montgomery, 1999; Manga and Kirchner, 2000; Curran and Wohl, 2003; Faustini and Jones, 2003). The hydraulic effects of wood are extremely complicated and not readily predictable. The effects of an individual wood piece depend on the blockage caused by the wood and the respective distances between the wood and the water surface and the wood and the streambed; for wood near the water surface, resistance increases as the Froude number increases, whereas for wood near the streambed, pieces with a diameter much greater than bedform or grain roughness exert a greater influence (Hygelund and Manga, 2003; Mutz, 2003). The effects also vary with time in channels with readily deformable boundaries; drag force decreases with time in sand-bed channels, for example, as the channel erodes around the wood (Wallerstein et al., 2001). The effects of wood accumulations depend on the arrangement, density, and mobility of the wood (Daniels and Rhoads, 2004; Daniels and Rhoads, 2007; Manners et al., 2007).

The work summarized in this chapter builds on the observations of wood dynamics in the preceding chapters by attempting to evaluate the geomorphic importance of wood in headwater tropical streams as compared to temperate zone streams. Wood in the Costa Rican study streams is similar to many temperate streams in terms of total load (see Chapter 2), but is more transient than wood in many temperate zone streams, potentially leading to reduced geomorphic effectiveness (see Chapter 3). A possible contributing factor to this reduced wood residence time is the prevalence of high magnitude, short duration floods. This flow regime likely impacts channel organization, grain size distribution, wood distribution, and therefore flow resistance, by altering the channel to be coarser bedded and rougher and concentrating wood load into low energy sites near the channel margins during floods. Because the recovery time between floods is short relative to the temperate zone, the morphology created during high flows will persist as the dominant form.

I hypothesize that discharge, grain size, bed form, and wood load will individually and collectively be predictors of flow resistance in headwater streams in Costa Rica (H_1). I selected these variables because they represent the primary divisions of resistance documented by previous studies (grain, form, spill, and wood), with the exception of spill resistance, which is excluded from the hypothesis because there is no plunging flow in four of the six study reaches, and only minimal plunging flow in the other two. Discharge was included because of its documented influence on the partition of energy between resistance and sediment transport. Alternately, I hypothesize that flow resistance will be best predicted by gradient, discharge, and wood load, in declining order of importance, based on previous studies in headwater streams of Colorado (David et al., 2010) (H_2). I also hypothesize that values of flow resistance will be lower in the Costa Rican streams than in analogous temperate zone streams (H_3) because of the transience of wood and the potential for wood to be transported during high flows and then deposited along channel margins during the falling limb of floods, rather than remaining in the central portions of the channel and substantially increasing boundary roughness and turbulence.

In order to test these hypotheses I collected a total of 32 flow resistance measurements from six stream segments at a variety of discharges. Regressions of resistance against discharge, mean grain size, variation in thalweg elevation, and wood load were used to test H_1. To evaluate the predictive value of this idealized variable set, I compared it with best subset models selected from a broader variable set using standard statistical criteria. Because previous research has indicated the presence of interaction effects among the variables in the *a priori* model (Wilcox and Wohl, 2006), I also analyzed the data to find statistically significant interaction regression terms. The results presented here represent the first published analysis of the effects of instream wood on hydraulic resistance in headwater tropical streams.

4.2 Study Site

Research was conducted at six of the 50-m-long study reaches within La Selva Biological Station (Figure 4.1). Of the six study sites where flow resistance was measured, three are located on Quebrada Esquina, which forms the eastern boundary of La Selva, two are on El Surà, which drains 4.8 km^2 of La Selva and Braulio Carillo, and one is on the Taconazo, a tributary of El Surà (Figure 4.1). The two lowest elevation sites (Taco 01 and Sura 03, Figure 4.1) are on the floodplain of the Rìo Puerto Viejo and backflooding is observed at these sites when the larger rivers flood. These two sites have sandy beds, whereas the three Esquina sites (Esquina 17, 20, and 21) are gravel-cobble bedded, and the higher Surà site (Sura 05) is boulder dominated (Table 4.1). Flood hydrographs at gaged streams at La Selva tend to be flashy.

4.3 Methods

I selected six representative study reaches from 10 reaches for which wood load was monitored for 3 years (see Chapter 3), which were themselves selected as representative of 30 reaches for which wood load was initially measured (see Chapter 2). The reaches were selected to cover the full range of bed material size and gradient observed at La Selva. All reaches were approximately 50 m in length. Flow resistance data were collected using field surveys and salt slug discharge and velocity measurements. Flow resistance was measured at as broad a range of stages as possible during the field campaigns and each study reach was measured from 4 to 8 times. At the time of each resistance measurement, water surface width (w) was surveyed in five locations and average water surface slope (S) was calculated using these same ten spatial data points. Conductivity probes set to a sampling frequency of 1 Hz were used to track the passage of a slug of salty water that was introduced to the stream about 50 m upstream of the top of the reach. One probe was placed at the top of the reach and one at the bottom. The harmonic mean travel time of the salt slug to each probe was calculated (Calkins and Dunne, 1970; Waldon, 2004), and the difference in mean times was divided by the reach length to find reach average flow velocity (V). Discharge (Q) was calculated using the known mass of salt added to the stream and the integral of salt concentration as a function of time derived from the conductivity probe data. Reach average cross-sectional area (A) was calculated from continuity as QV^{-1}, and reach average depth (d) was calculated as $QV^{-1}w^{-1}$. Two measures of flow resistance were calculated, the Darcy-Weisbach friction factor (ff) and the Manning's n coefficient (n):

$$ff = 8gdSV^{-2} \qquad (1)$$

and

$$n = R_h^{2/3} S^{1/2} V^{-1} \qquad (2)$$

where g is acceleration due to gravity (9.8 m/s^2) and R_h is hydraulic radius. I calculated R_h as AP^{-1}, where P is wetted perimeter. I assumed a rectangular cross section in the estimate of P, so that P=w+2d. Detailed cross section surveys indicate that this estimate of P may underestimate the actual value by as much as 6% in the boulder-bed reaches, but by less than 1% in the sand-bed reaches.

Wood within the bankfull limits of each stream was surveyed prior to each flow resistance measurement. The length and midpoint diameter of each piece were measured, and the volume of each piece was calculated assuming a cylindrical form. Total wood volume was divided by channel area to find wood load (W_A) in units of m^3/m^2. Wood was included in the survey if it was in or above the bankfull channel as identified visually by bank slope changes and vegetation distribution. Wood that was not in contact with the water during any given flow measurement is not expected to alter flow dynamics. The wood volume data were post-processed to remove 'bridged' pieces that were suspended over the water surface and 'ramped' pieces that rested on the bank above the water surface at the time of each flow measurement, resulting in a reduced in-flow wood load value (W_{Ai}), also in units of m^3/m^2.

Surface grain characteristics were quantified for each reach. One hundred clasts were randomly sampled, and the intermediate diameter was measured. Mean diameter (D_{ave}) and the 84th percentile of the grain size distribution (D_{84}) were found. Sorting of the surface sediment was calculated as the inclusive graphic standard deviation in phi units of the 100 sampled clasts (s_{sd}) (Folk, 1980). A thalweg survey was performed once for each reach and the root mean square error of the bed elevation relative to the average bed slope was calculated as a measure of bed form roughness (T_{RMSE}).

Multiple regression models of *ff* and *n* were tested using the R statistical software package. I first tested the *a priori* model, with the predictor variables Q, T_{RMSE}, D_{ave}, and W_{Ai}, for significance and for significant two-way interactions among variables. I did not extend the analysis to higher order interactions because of the small sample size (n = 32). I then conducted a best subsets test of the predictor variables Q, T_{RMSE}, D_{ave}, D_{84}, R_h/D_{84}, s_{sd}, W_A, W_{Ai}, width to depth ratio (w:d), and their two-way interactions. V, d, and S were not used as predictor variables because they are used to calculated *ff* and *n*. Subset models were evaluated using the Bayesian Information Criterion (BIC) (Schwarz, 1978), in order to select parsimonious variable subsets. Only models in which all parameter estimates were significant at the p<0.1 level were considered. Models that included variable combinations with high variance inflation factors (VIF) were excluded for failing assumptions of non-collinearity. For example, D_{ave} and D_{84} were collinear and so were not allowed in a subset together.

To better constrain the contribution of each variable to the predictive power of the model, I standardized the variables by subtracting the mean and dividing by the standard deviation. In regressions using standardized variables, parameter values will be roughly comparable, with larger absolute values indicating higher influence. I also calculated the coefficients of partial determination (e.g., $R^2_{Y\ X1\ |\ X2\ X3 \ldots Xi}$) for each model component, which indicates how much each component improves the model. The value of $R^2_{\ |}$ is equivalent to the coefficient of simple determination between the two variables to the left of the bar in the subscript when their linear relationships with the variables to the right of the bar have been accounted for.

In addition to modeling the full data set, I also modeled a sample that included one low-flow measurement from each site, a sample that included one high-flow measurement from each site, and a sample limited to the measurements taken at site Sura 05 (n = 6, 6, and 8, respectively). The three smaller data sets were limited to a maximum of 2 predictor variable because of their very small sample size. These smaller data sets were analyzed in order to isolate intra-stream variation and inter-stream variation, in case one was so dominant as to mask trends in the other within the full data set.

4.4 Results

Calculated values of ff varied from 0.17 to 12.16 and values of n varied from 0.029 to 0.297, both of which tended to decrease at a site with increasing discharge (Figure 4.2). Both W_A and W_{Ai} were fairly constant at each site through time (Table 4.1). Two sites had sand-dominated bed material. The mean grain size at the other four sites ranged from 73-435mm. Average water surface slopes range from 0.003-0.032.

The best single predictor of flow resistance was Q within a site and D_{84} between sites (Figure 4.2, Figure 4.3). Best subset multiple regression analysis found that for the site Sura 05 data set, the simple regression against Q had the lowest BIC value. For the low flow data set, the best regression subset was also a single variable, D_{ave}. Analysis of the high-flow data set yielded significant two parameter models, the best of which included D_{ave} and s_{sd} and had a coefficient of multiple determination (R^2) value of 0.93. Higher values of ff were associated with higher values of D_{ave} and lower values of s_{sd}. Although both parameter estimates were significant at the 0.05 level, it is possible that the inclusion of sorting in this model is spurious due to the very small sample size. In each case, the best model subsets were the same when modeling *ff* or *n*.

For the full data set *a priori* models, regressing *ff* and *n* against Q, D_{ave}, T_{RMSE}, and W_{Ai}, both models have highly significant p-values, all < 0.01, and multiple R^2 values of 0.78 and 0.81 (Table 4.2, Table 4.3). Standardized regression parameters and coefficients of partial determination ($R^2_{|}$) suggest that D_{ave} is the most influential component by a wide margin, with $R^2_{ff\ D\mathrm{ave}\ |\ Q\ T\mathrm{rmse}\ W\mathrm{ai}}$ equal to 0.74 and $R^2_{n\ D\mathrm{ave}\ |\ Q\ T\mathrm{rmse}\ W\mathrm{ai}}$ equal to 0.78. There is only one significant two-way interaction that can be added to the *ff* model, between D_{ave} and Q, and no significant interactions for the *n* model. This interaction increases model R^2 to 0.83 for the *ff* model, and the parameter estimate is negative, suggesting that for streams with large bed material the reduction in *ff* with rising Q is steeper than for streams with small bed material. Or, at low flows the increase in *ff* caused by increasing D_{ave} is steeper than at high flows. It should be noted that this model has a lower BIC than any subset without interactions. The results thus partially support H_1; although Q, grain size, bedform dimensions, and wood load do correlate significantly with flow resistance, very little explanatory power is gained by including bedform dimensions and wood load.

The alternate regression using the variables S, Q, and W_{Ai} was less successful (Table 4.4). The R^2 value for the *ff* model was 0.21, and for the *n* model was 0.18. The results thus do not support H_2; S, Q, and wood are not the best predictors of resistance, in contrast to the findings of David et al. (2010) for headwater streams in the Colorado Rocky Mountains.

The *a priori* models for *ff* and *n* compare favorably with the models chosen using exhaustive best subset testing, with BIC as the selection criterion. The best variable subset for *ff* used the variables D_{ave}, Q, w:d, and the interaction $D_{\text{ave}} \times Q$, and the best subset for *n* included Q, w:d, D_{ave}, T_{RMSE}, and W_{Ai} (Table 4.5, Table 4.6). However, in both cases the w:d parameter had a negative sign, which is counterintuitive, suggesting that wider, shallower channels have lower flow resistance than narrower, deeper channels. Therefore, I also found the best subsets excluding w:d from the analysis. For *ff* this limited best subset included the variables D_{ave}, Q, T_{RMSE}, s_{sd}, and the interaction $D_{\text{ave}} \times Q$ (Table 4.7). For *n*, the limited best subset included the variables D_{ave}, Q, T_{RMSE}, and s_{sd} (Table 4.8). The variables Q, s_{sd}, and $D_{\text{ave}} \times Q$ had negative parameters, and the variables T_{RMSE}, and D_{ave} had positive parameters.

Comparing these more complex models with the simple regressions of *ff* and *n* against D_{ave} reveals significant improvement in model R^2, from values near 0.65 for the simple regressions (Figure 4.4) to values ranging from 0.78-0.89 for the more complex regressions. A basic interaction model for *ff* using D_{ave}, Q, and $D_{\text{ave}} \times Q$ has a model R^2 of 0.78 (Table 4.9), close to the level achieved using the more complex models, but modeling *n* with this basic interaction only yielded a model R^2 of 0.70.

The gradients of Esquina 17 overlap with those of the plane-bed segments of Reid and Hickin (2008) in the temperate zone. The measured range of *ff* values (0.2-12.2) are lower than the highest values measured for the temperate streams (20-53 on 3 of the 10 cross sections most comparable to the La Selva study sites), but coincide well with the range for the remaining 7 cross sections (0.7-18). Although this represents a very limited test of H_3, this comparison indicates partial support of the hypothesis.

4.5 Discussion

Most variation in flow resistance was explained by variation in grain size and discharge and their interaction. Wood load variables were occasionally selected in best subset models, but in spite of significant parameter estimates they added very little explanatory power, and in some cases the variation explained by wood was explained just as well or better by other variables such as s_{sd}. Thus there is very limited support for wood playing a significant role in controlling flow resistance in these streams.

There is a possibility that some variables that were included in the models were spurious, with statistically significant relationships being found by chance. Although I employed the BIC to avoid inclusion of spurious variables, the small sample size may have undermined this effort. The fact that w:d was found to be an important component of highly predictive models, but with a parameter value that indicates that flow resistance decreases as w:d increases, suggests that the sample size might be too small to accurately characterize flow resistance across the range of measured conditions. And the nearly equal performance of models which interchanged uncorrelated variables suggests that variation among so few sites was easily explained. Yet the parameters associated with the variables Q, s_{sd}, T_{RMSE}, D_{ave}, D_{84}, and W_{Ai}, make intuitive sense, which supports the validity of the analysis. The significance of all parameters in the significant models discussed here had p-values less than 0.05, in most cases less than 0.005, also supporting the validity of the analysis. Even if the regressions with four or more variables are legitimate, s_{sd}, T_{RMSE}, and W_{Ai} explain only a very small proportion of flow resistance variation relative to Q and D_{ave}.

The study streams are best described as pool-riffle in morphology. There is one bedrock step in reach Esquina 17 and one boulder step in reach Sura 05 at low flows, but none in the other four reaches. Wood in the study streams does not form steps with plunging flow, which is the best-studied mechanism by which wood increases flow resistance (Curran and Wohl, 2003; MacFarlane and Wohl, 2003; Wilcox and Wohl, 2006). Any flow resistance induced by wood in the La Selva study streams will be from form drag, skin friction, or redirection of flow toward the bed or banks. As noted in the introduction, the flow resistance caused by wood in sand-bed streams decreases as the channel erodes around the wood (Wallerstein et al., 2001; Wallerstein and Thorne, 2004), which may help to explain why the sand-bed segments Taconazo 01 and Sura 03 had relatively low *ff* values despite having values of W_{Ai} that were approximately double those of the other channel segments (0.02-0.05 W_{Ai} versus 0.01-0.02, respectively). Interpretation of the parameters in the *a priori* models suggests that increasing wood load by 0.01 m^3/m^2 will increase *ff* by about 1.2 and *n* by about 0.03, all else being equal. As a reference for this scale of change in wood load, average W_{Ai} in the six study reaches ranged from 0.011 to 0.046 m^3/m^2, and an increase in 0.01 m^3/m^2 is equivalent to adding four logs with a diameter of 0.25 m and a length of 5 m to the narrowest stream, or sixteen such logs to the widest stream.

The finding of minimal wood contribution to flow resistance contrasts with work done in a spring-fed stream in Oregon, USA (Manga and Kirchner, 2000), where it was estimated that wood contributes half the flow resistance. The differing findings may be attributable to the differing natures of the study sites. The spring-fed stream had minimal bed elevation variation, median grain sizes between 10-30 mm, average bed slope of

0.0035, an approximate width of 25-30 m, a much larger width to depth ratio than any of the Costa Rican streams, and wood that was uniformly oriented perpendicular to flow and typically suspended in the water column, although that wood was estimated to cover < 2% of the streambed (Manga and Kirchner, 2000). These features will tend to increase the proportion of resistance attributable to wood relative to the La Selva study streams. Additionally, this study covers a broader range of bed material conditions than wood load conditions, and the relatively large magnitude of the bed and grain effects may mask the wood effects. Perhaps a study design that minimizes inter-site variation in bed form and grain size would find statistical models more dependent on wood load.

An alternate possibility is that wood in tropical streams is relatively less important to flow resistance because of its transience. If the channel is organized by high flows and wood is mobile at high flows, then wood may have a smaller role than the immobile fraction of the bed material. Likewise, wood is liable to be redeposited in low-energy channel zones in streamlined positions, both of which would reduce drag and flow resistance. I did not measure flow resistance at any discharges that approach the annual flood, so I have little direct knowledge of channel-forming flows. For example, in three years of monitoring stage at the site Sura 05, the highest recorded stage was 1.4 m, which I estimated to represent a discharge of 10 m^3/s, but the highest stage during a flow resistance measurement there was 0.53 m, with a measured discharge of 0.64 m^3/s. However, within the limitations of the dataset, it appears that wood is not a primary contributor to flow resistance in these headwater streams.

In this context, it is interesting to compare the results of Reid and Hickin's (2008) work in plane-bed channels in Canada from which wood is largely absent. The *ff* values from seven of the ten cross sections with gradients comparable to Esquina 17 lie in a similar range to the estimated *ff* values for Esquina 17. These cross sections have very similar values for D_{50} and D_{84}, d, average velocity, and grain resistance calculated using the Millar and Quick (1994) equation, although they tend to be wider (Reid and Hickin, 2008). The fact that the wood present in Esquina 17 does not produce notably higher *ff* values than those for the Canadian plane-bed channels suggests that this wood makes a relatively minor contribution to total resistance.

4.6 Conclusions

The statistical regression that I hypothesized would best explain variation in flow resistance, using the variables D_{ave}, Q, T_{RMSE}, and W_{Ai} performed very well, with statistically significant parameter estimates, but was not the best model found using the full set of measured explanatory variables. When supplemented with an interaction term between Q and D_{ave}, the *a priori* model explained 82% of the variation in *ff*. In comparison, the best subset model, which selected the variables D_{ave}, Q, $w{:}d$, and $D_{ave} \times Q$, explained 89% of the variation in *ff*. Grain size was the most influential component of all the statistical models. Wood was not found to be a dominant component of flow resistance, whereas previous studies in streams of the temperate zone have found it to be very important (e.g., Manga and Kirchner, 2000; Wilcox and Wohl, 2006). This may be because of the small range of wood loads in the study streams relative to the wide ranges of flow and bed material, but it also may reflect the fact that frequent high flows mobilize wood so that the channel is adjusted to maximize energy dissipation by other mechanisms. Determining which of these alternative explanations is more appropriate requires further data on flow resistance in relation to wood load and other channel characteristics from both temperate and tropical headwater streams.

4.7 Tables

Table 4.1. Flow resistance, bed surface material, and wood data for all runs.

(shown on next page)

Site	Date (mo/day/yr)	w (m)	d (m)	$w{:}d$ ratio	S (m/m)	V (m/s)	A (m^2)	Q (m^3/s)	ff	n	T_{RMSE} (m)	D_{ave} (mm)	D_{84} (mm)	R_h / D_{84}	s_{sd} (φ)	W_A (m^3/m^2)	W_{Ai} (m^3/m^2)
Taco 01	7/9/2007	2.3	0.14	16	0.0032	0.127	0.33	0.042	2.27	0.1137	0.110	2.00	2	64.2	0.60	0.116	0.023
Taco 01	3/4/2009	2.5	0.12	20	0.0021	0.122	0.30	0.036	1.31	0.0853	0.110	2.00	2	55.2	0.60	0.107	0.019
Taco 01	6/20/2009	1.8	0.09	20	0.0035	0.089	0.16	0.014	3.04	0.1233	0.110	2.00	2	40.3	0.60	0.147	0.027
Taco 01	11/13/2008	1.8	0.09	21	0.0025	0.081	0.16	0.013	2.54	0.1128	0.110	2.00	2	39.7	0.60	0.143	0.026
Sura 03	7/6/2007	7.9	0.46	17	0.0023	0.390	3.64	1.420	0.54	0.0676	0.126	1.00	1	414.0	0.70	0.042	0.040
Sura 03	7/16/2007	7.6	0.48	16	0.0024	0.245	3.63	0.888	1.49	0.1127	0.126	1.00	1	423.1	0.70	0.043	0.042
Sura 03	11/21/2008	7.3	0.32	23	0.0023	0.317	2.31	0.734	0.56	0.0657	0.126	1.00	1	291.4	0.70	0.048	0.047
Sura 03	11/13/2008	6.9	0.36	19	0.0023	0.285	2.53	0.722	0.79	0.0794	0.126	1.00	1	329.8	0.70	0.051	0.049
Sura 03	3/3/2009	7.8	0.27	29	0.0031	0.327	2.15	0.702	0.62	0.0682	0.126	1.00	1	256.3	0.70	0.045	0.043
Sura 03	6/18/2008	6.9	0.41	17	0.0032	0.246	2.80	0.689	1.70	0.1175	0.126	1.00	1	365.5	0.70	0.056	0.054
Sura 05	7/6/2007	7.8	0.35	22	0.0098	0.235	2.74	0.643	4.92	0.1986	0.111	434.50	630	0.513	1.45	0.017	0.016
Sura 05	11/19/2009	6.8	0.33	21	0.0119	0.197	2.20	0.433	7.86	0.2469	0.111	434.50	630	0.472	1.45	0.027	0.026
Sura 05	11/18/2008	7.0	0.29	24	0.0124	0.201	2.04	0.410	7.01	0.2308	0.111	434.50	630	0.428	1.45	0.021	0.020
Sura 05	7/16/2007	7.0	0.29	24	0.0107	0.171	2.05	0.351	8.46	0.2538	0.111	434.50	630	0.431	1.45	0.019	0.018
Sura 05	3/3/2009	7.2	0.28	26	0.0113	0.170	2.02	0.345	8.53	0.2538	0.111	434.50	630	0.414	1.45	0.019	0.018
Sura 05	11/21/2008	6.6	0.24	27	0.0126	0.168	1.62	0.272	8.49	0.2479	0.111	434.50	630	0.360	1.45	0.022	0.021
Sura 05	11/15/2008	6.8	0.25	28	0.0127	0.142	1.68	0.238	12.16	0.2974	0.111	434.50	630	0.364	1.45	0.022	0.021
Sura 05	6/19/2009	7.2	0.19	37	0.0117	0.121	1.40	0.169	12.07	0.2880	0.111	434.50	630	0.292	1.45	0.018	0.017
Esq 17	3/7/2009	4.9	0.16	32	0.0309	0.494	0.77	0.383	1.56	0.0993	0.176	204.75	350	0.421	1.57	0.014	0.012
Esq 17	7/8/2007	4.5	0.19	24	0.0317	0.400	0.83	0.333	2.90	0.1378	0.176	204.75	350	0.492	1.57	0.018	0.016
Esq 17	6/19/2008	4.5	0.12	37	0.0325	0.221	0.54	0.120	6.33	0.1929	0.176	204.75	350	0.329	1.57	0.017	0.015
Esq 17	11/19/2008	3.8	0.15	26	0.0313	0.189	0.55	0.104	9.93	0.2454	0.176	204.75	350	0.386	1.57	0.020	0.017
Esq 20	3/7/2009	5.9	0.29	21	0.0049	0.458	1.68	0.768	0.52	0.0620	0.209	72.65	110	2.363	1.31	0.013	0.013
Esq 20	7/8/2007	6.4	0.30	21	0.0079	0.239	1.94	0.463	3.27	0.1574	0.209	72.65	110	2.500	1.31	0.010	0.010
Esq 20	6/21/2009	5.4	0.10	57	0.0094	0.340	0.51	0.174	0.60	0.0579	0.209	72.65	110	0.836	1.31	0.014	0.014
Esq 20	6/19/2008	5.8	0.16	36	0.0114	0.180	0.92	0.166	4.41	0.1683	0.209	72.65	110	1.373	1.31	0.011	0.010
Esq 20	6/24/2008	5.9	0.17	35	0.0110	0.166	0.99	0.165	5.27	0.1856	0.209	72.65	110	1.452	1.31	0.011	0.010
Esq 20	11/19/2008	5.1	0.15	34	0.0111	0.208	0.76	0.157	3.02	0.1375	0.209	72.65	110	1.282	1.31	0.012	0.011
Esq 21	3/7/2009	6.3	0.17	37	0.0082	0.663	1.07	0.711	0.25	0.0403	0.077	120.90	220	0.730	1.52	0.024	0.015
Esq 21	6/21/2009	6.3	0.07	93	0.0073	0.480	0.42	0.203	0.17	0.0291	0.077	120.90	220	0.300	1.52	0.024	0.015
Esq 21	11/19/2008	5.9	0.10	61	0.0078	0.298	0.57	0.171	0.67	0.0613	0.077	120.90	220	0.427	1.52	0.026	0.016
Esq 21	6/24/2008	4.8	0.09	52	0.0074	0.347	0.44	0.154	0.44	0.0492	0.077	120.90	220	0.404	1.52	0.030	0.019

Table 4.2. Hypothesis 1 model: *ff* as a linear combination of D_{ave}, Q, T_{RMSE}, and W_{Ai}

Variable	parameter estimate	p-value	standardized parameter est.	VIF	Partial R^2	
intercept	-2.35	0.129	--	--	--	
D_{ave}	0.0203	<0.0001	0.95	1.37	$R^2_{ff\ Dave\ \mid\ Q\ Trmse\ Wai}$:	0.75
Q	-4.42	0.0019	-0.39	1.57	$R^2_{ff\ Q\ \mid\ Dave\ Trmse\ Wai}$:	0.31
T_{RMSE}	25.2	0.0071	0.31	1.37	$R^2_{ff\ Trmse\ \mid\ Dave\ Q\ Wai}$:	0.24
W_{Ai}	115	0.0065	0.39	2.18	$R^2_{ff\ Wai\ \mid\ Dave\ Q\ Trmse}$:	0.24

Model statistics: R^2 = 0.78, Adjusted R^2 = 0.75, p-value <0.00001

Table 4.3. Hypothesis 1 model: *n* as a linear combination of D_{ave}, Q, T_{RMSE}, and W_{Ai}

Variable	parameter estimate	p-value	standardized parameter est.	VIF	Partial R^2	
intercept	-0.0623	0.118	--	--	--	
D_{ave}	0.000466	<0.0001	1.00	1.37	$R^2_{n\ Dave\ \mid\ Q\ Trmse\ Wai}$:	0.79
Q	-0.0894	0.0024	-0.35	1.57	$R^2_{n\ Q\ \mid\ Dave\ Trmse\ Wai}$:	0.29
T_{RMSE}	0.722	0.0004	0.40	1.37	$R^2_{n\ Trmse\ \mid\ Dave\ Q\ Wai}$:	0.37
W_{Ai}	2.90	0.0013	0.45	2.18	$R^2_{n\ Wai\ \mid\ Dave\ Q\ Trmse}$:	0.32

Model statistics: R^2 = 0.81, Adjusted R^2 = 0.78, p-value <0.00001

Table 4.4. Hypothesis 2 model: *ff* as a linear combination of S, Q, and W_{Ai}

Variable	parameter estimate	p-value	standardized parameter est.	VIF	Partial R^2	
intercept	3.20	0.104	--	--	--	
S	145	0.074	0.35	1.30	$R^2_{ff\ S\ \mid\ Q\ Wai}$:	0.11
Q	-2.69	0.261	-0.23	1.49	$R^2_{ff\ Q\ \mid\ S\ Wai}$:	0.04
W_{Ai}	8.29	0.900	0.03	1.75	$R^2_{ff\ Wai\ \mid\ S\ Q}$:	0.001

Model statistics: R^2 = 0.21, Adjusted R^2 = 0.13, p-value 0.075

Table 4.5. Best subset model: *ff* as a linear combination of D_{ave}, Q, w:d, and $D_{ave}\times Q$. Variables were standardized to better enable parameter comparison

Variable	parameter est. (stand.)	p-value	VIF	Partial R^2	
intercept	-0.09	0.174	--	--	
D_{ave}	0.74	<0.0001	1.03	$R^2_{ff\ Dave\ \mid\ Q\ w:d\ Dave\times Q}$:	0.82 [1]
Q	-0.74	<0.0001	2.73	$R^2_{ff\ Q\ \mid\ Dave\ w:d\ Dave\times Q}$:	0.64 [1]
w:d	-0.35	<0.0001	1.16	$R^2_{ff\ w:d\ \mid\ Dave\ Q\ Dave\times Q}$:	0.48
$D_{ave}\times Q$	-0.61	<0.0001	2.44	$R^2_{ff\ Dave\times Q\ \mid\ Dave\ Q\ w:d}$:	0.51

Model statistics: R^2 = 0.89, Adjusted R^2 = 0.87, p-value <0.00001

[1] The reduced model does not individually include both variables used in the interaction term.

Table 4.6. Best subset model: *n* as a linear combination of D_{ave}, *Q*, *w*:*d*, T_{RMSE}, and W_{Ai}. Variables were standardized to better enable parameter comparison

Variable	parameter est. (stand.)	p-value	VIF	Partial R^2	
intercept	0	--	--	--	
D_{ave}	0.92	<0.0001	1.58	$R^2_{n\ Dave\ \mid\ Q\ w:d\ Trmse\ Wai}$:	0.80
Q	-0.38	0.0003	1.59	$R^2_{n\ Q\ \mid\ Dave\ w:d\ Trmse\ Wai}$:	0.40
$w:d$	-0.30	0.0014	1.38	$R^2_{n\ w:d\ \mid\ Dave\ Q\ Trmse\ Wai}$:	0.33
T_{RMSE}	0.29	0.0046	1.73	$R^2_{n\ Trmse\ \mid\ Dave\ Q\ w:d\ Wai}$:	0.27
W_{Ai}	0.30	0.0201	2.93	$R^2_{n\ Wai\ \mid\ Dave\ Q\ w:d\ Trmse}$:	0.19

Model statistics: R^2 = 0.87, Adjusted R^2 = 0.84, p-value <0.00001

Table 4.7. Best subset model excluding *w*:*d*: *ff* as a linear combination of D_{ave}, *Q*, T_{RMSE}, and s_{sd}, and $D_{ave}\times Q$. Variables were standardized to better enable parameter comparison

Variable	parameter est. (stand.)	p-value	VIF	Partial R^2	
intercept	-0.08	0.253	--	--	
D_{ave}	1.09	<0.0001	2.24	$R^2_{ff\ Dave\ \mid\ Q\ Trmse\ Ssd\ Dave\times Q}$:	0.81 [1]
Q	-0.61	<0.0001	2.51	$R^2_{ff\ Q\ \mid\ Dave\ Trmse\ Ssd\ Dave\times Q}$:	0.55 [1]
T_{RMSE}	0.26	0.0020	1.25	$R^2_{ff\ Trmse\ \mid\ Dave\ Q\ Ssd\ Dave\times Q}$:	0.31
s_{sd}	-0.42	0.0004	2.27	$R^2_{ff\ Ssd\ \mid\ Dave\ Q\ Trmse\ Dave\times Q}$:	0.39
$D_{ave}\times Q$	-0.53	0.0002	2.39	$R^2_{ff\ Dave\times Q\ \mid\ Dave\ Q\ Trmse\ Ssd}$:	0.43

Model statistics: R^2 = 0.88, Adjusted R^2 = 0.85, p-value <0.00001

[1] The reduced model does not individually include both variables used in the interaction term.

Table 4.8. Best subset model excluding *w*:*d*: *n* as a linear combination of D_{ave}, *Q*, T_{RMSE}, and s_{sd}

Variable	parameter est. (stand.)	p-value	VIF	Partial R^2	
intercept	0	--	--	--	
D_{ave}	1.21	<0.0001	2.25	$R^2_{n\ Dave\ \mid\ Q\ Trmse\ Ssd}$:	0.80
Q	-0.20	0.0176	1.07	$R^2_{n\ Q\ \mid\ Dave\ Trmse\ Ssd}$:	0.19
T_{RMSE}	0.38	0.0002	1.25	$R^2_{n\ Trmse\ \mid\ Dave\ Q\ Ssd}$:	0.41
s_{sd}	-0.52	0.0001	2.27	$R^2_{n\ Ssd\ \mid\ Dave\ Q\ Trmse}$:	0.43

Model statistics: R^2 = 0.84, Adjusted R^2 = 0.81, p-value <0.00001

Table 4.9. Simple interaction model: *ff* as a linear combination of D_{ave}, *Q*, and $D_{ave}\times Q$

Variable	parameter est. (stand.)	p-value	VIF	Partial R^2	
intercept	-0.08	0.390	--	--	
D_{ave}	0.75	<0.0001	1.03	$R^2_{ff\ Dave\ \mid\ Q\ Dave\times Q}$:	0.72 [1]
Q	-0.56	0.0004	2.42	$R^2_{ff\ Q\ \mid\ Dave\ Dave\times Q}$:	0.37 [1]
$D_{ave}\times Q$	-0.52	0.0022	2.38	$R^2_{ff\ Dave\times Q\ \mid\ Dave\ Q}$:	0.29

Model statistics: R^2 = 0.78, Adjusted R^2 = 0.76, p-value <0.00001

[1] The reduced model does not individually include both variables used in the interaction term.

4.8 Figures

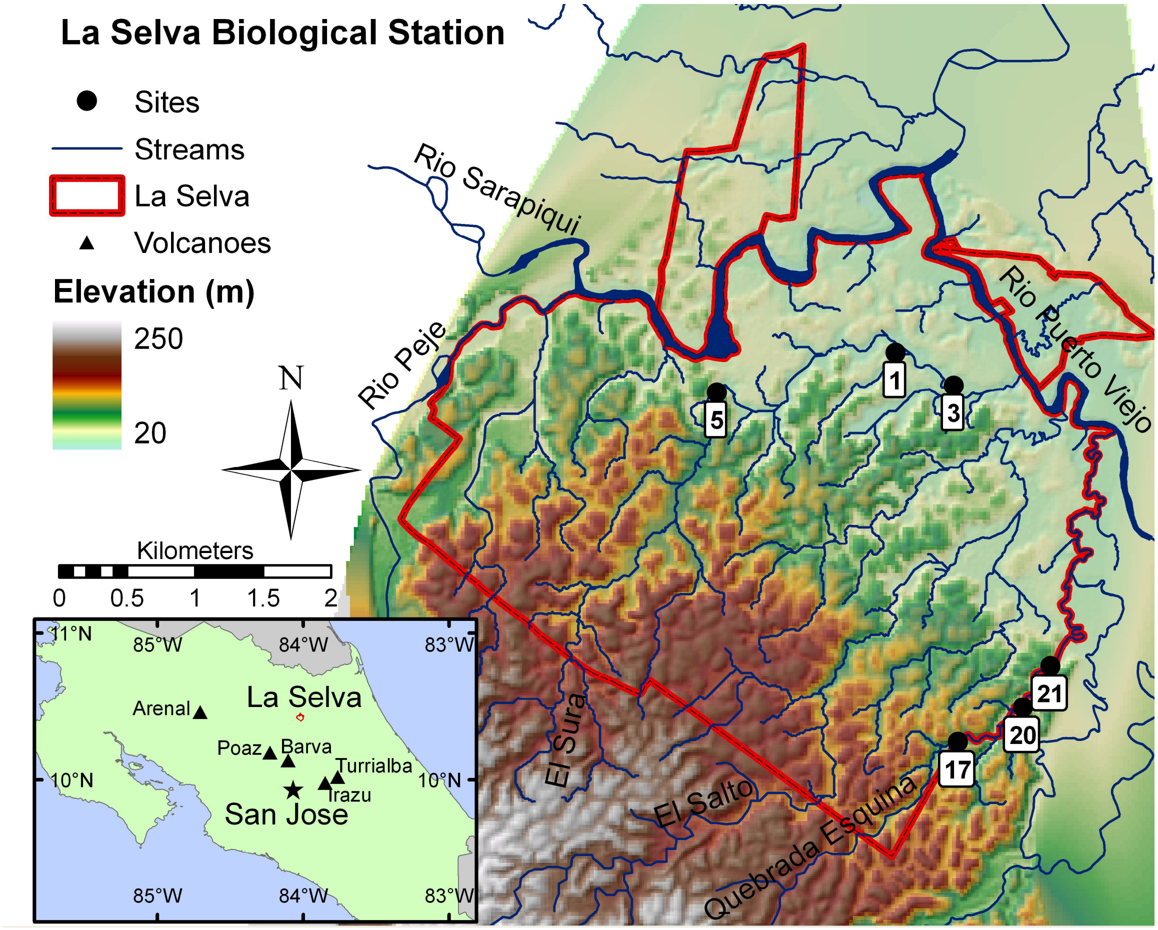

Figure 4.1. Site map showing location of the six flow resistance study reaches. Each is 50 m long.

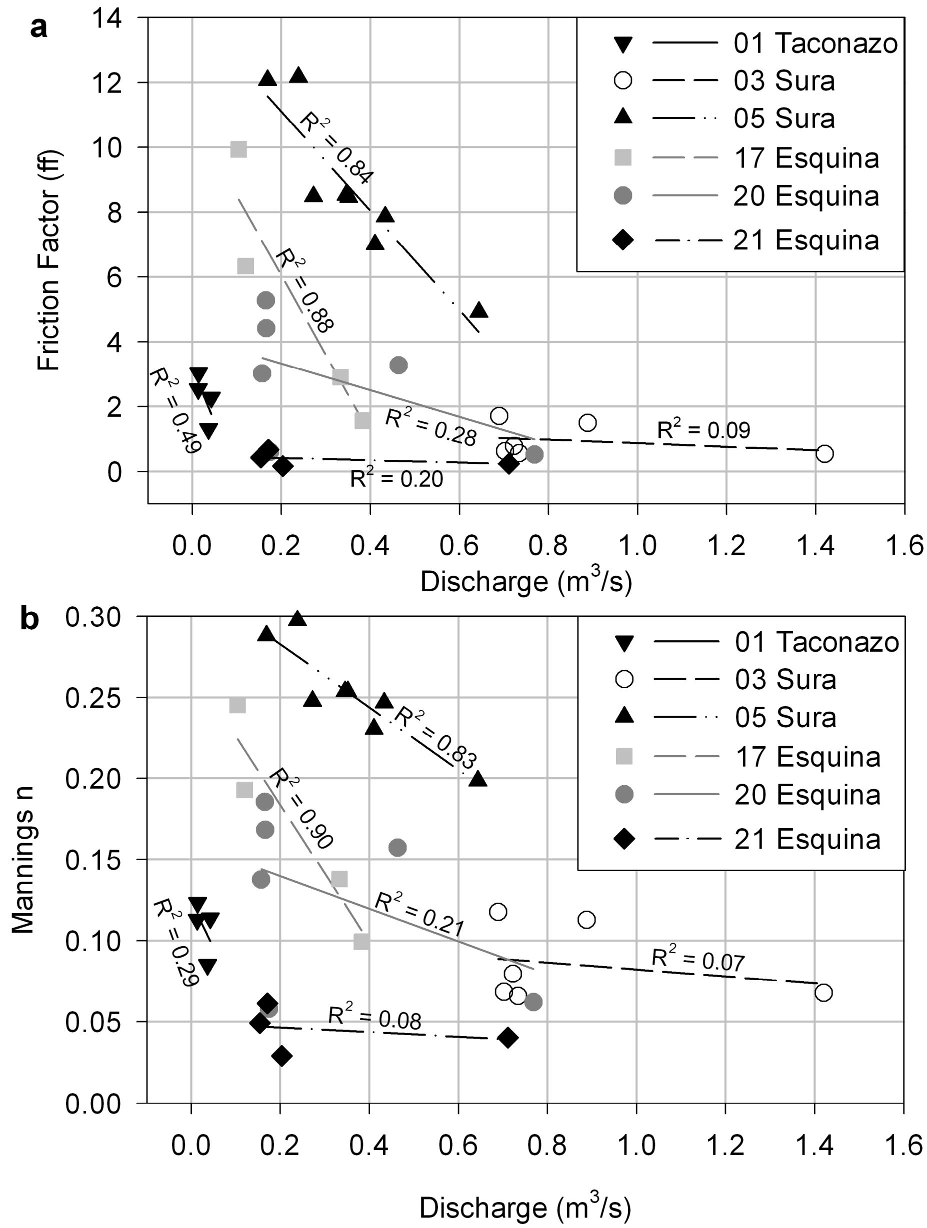

Figure 4.2. A) Variation of friction factor (*ff*) with discharge. B) Variation of Mannings *n* with discharge.

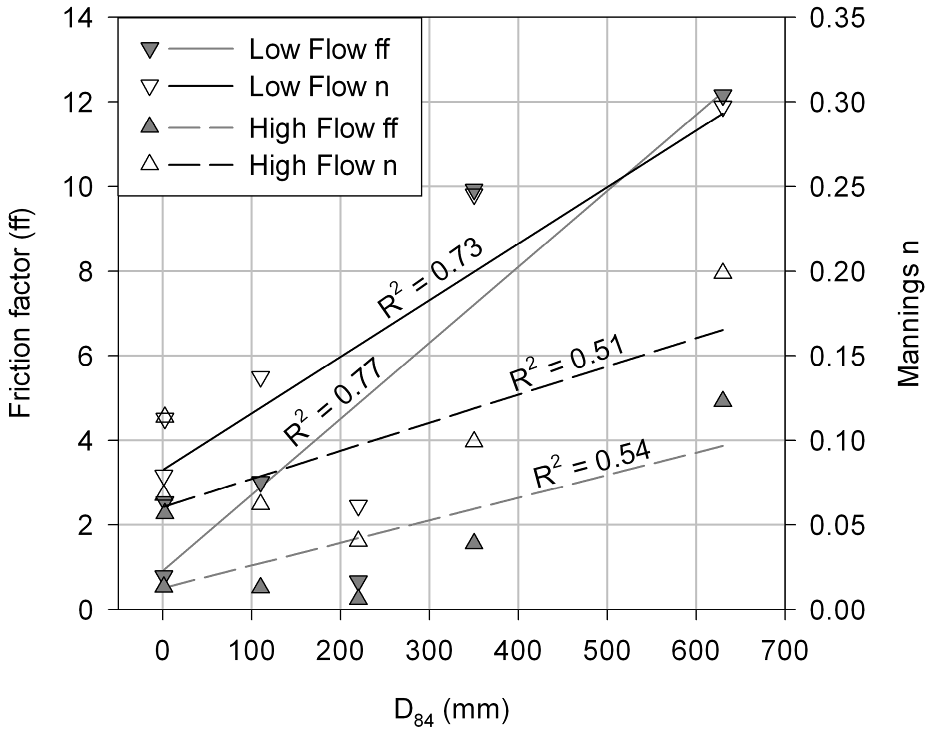

Figure 4.3. Variation of friction factor (*ff*) and Mannings *n* with D_{84}.

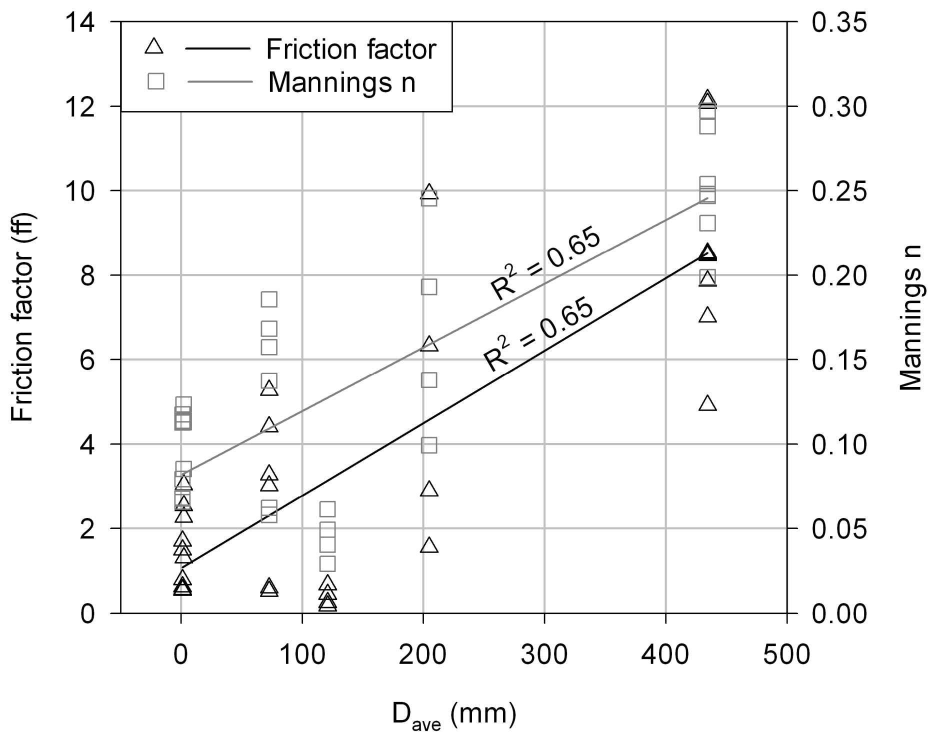

Figure 4.4. Full data set *ff* and *n* variation with D_{ave}.

5 COARSE SEDIMENT MOVEMENT NEAR A JAM

5.1 Introduction

Wood has been entering and modifying channels for more than 400 million years (Montgomery and Piégay, 2002), yet human impacts have altered this dynamic. In historical times, humans have reduced global forest cover to about half its maximum Holocene extent, and harvested all but a fraction of the world's aboriginal forests. Also, most management efforts, until very recently, focused on removing wood from channels to facilitate navigation, increase flood conveyance, or for use as fuel. Modern forests still cover almost a third of Earth's land surface, and many channels, especially low-order channels, contain significant wood loads. Nonetheless, the prevalence of anthropogenic instream wood reduction has the potential to increase sediment mobility and yield because wood increases flow resistance (Keller and Tally, 1979b; Curran and Wohl, 2003; MacFarlane and Wohl, 2003; Daniels and Rhoads, 2004; Wilcox and Wohl, 2006), reducing the energy available for sediment transport, and forms jams, which act as barriers to sediment movement and create low-velocity backwater storage locations (Keller and Swanson, 1979; Lisle, 1995; Abbe and Montgomery, 1996; Brooks et al., 2003; Comiti et al., 2008). In most of these studies, wood has been observed to affect channel morphology through its effect on sediment mobility. An extreme example of increased sediment storage are forced alluvial reaches (Montgomery et al., 1996; Massong and Montgomery, 2000; Montgomery et al., 2003b). In forced alluvial reaches jams alter the relationship between sediment supply, transport capacity, and channel type, initiating sedimentation where degradation to bedrock would otherwise occur.

A major mechanism by which wood interacts with sediment transport is the trapping of sediment behind jams, as documented in studies throughout the temperate zone. Log obstructions in seven 1st to 3rd order streams in central Idaho, USA stored 13 m^3/km of sediment on average, and 2-16 times the annual sediment yield in total (Megahan, 1982). Log steps are estimated to store a total of 15,600 m^3 of sediment in 13 5th order stream basins in the central Coast Range of Oregon, USA, which is estimated to represent 123% of the mean annual sediment yield from these basins (Marston, 1982). Wood jams store 26.1 m^3 of sediment in a 412-m-long reach of a 3rd order stream with a bedrock channel in central Vermont, USA, which is about 1.5 times the sediment stored in riffles (Thompson, 1995). In an alluvial stream in southwestern Australia that drains a 187 km^2 basin, wood was estimated to cause 5700 m^3 of sediment storage within the 715-m-long study reach, or about 49% of the total sediment stored in the reach (Webb and Erskine, 2003). In a 3rd order stream in the Cascade Range of Oregon, comparison of a logged reach with no large wood jams, versus an upstream unlogged reach with numerous large wood jams, found net cross-section scour in the logged reach averaging 1.5 m^2, but no net scour in the unlogged reach and >3 m^2 of cross section fill behind jams following a 25-year flood (Faustini and Jones, 2003). Wood jams in three 3rd order mountain streams in the southern Andes trap approximately 1000 m^3/km, which is of the same order of magnitude as the annual sediment yield (Comiti et al., 2008). Fisher et al. (2010) document greater frequency of sediment storage sites and increased sediment volumes and storage times in reaches with wood on the Ducktrap River in Maine, USA.

Synthesizing across all of these studies, one can roughly generalize that wood jams in small temperate streams double in-stream sediment storage and impound sediment volumes exceeding the mean annual sediment yield.

The longitudinal spacing, size, and average longevity of jams in a given system are expected to be major controls on the ability of wood to reduce sediment transport. Jams may be persistent features even in streams where wood is relatively transient, in part because they are commonly anchored by immobile ‘key pieces’ that may take tens to hundreds of years to decay (Abbe and Montgomery, 1996) and in part because the feature may persist even as individual pieces are exchanged (Gregory et al., 1985; Wohl and Goode, 2008). Annual flood flows commonly modify jams and cause secondary piece exchange, but jams typically persist until the key piece decays and breaks. Some jams persist for decades, although even the largest jams are susceptible to removal during large flows (Wohl and Goode, 2008). In the New Forest of southwest England, 20% of jams on the Highland Water persisted for 30 years, but 36% were removed within one year (Gregory et al., 1985; Sear, pers. comm. 2010). In Idaho, over half of all log obstructions persisted less than 1 year, and approximately 5% persisted over 6 years (Megahan, 1982). Jam frequency is also variable in the temperate zone, and may decrease with increasing drainage area (Martin and Benda, 2001). Observed jam frequencies in minimally disturbed low-order streams include values of 10-60 jams/km in Britain (Gurnell and Sweet, 1998), 19-55 jams/km in the southern Andes (Comiti et al., 2008), 10-30 jams/km in central Idaho (Megahan, 1982), 10-53 jams/km in Michigan (Morris et al., 2007), and 54 jams/km in the Colorado Rocky Mountains (Wohl and Cadol, in review). Variation in the definition of a jam makes comparison problematic, but the range of variability in most studies overlaps in the 10-60 jams/km range.

The ability of wood in tropical settings to alter sediment dynamics may be reduced relative to the temperate zone because of differences in prevailing jam characteristics. Wood in our study site is more transient than in comparable temperate zone streams. Wood transience in tropical streams is likely attributable to higher discharge per unit of contributing area and higher decay rates relative to temperate zones. Key pieces are expected to be equally affected by these controls that increase transience, and thus jam transience is also expected to be high in the tropics. Reduced jam residence time may in turn reduce either the volume or duration of wood-induced sediment storage. Likewise, low jam frequencies may reduce sediment storage. Seven channel-spanning jams were found in 600 m of surveyed streams at La Selva Biological Station, Costa Rica, creating an average of 12 jams/km, which is at the lower end of the range observed in the temperate zone.

The use of tracer clasts to study sediment movement in gravel-bed streams is well established (e.g., Church and Hassan, 1992; Foster et al., 2000). Haschenburger and Rice (2004) used magnetic tracer clasts to study sediment movement around three jams on Vancouver Island, Canada.

In order to evaluate one aspect of the influence of wood on sediment transport in tropical streams, I monitored tracer clasts, scour chains, and wood piece locations in the vicinity of a channel-spanning wood jam on a small channel in Costa Rica from June 2007 to November 2009. I tested two hypotheses relating to the impact of the jam on sediment transport. The first hypothesis (H_1) is that clast position with respect to the jam will have the greatest influence on transport distance. Although I expect flow history and clast size will affect clast transport distance (Church and Hassan, 1992; Haschenburger and Rice, 2004), I hypothesize that clast position with respect to the jam will be a more influential variable. The second hypothesis (H_2) is that morphological changes to the jam will increase sediment transport. I hypothesize that periods with high rates of piece turnover in the jam correlate to increased rates of sediment passage through the jam, and that alterations to jam structure, density, or key piece location influence upstream clast mobility.

5.2 Study Site

The study site is located on Quebrada Esquina, in La Selva Biological Station, Costa Rica (Figure 5.1). At the study site, Quebrada Esquina drains 1.6 km^2 of preserved old-growth tropical wet forest and has an average gradient of 3.2%. Bed-material particles range from coarse sand to boulders, with a mean grain size of 205 mm and 84th percentile size of 350 mm. The inclusive graphic standard deviation, a measure of sorting (Folk, 1980), is 1.57 phi. Particles are moderately rounded and frequently have concave depressions, knobs, and necks or waists. Channel morphology varies between step-pool and pool-riffle (Montgomery and Buffington, 1997) (Figure 5.2). The bedrock at La Selva consists of highly weathered andesitic lava flows, with the basin upstream of the study site being composed almost entirely of the Esquina Andesite (Alvarado, 1990, in Kleber et al., 2007). Bedrock outcrops are common in the stream bed and banks near the study site. The upper meter of bedrock is typically weathered into a weak saprolite and the clasts that compose the bedload are also weakened by weathering. The bed clasts could not be used to drive rebar into gravel; even 20 cm diameter cobbles broke in half after a few strikes.

Discharge was measured at a site approximately 650 m downstream of the study site. Stage data were collected by a pressure sensor at 15-minute intervals and converted to discharge using a rating curve based on 6 salt-slug discharge measurements. Discharge data are only available from March 2008 to September 2008 and from February 2009 to June 2009 because of frequent failure of the pressure sensor. Flow depth exceeded 1 m four times in the first monitored period and twice in the second, with a maximum measured depth of 1.25 m on June 3, 2008. These 6 events occurred on days with 75-160 mm of rainfall, as measured at a meteorological tower approximately 2.5 km from the gage. There were 15 days in 2009 when 24-hour rainfall exceeded 75 mm, the greatest being July 18, when 217 mm fell in 24 hours. Base flow stage at the gage site was approximately 0.2 m. Flood hydrographs are extremely flashy (Figure 5.3) with baseflow maintained by groundwater and declining only slowly between floods.

5.3 Methods

A channel-spanning jam on the gravel-bedded Quebrada Esquina was selected (). The site was visited at approximately 4-month intervals to survey clast and log locations and to check for scour at the installed scour chains. Tracers clasts were introduced in two distinct groups. The first set, introduced in July 2007, consisted of 80 painted clasts between 28-220 mm and 19 in-stream boulders that were marked with paint spots. The second set, introduced in November 2008, consisted of 90 unpainted clasts ranging in size from 26 to 200 mm. All clasts smaller than 220 mm were also marked with brightly colored flagging labeled with a unique number. Flagging was used because paint did not dry on the clasts because of the frequent rain and nightly condensation. Flagging was cut to limit the loose ends beyond the knot used to tie the flagging to the clast, but the presence of flagging does have the potential to exert a greater influence on the drag of individual clasts, and therefore clast movement, than does paint or other forms of marking clasts. I did not drill holes and insert magnets or radios into clasts because the intense weathering of the clasts would likely have caused any clast smaller than a medium boulder to disintegrate under such treatment. Tracer clasts were removed from the bed, marked, and then returned to the same section of the study reach from which they came. Clasts were emplaced in a 20 m reach above the jam, adjacent to the jam, and in a 5 m reach below the jam. In subsequent visits I surveyed the location of all clasts that were visible on the bed surface. The search for clasts extended from the emplacement areas to a depositional zone at the head of a mid-channel island 55 m below the jam, beyond which a bend obscured the channel from the survey instrument location.

I installed 1-m-long scour chains by loosely attaching the chain end to a piece of rebar, driving it into the channel bed, and removing the rebar. I was able to install 2 scour chains to depths of 60 cm and 70 cm in localized gravel bars (). Most of the channel bed was too coarse to install chains, and even where surface gravel was present, coarse material or bedrock were frequently hit within 20 cm of the surface, suggesting that scour during high flows is also limited by very coarse or immobile substrate.

All wood pieces were surveyed during each site visit. Logs were flagged and numbered so that individual piece retention could be determined. The length and diameter of pieces were recorded and used to calculate total wood volume. Retention rates were calculated for wood pieces and wood volume. There were three key pieces to the jam, each 35 cm in diameter, and ranging from 4-9 m in length. The movement of these three pieces was considered separately from the rest of the pieces in the jam, and indicated structural changes in the jam. Jam density was calculated by dividing the total wood volume by the volume of the macro-scale shape of the jam (Thevenet et al., 1998; Gurnell et al., 2000a; Andreoli et al., 2007). The jam was best described as a triangular prism, thus the length, average height, and base width were estimated from the 3-dimensional survey data taken during each site visit.

Hypothesis 1 (transport distance correlates with clast position relative to the jam) was tested by analyzing correlations between distance travelled by recovered clasts and the potential control variables grain size, peak 24-hour rainfall, and placement location. In these analyses, peak 24-hour rainfall is used as a surrogate for flow because the discharge record was incomplete, but it did show a good correlation between daily rainfall and flood stage. Correlations between recovery rate and the three control variables were also investigated because distance traveled by recovered clasts may not be a reliable measurement of mobility. The distance traveled is an average distance traveled only for clasts that were recovered, but the moderate to low recovery rates cause this metric to be unstable. For example, very few gravel sized clasts that were placed downstream of the jam in the second set were recovered. Those that were recovered had been placed on a stable bar and did not move, and the average travel distance for this class of clasts was less than a meter. However, the majority of the downstream gravel clasts were not recovered and it is likely they were transported out of the reach. Thus, distance traveled may not be a good indicator of mobility in this case.

Hypothesis 2 (morphological changes to the jam increase sediment transport) was tested by comparing jam density and the retention rate of wood pieces in the jam to the transport-related clast parameters, distance travelled and recovery rate. In calculating the transport parameters in this case, I limited the analysis to the clasts placed upstream of the jam. I then compared mobility of the upstream clasts with those placed beside and below the jam. Jam density was estimated by dividing the volume of the wood in the jam by the volume of a triangular prism that approximated the dimensions of the jam. Wood volume in the jam was calculated from the length and average diameter of all pieces, assuming that the pieces had the shape of a cylinder. I used thalweg surveys to estimate the volume of a sediment wedge temporarily stored upstream of the jam. The presence of the wedge, flow routing around the jam, and key piece stability also served as qualitative measures of jam density and permeability.

5.4 Results

Distances traveled by tracer clasts that were recovered from the two sets were negatively correlated with clast diameter, with Pearson correlation coefficients (r) of -0.44 for Set 1 and -0.34 for Set 2. The trends are better described with power functions (Figure 5.5). Average distance traveled by recovered clasts was unrelated to peak rainfall between surveys and unrelated to placement location relative to the jam in both sets (Table 5.1, Figure 5.6). Recovery rate may be a better metric of mobility. Recovery rates were higher for larger caliber material (Table 5.1), and in visits subsequent to periods with low to moderate peak rainfalls (Figure 5.7). Recovery was only 4% for gravel and cobbles after the highest flow of the study period in late July 2009. No marked boulder-sized clasts were transported in the two years of monitoring, so recovery was 100%.

Unrecovered clasts may be lost as a result of transport beyond the 50-m-long collection reach, burial, removal of flagging by highly turbulent flow, or clast breakage in transport. The strong relationship between recovery rate and size at all time periods suggests that clasts are lost because of their mobility and supports the idea that lost clasts are generally transported beyond the recovery reach. The strong relationship between rainfall and cobble recovery rate also supports this. However, the lower gravel recovery rate in set 1 compared to set 2 requires an alternate explanation. For these clasts, burial in a sediment wedge that developed upstream of the jam after tracer deployment, a feature that will be discussed below, seems the most likely cause of loss. Using recovery rate as an indicator of mobility indicates that clast size and streamflow control transport, but not position relative to the jam (Table 5.2). The results thus do not support H_1.

All but 9 of the gravel and cobble clasts were eventually lost. Seven of these were beside the jam and two were on the gravel bar just downstream. Low-velocity zones around the jam appear to retain clasts, but delay of passage of clasts through the jam was not documented with the tracer clasts. However, morphological changes observed in the channel do indicate temporary sediment storage behind the jam.

Changes in jam morphology through time appeared to affect sediment transport. The jam was complex, with two outlets (). Each outlet carried the majority of flow at different times during the study. Flow paths evolved as wood pieces were delivered to the jam from upstream. Early in the study, most flow passed under a key piece near the right margin of the jam. Between July and November 2008 this path became blocked with wood and large leaf debris, causing accumulation of a sediment wedge behind the jam and forcing the majority of flow around the left margin of the jam (Figure 5.8). This flow alteration also modified a gravel bar deposited downstream of the jam, dissecting the upstream portion and depositing gravel on the downstream portion, effectively shifting the feature downstream. The flow alteration also increased scour in a pool along a bedrock portion of the left stream bank next to the altered gravel bar. Between March and June 2009, the wood and smaller organic materials that had obstructed the original flow path decayed and were removed, causing a return of flow to the right side of the jam. This caused the sediment wedge to be eroded, and the sediment was transported beyond the jam. Thalweg surveys conducted in March 2007, November 2008, and March 2009 record the formation and removal of the sediment wedge (Figure 5.9). I estimate that the wedge contained about 5 m^3 of sediment. Marked clasts that had not been found on the surface of the bed since the development of the wedge were subsequently found downstream. I infer that they were trapped in the sediment wedge and then released. The jam was finally breached in July 2009 with removal of the key piece on the right side of the jam (Figure 5.8).

Following introduction of the second set of clasts in November 2008, recovery was initially high; 54% and 44% of the non-boulder clasts after 4 and 8 months, respectively. Of the 59 gravel and cobble clasts placed upstream of the jam, within 8 months 25 clasts were lost, 20 were found downstream of the jam or beside the jam, 9 moved but stayed upstream of the jam, and 8 were stationary. However, a large flood prior to the final survey (12 months after emplacement) caused the loss of all but 3 of the upstream clasts and caused the greatest modification to the jam that was observed. A wood piece that was 5.5 m long and 0.35 m in diameter, which had been the key piece on the right side of the jam, was moved to a position leaning high on the other key piece

(Figure 5.8). The clast recovery rate dropped to 4% following this major modification of the jam. All 4 of the clasts recovered in November 2009 were located beside the jam, on river left.

Jam density was nearly constant through time at 0.32, although it dipped to 0.24 in March 2009 as the jam began to deteriorate, but had not yet shrunken in overall dimensions. Jam density has no relation to recovery rate or travel distance of recovered clasts and thus results do not support H_2. The number of wood pieces included in the jam remained fairly constant until November 2008, but individual pieces within the jam had a high turnover rate even during this time period (Table 5.1). Neither recovery rate nor travel distance of recovered clasts had a consistent relationship with jam piece turnover rate. The recovery rates of clasts placed upstream of the jam were similar to those of clasts placed beside and downstream of the jam (collectively referred to as downstream). Trends with peak rainfall are observed both upstream and downstream of the jam for cobble clasts (Figure 5.7b). Recovery rate of gravel clasts placed below the jam in the second set are lower than the trend, as is recovery of gravel clasts placed upstream of the jam in the first set. The downstream clasts may have been transported beyond the recovery reach, whereas upstream clasts may have been lost by burial in the sediment wedge.

Bedrock is close to the channel surface throughout the study reach, thwarting attempts to install scour chains in most locations. I could only install chains on two distinct gravel bars (), to depths of about 70 cm. I observed no scour around the two installed chains, although gravel bar migration was observed in other locations, where 50-

cm-long rebar survey benchmarks which had been driven into a gravel bar were exposed and removed (Figure 5.10).

5.5 Discussion

The initially high recovery rate of the tracer clasts, and the frequent bedrock outcrops, suggest that the layer of actively moving sediment is thin for most floods. The large flood near the end of the study period may have mobilized sediment to bedrock, mixing and burying the tracer clasts, it may have transported the tracer clasts beyond the recovery zone, or it may have removed the flagging used to mark the tracer clasts. Any or all of these processes could have contributed to the 4% recovery rate in the final survey.

The tracer clast data do not support H_1, that placement location is the dominant control on transport distance and mobility. Rather, clast size and flow history appear to control clast movement, as demonstrated in previous studies (Church and Hassan, 1992; Haschenburger and Rice, 2004). There is some anecdotal evidence, however, for sediment transport disruption by the jam. For example, all clasts that survived to the end of the study were located next to the jam in a low-energy zone associated with the leftward flow path around the jam ().

Tracer clast mobility was likewise not correlated to jam density, which leads to rejection of H_2. The development and destruction of a 5-m^3 sediment wedge, however, was clearly related to jam morphology (Figure 5.8). Although the analysis of tracer clast data did not support the hypotheses, the lack of support may be caused by inadequacies in the methodology. More tracer clasts, longer delivery and recovery reaches, better marking techniques, and more frequent sampling may have enabled detection of a transport effect from the jam. For example, Haschenburger and Rice (2004) used over

2000 magnetically marked tracers, excavated in recovery operations, and searched for tracers nearly 2 km beyond the release site. They also found strong correlations among transport distance, clast size, and flow history, however, which supports the validity of my inferences from Quebrada Esquina.

Previous work in gravel-bed channels indicates that clast transport distance is size-dependent when the Shields stresses, τ^*_{50}, are 1.5-2 times the dimensionless critical shear stress of the D_{50}, or τ^*_{c50} (Ferguson and Wathen, 1998; Wilcock and Crowe, 2003; Parker, 2008), conditions which were met during this study on the Quebrada Esquina. Movements of tracer clasts along a bedrock-dominated channel with substantial bed roughness and poorly sorted grains, however, indicated that clast transport distance correlated more strongly with local hydraulic environment, as defined by bed irregularities caused by protruding bedrock, than with clast size (Goode and Wohl, in press), along channel reaches with Manning's *n* coefficients and bed gradients roughly comparable to those at the Quebrada Esquina site. Given the substantial effect of wood on boundary roughness and local variability of bed elevation (Manga and Kirchner, 2000; David et al., 2010), the correlations between bed-surface grain size and hydraulic roughness associated with wood (Buffington and Montgomery, 1999), and documented increases in bedload transport following wood removal (Smith et al., 1993a; Smith et al., 1993b; Assani and Petit, 1995), it is reasonable to expect that wood might also exert a strong influence on clast transport. The relatively poor correlations between clast transport and characteristics of the logjam on Quebrada Esquina, however, suggest that this is not the case. The differences between clast transport patterns in channels with wood- versus bedrock-dominated bed roughness might reflect the ability of wood to respond to hydraulic forces and sediment movement during a single large flow, as opposed to the typically longer response time of bedrock channel features; this could cause the hydraulic effects of the wood to decrease during the higher flows capable of mobilizing coarse bed sediment. I might also have found correlations between clast placement with respect to the logjam and transport distance if I had been able to recover more of the tracer clasts, or if I had also documented transport of comparably sized clasts on a channel reach without a logjam. Based on the results thus far, however, I assume that clast size is the best predictor of transport distance in tropical gravel-bed channels, whether or not wood is present.

5.6 Conclusions

The transience of wood in tropical streams should contribute to lessening the impact of jams on sediment transport relative to the temperate zone. Nonetheless, I hypothesized that jams would have some measurable affect on clast transport rates. However, the tracer clast data do not indicate any alteration of clast mobility by jams. Rather, grain size and flow history controlled both transport distance and recovery rate. Frequent changes in jam morphology did alter channel morphology, forcing deposition of a 5 m^3 sediment wedge that persisted for about one year. But the observation that all gravel and cobble size tracer clasts either passed the jam or were lost suggests that sediment flux is considerably higher than the volume stored in the sediment wedge.

In high-energy locations such as this site, thalweg surveys and sediment size sampling are likely to have better success at documenting jam trapping of sediment than tracer clast studies. In order for tracers to effectively measure sediment flux at La Selva, larger numbers of clasts are probably necessary along with a longer recovery reach and more definitive marking techniques. But, in spite of the limitations of the methods, it appears that sediment flux was only weakly affected by the jam, even when it was most effectively altering flow dynamics.

5.7 Tables

Table 5.1. Clast recovery rate

	First Set (introduced July 07)				Second Set (introduced Nov 08)			
	# of clasts	Recovery Rate			# of clasts	Recovery Rate		
		Nov 07	Mar 08	Jun 08		Feb 09	Jun 09	Nov 09
Gravel (26-64 mm)	50	0.22	0.16	0.16	48	0.46	0.38	0.00
Cobble (65-256 mm)	30	0.63	0.4	0.43	42	0.6	0.52	0.10
Gravel+Cobble	80	0.38	0.25	0.26	90	0.52	0.44	0.04
Boulder [1] (257-1210 mm)	19	1	1	1	19	1	1	1
		Nov 07	Mar 08	Jun 08		Feb 09	Jun 09	Nov 09
Peak 24-hour rainfall (mm)		134	170	175		144	161	217
Jam wood retention rate		0.56	0.78	0.79		0.79	0.92	0.45

[1] The boulders were the same individuals in both tracer clast sets.

Table 5.2. Clast recovery rate by grain size, location, and time period (excluding boulders)

	Set 1	Initial number of tracer clasts				Set 2	Initial number of tracer clasts			
		US	Side	DS	Total		US	Side	DS	Total
<64 mm	Gravel	20	16	14	50	Gravel	32	9	7	48
64-128 mm	Cobble I	8	3	6	17	Cobble I	19	4	5	28
128-256 mm	Cobble II	7	5	1	13	Cobble II	8	4	2	14
	Total	35	24	21	80	Total	59	17	14	90

	Set 1	4 month recovery rate				Set 2	4 month recovery rate			
		US	Side	DS	Total		US	Side	DS	Total
<64 mm	Gravel	0.10	0.38	0.21	0.22	Gravel	0.56	0.33	0.14	0.46
64-256 mm	Cobble	0.73	0.50	0.57	0.63	Cobble	0.59	1.00	0.14	0.60
	Total	0.37	0.42	0.33	0.38	Total	0.58	0.65	0.14	0.52

	Set 1	8 month recovery rate				Set 2	8 month recovery rate			
		US	Side	DS	Total		US	Side	DS	Total
<64 mm	Gravel	0.10	0.31	0.29	0.22	Gravel	0.41	0.44	0.14	0.38
64-256 mm	Cobble	0.33	0.50	0.57	0.43	Cobble	0.48	1.00	0.29	0.55
	Total	0.20	0.38	0.38	0.30	Total	0.44	0.71	0.21	0.46

	Set 1	12 month recovery rate				Set 2	12 month recovery rate			
		US	Side	DS	Total		US	Side	DS	Total
<64 mm	Gravel	0.15	0.13	0.36	0.20	Gravel	0.06	0.00	0.00	0.04
64-256 mm	Cobble	0.40	0.38	0.57	0.43	Cobble	0.04	0.13	0.00	0.05
	Total	0.26	0.21	0.43	0.29	Total	0.05	0.06	0.00	0.04

5.8 Figures

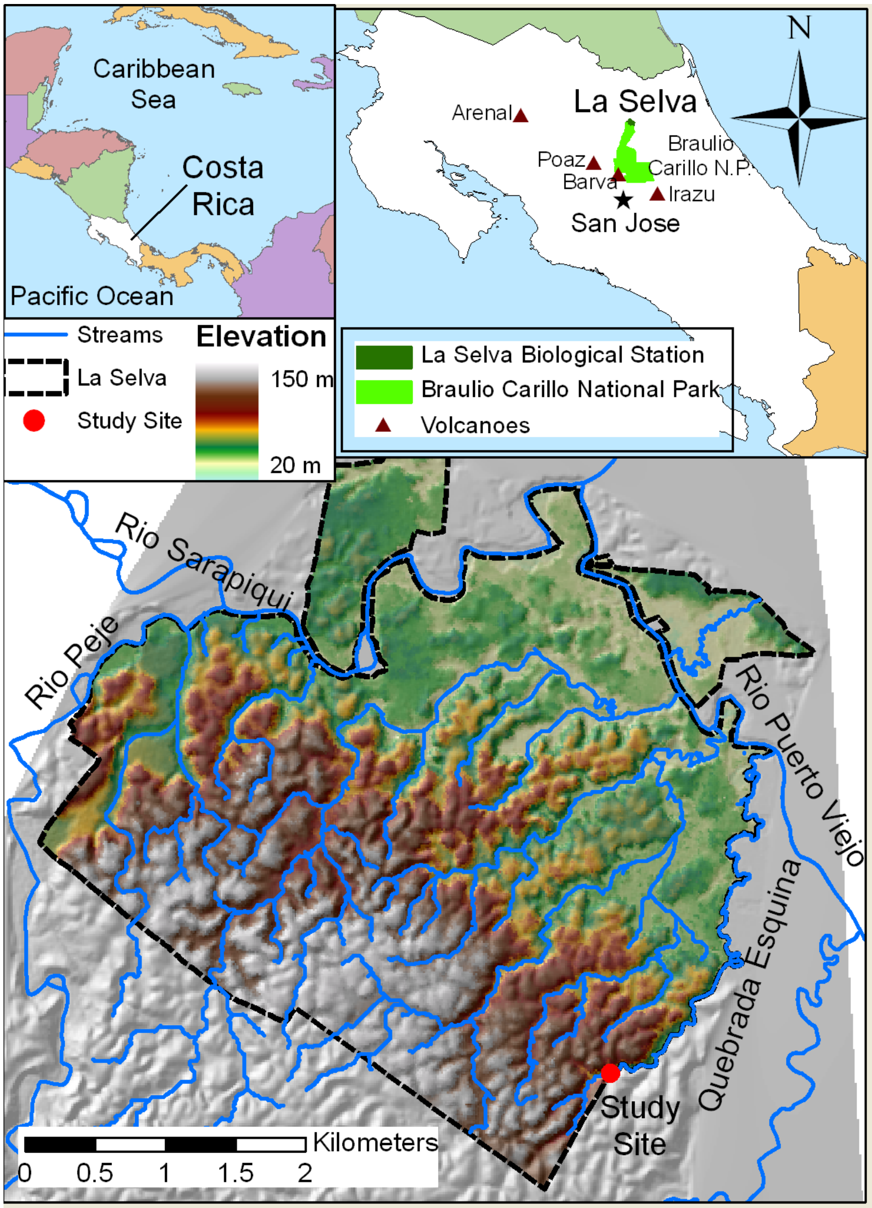

Figure 5.1. Location of study jam.

Figure 5.2. View looking downstream toward the jam. View encompasses most of the upstream clast emplacement reach.

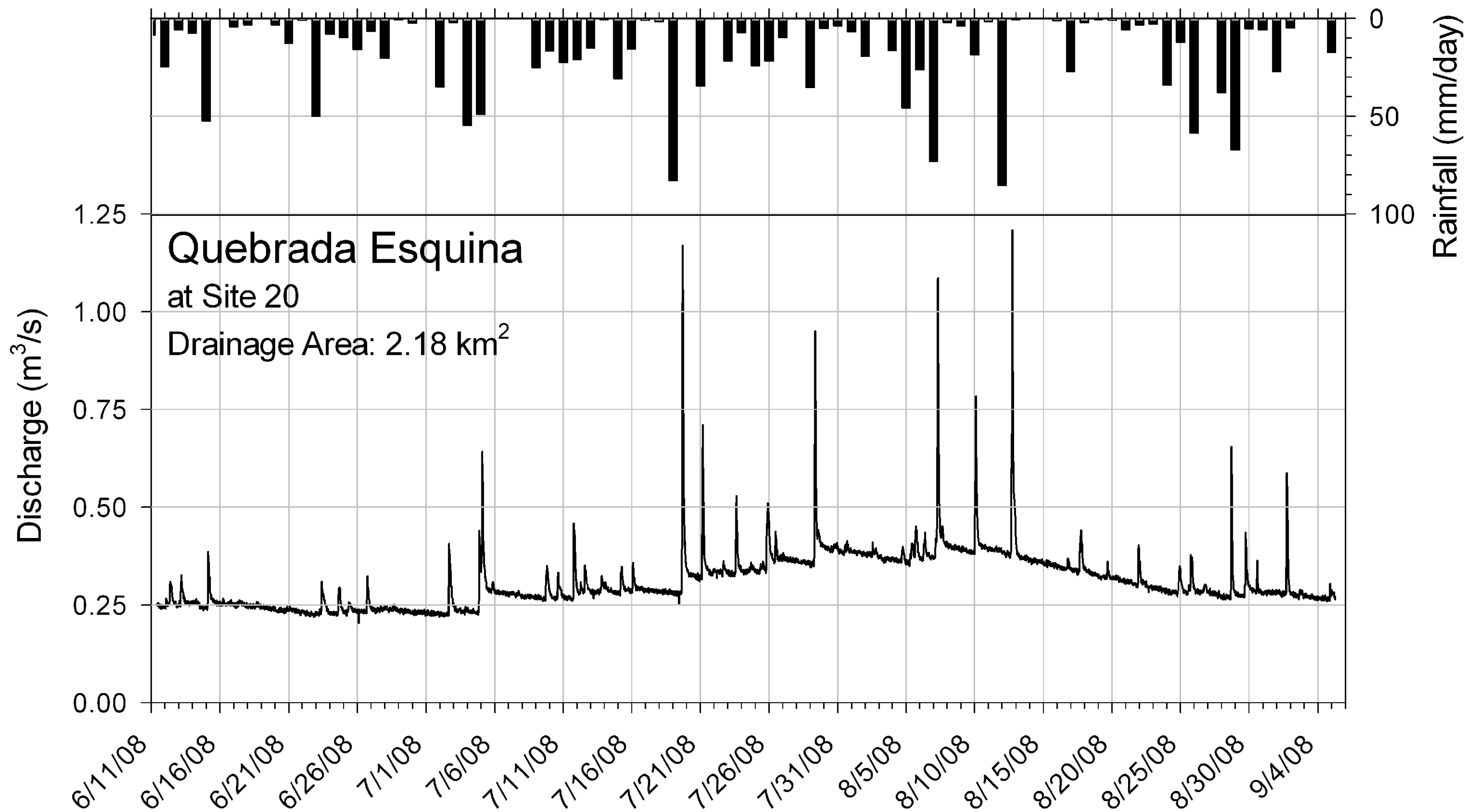

Figure 5.3. Hydrograph at a site 650 m downstream of the study jam from June 11 to September 5, 2008.

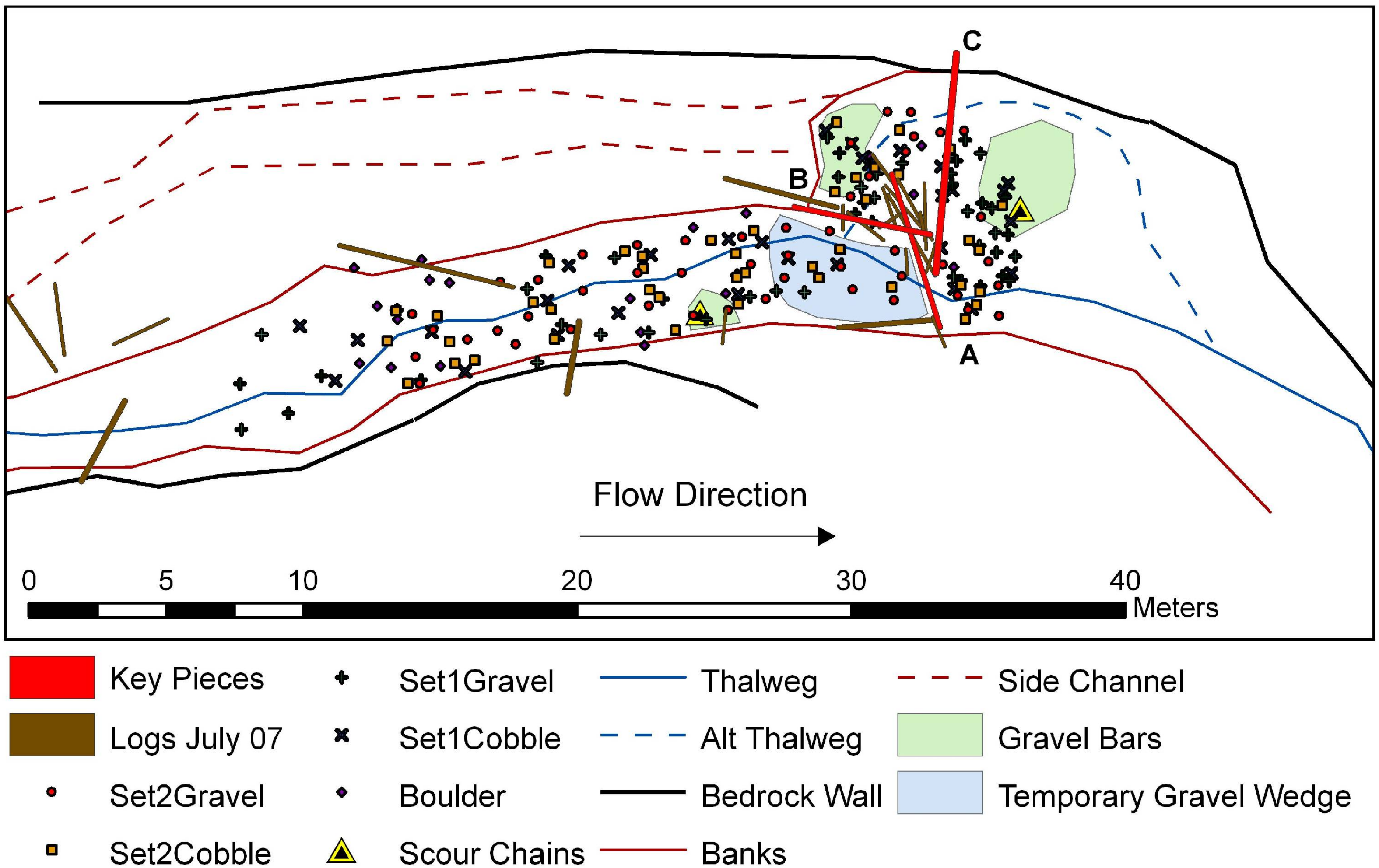

Figure 5.4. Jam survey, with tracer clast emplacement locations and channel features. The labels of the three key pieces (A, B, and C) are for use with the photographs in Figure 5.8.

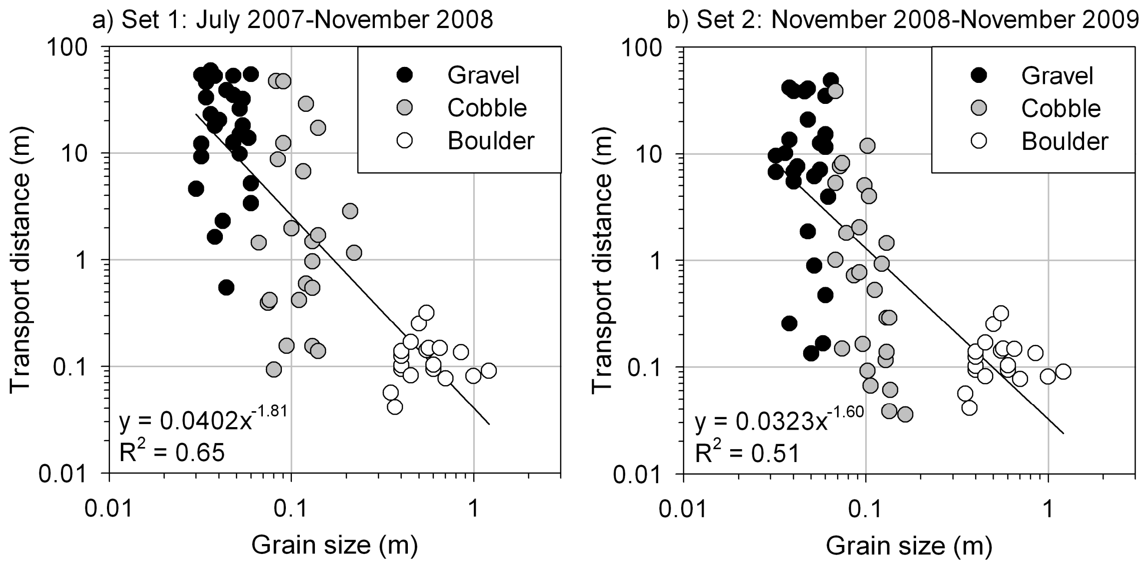

Figure 5.5. Clast size (median diameter, mm) as a control on distance traveled. Gravel is shown in black, cobbles in gray, and boulders in white. Apparent boulder movement is most likely due to inconsistency in survey point selection.

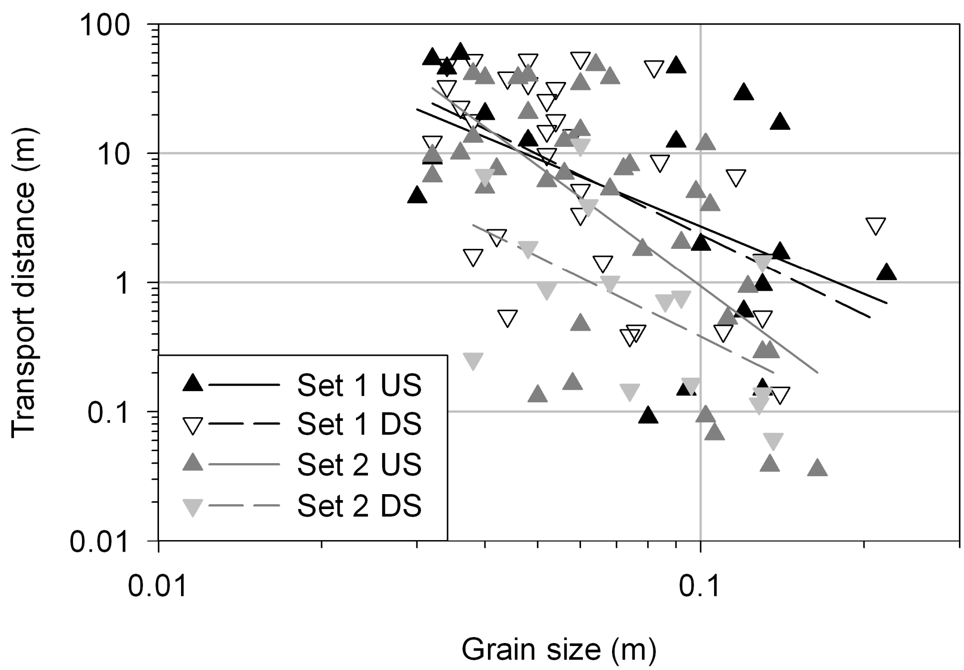

Figure 5.6. Distance traveled by the recovered gravel and cobble tracer clasts, separated into groups based on introduction date (Set 1: July 2007; Set: November 2008) introduction location (US: upstream of jam; DS: downstream of jam).

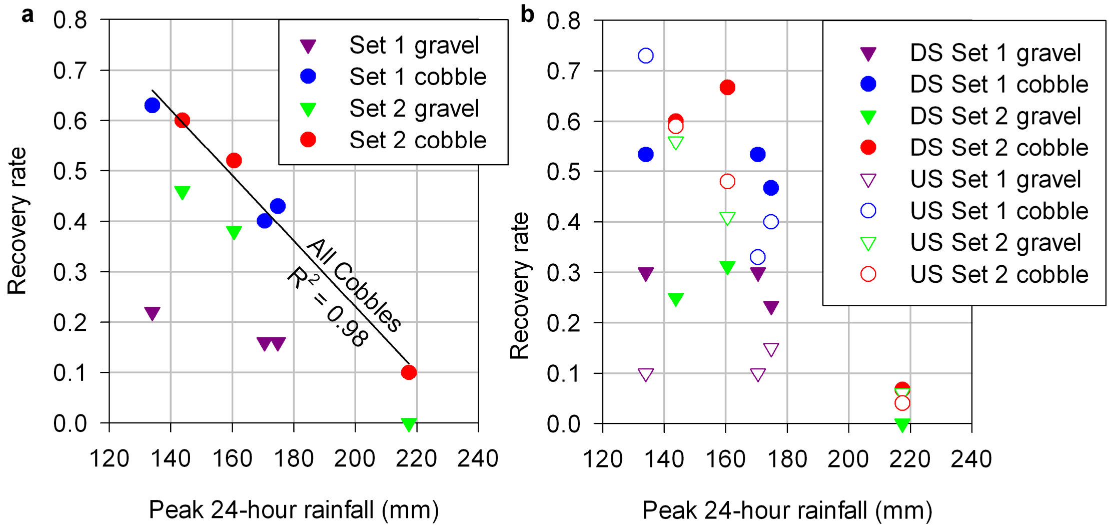

Figure 5.7. Recovery rate versus peak 24-hour rainfall (a) for all gravel and cobble clasts, and (b) separated by placement location, either downstream of or beside the jam (DS) or upstream of jam (US).

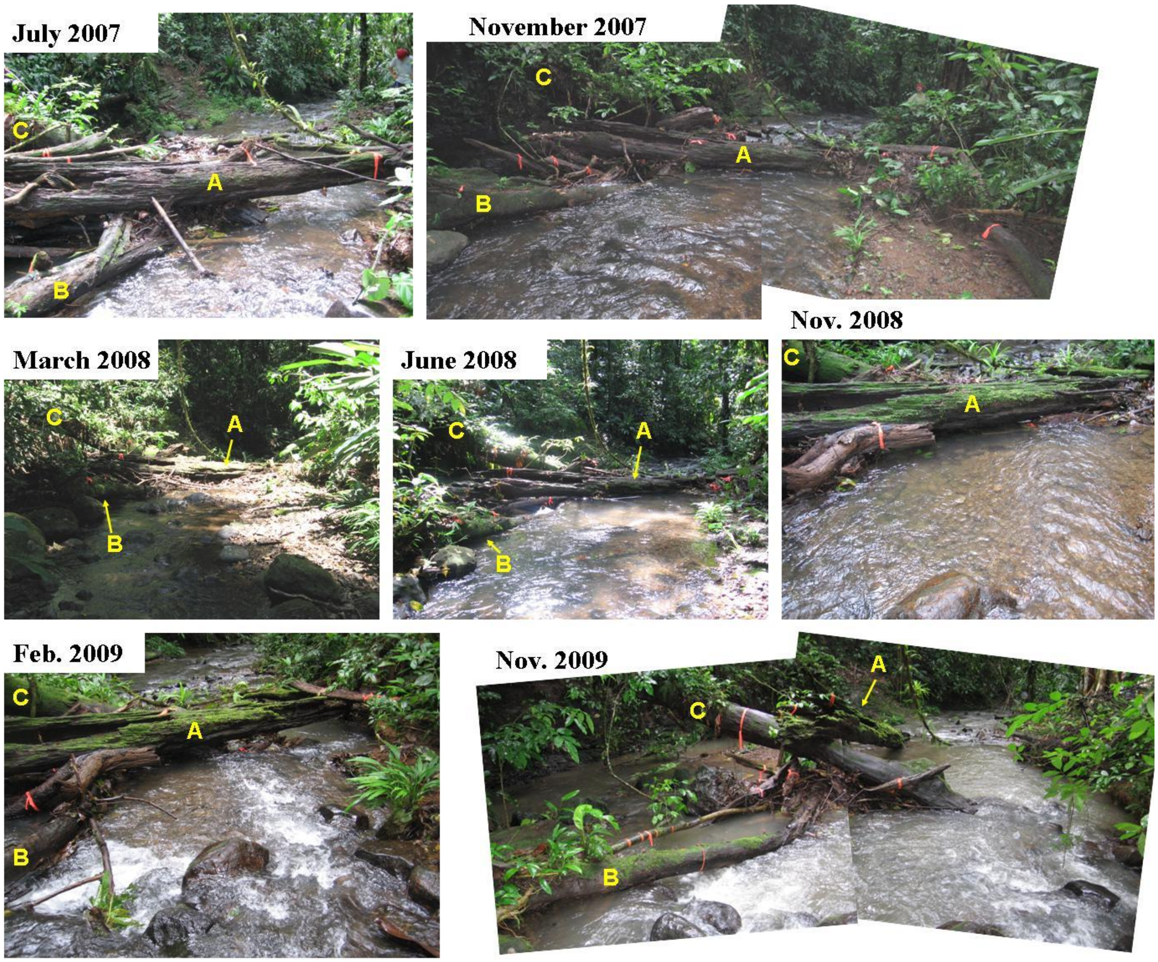

Figure 5.8. Evolution of the jam through time; view is downstream. The three key pieces are labeled A, B, and C, as in Figure 5.4. Upstream gravel wedge is present from November 2007 to November 2008. June 2009 configuration (not pictured) was nearly identical to March 2009, but differed dramatically from November 2009, when the key piece on the right side of the jam was moved and lay parallel to flow on top of the large ramped key piece.

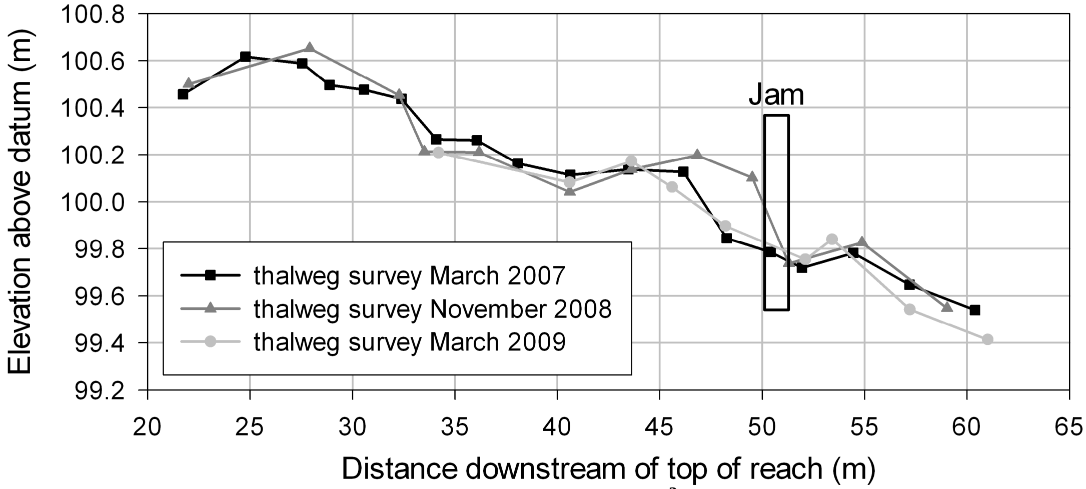

Figure 5.9. Thalweg elevation variation through time. A 5 m^3 wedge of sediment was present behind the jam in November, 2008.

Figure 5.10. Gravel bar scour following closing of right side flow path around jam. Exposed portion of rebar at center of photograph is approximately 30 cm long, about 20 cm more exposure than immediately following installation. Note surviving tracer clast below leaf at right. This rebar was subsequently removed by flow prior to the November 2009 site visit. Flow is left to right in this view.

6 EFFECTS OF EVAPOTRANSPIRATION ON BASEFLOW

6.1 Introduction

In forested catchments, forests affect stream function through mechanisms such as evapotranspiration (ET) (Link et al., 2005), delivery of instream wood (Benda and Sias, 2003), control of sediment delivery (Piégay et al., 2004), temperature control/shading (Gregory et al., 1991), and allochthonous nutrient delivery (Fisher and Likens, 1973; Naiman et al., 2005). Most of these forest-stream interactions directly impact stream ecosystems and biota (Harmon et al., 1986; Beschta et al., 1987; Gregory et al., 1991; Wallace et al., 1997; Allan, 2004). The wholesale breakage of these links by logging has been well studied (Hibbert, 1967; Bosch and Hewlett, 1982; Bruijnzeel, 1990; Stednick, 1996). It is less clear how subtler impacts, such as climate variation or invasive species introduction might alter stream-forest interactions, and thereby the physical and ecological function of streams. Climate components such as precipitation and temperature impact forests, potentially leading to changes in growth rates, species composition, or disturbance regime (drought, fire, insect infestation), and the impacts of a change in any of these may be transferred to streams by the interaction agents (wood, ET, etc.) listed above. While long-term effects of climate change on riparian forests are difficult to predict, daily and seasonal effects of climate on forest transpiration are easier to explore. At this short-response-time scale, climate variations have the potential to impact ET by changing precipitation amounts and patterns, soil moisture content, cloud cover (and thereby photosynthetically available radiation (PAR)), humidity, and temperature, and thereby vapor pressure differential (VPD).

Consideration of such impacts is important because ET is a fundamental component of water budgets. A significant percentage of rainfall in tropical environments is exported as ET (Leigh, 1975). Between 54% and 66% of rainfall at La Selva Biological Station, Costa Rica, was exported as ET during the years 1998-2000 (Loescher et al., 2005). But ET also has the potential to affect streamflow at much smaller scales than the whole water budget. Diurnal variation in ET demand can lead to complementary diel cycles in stream discharge (Bond et al., 2002). Researchers in semi-arid and temperate zone sites have used fluctuations in groundwater levels to estimate ET (Loheide, 2008). These groundwater fluctuations can in turn influence streamflow (Rowe and Pearce, 1994; Dye et al., 2001). Studies at H.J. Andrews Experimental Forest in Oregon, USA, have documented a link between ET and streamflow (Bond et al., 2002; Wondzell et al., 2007).

Sap flow is the means by which groundwater is transferred to leaves and thence to the atmosphere, and diel cycles in sap flow have been observed at numerous study sites in the neotropical region (Granier et al., 1996; Andrade et al., 1998; Meinzer et al., 2001; O'Brien et al., 2004). To my knowledge the link between ET and streamflow has not been quantified in the tropics, however, perhaps because of the confounding influence of the frequent precipitation events.

The impact of forest ET on streamflow is mediated through groundwater flow (Bond et al., 2002; Wondzell et al., 2007). The hydraulic gradient of groundwater flow into the channel will influence the transfer rate of subsurface water to the stream, and it is this gradient that is altered by forest water use lowering the water table. Groundwater flow rates are further affected by the transmissivity of the substrate, which influences both the speed with which water withdrawal by vegetation will become apparent in the stream and the rate at which streamflow recovers each night when ET ceases activity. Groundwater characteristics influence the source of water available to trees, and in areas where roots usually extend to the water table, such as riparian areas, trees can access either soil water or groundwater. The volume of water lost to the stream due to riparian forest transpiration should equal the volume of water transpired by the forest over an area of influence adjacent to the stream. Bond et al. (2002) estimated the aerial extent of direct tree-groundwater connection by scaling up locally measured ET rates to match daily stream discharge variation (Bond et al., 2002).

Exploration of the connections between diel cycles and ET could be conducted using a physically-based model. However, such a model of riparian zone ET effects on discharge would require a map of riparian zone boundaries, subsurface hydraulic properties, vegetation distribution, potential ET, boundary conditions along adjacent hillslopes, and ideally, spatial distributions of hydraulic head throughout the domain. In many cases, such as in this study, a model of this complexity is not feasible based on available data. Hillslope inputs to the riparian zone are typically unknown, as are the subsurface hydraulic properties and the ET dynamics. Nevertheless, clear diel fluctuations are present in the discharge signal, and a simpler spatially lumped model may represent the key features of the riparian zone ET process.

By monitoring flow cycles during baseflow, it may be possible to deduce certain ET characteristics, such as the amount of groundwater used by the forest, as well as subsurface hydraulic characteristics, such as variations in transmissivity. This effort is motivated by the fact that streamflow monitoring is typically easier than sapflow or groundwater flow monitoring, and the streamflow signal integrates the riparian ET response over a larger area. In this chapter, I use the diel fluctuations in discharge themselves as signatures of riparian zone ET, presenting a method to derive key features of the riparian zone flow process using only stage and standard meteorological data. The variations in lag time between ET demand (as estimated with VPD) and streamflow response at various stream stages may reflect groundwater routing or soil characteristics. The daily variation in flow enables an estimation of water lost to the stream because of ET, and thus an approximation of riparian forest water use. I hypothesize that observed diel cycles in streamflow are caused by ET withdrawal during the day and groundwater recharge at night. I present a simple model of baseflow discharge variation that uses measured VPD and empirical relationships between stage and nightly flow recovery to test this hypothesis. The characteristics of the rising limb of each cycle enable a simple evaluation of transmissivity variation.

6.2 Study Site

I installed a gage to monitor the flow of El Surà at the final bedrock macro-step before the stream reaches the Rìo Sarapiquì floodplain at an elevation of approximately 55 m (Figure 6.1). Drainage area at the gage is 3.4 km^2, and the basin supports a mix of old-growth and 30+ year-old second-growth forest. There is a very limited floodplain at the gage site, extending 2-9 m on either side of the channel before transitioning into valley sides with slopes of 10°-30°. Although inter-basin groundwater flow has been documented to be a major source of water in some watersheds at La Selva, solute contents of samples taken at the gage site indicate that less than 1% of base flow is from inter-basin groundwater transfer (Genereux et al., 2002). Streamflow is flashy (Figure 6.2), and baseflow periods are rare because of the frequency of rainfall events. Stream water temperature ranged from 22-26 °C during the study, with baseflow generally warmer, and storm flow generally cooler.

6.3 Methods

6.3.1 Data collection

From November 21, 2007 to June 15, 2009, stage was continuously monitored at a stable cross section of El Surà using a vented pressure sensor (LevelTroll700, InSitu Inc., Fort Collins, CO) set on a 10-minute recording interval. Discharge was measured using a salt slug dilution technique for nine flows ranging from 0.17-0.67 m^3/s, and two more flows up to 1.25 m^3/s were measured using a velocity meter and cross section survey at a nearby bridge, enabling establishment of a stage-discharge relationship. The stage data were converted to discharge by fitting a power function to these measurements. Discharge was then averaged to a 30-minute interval in order to match the meteorological data (Figure 6.2).

Meteorological data were collected by the staff of La Selva Biological Station at a tower in a clearing approximately 2 km from the stream gage. The variables precipitation (mm), average temperature (°C), average relative humidity (%), average solar radiation (SR, units of $\mu mol/s/m^2$), average photosynthetically available radiation (PAR, units of $\mu mol/s/m^2$), and maximum PAR were recorded for 30 minute intervals. Vapor pressure differential (VPD, units of kPa) was calculated from temperature and relative humidity.

In this flashy stream, diel flow patterns are easily masked by flood hydrographs (Figure 6.2), so I limited the analyses to times with little precipitation. I identified 12 time periods ranging from 2-17 days that exhibited distinct diel flow cycles (Figure 6.3). Within these identified baseflow periods, the daily flow cycle was superimposed on a falling hydrograph. In order to isolate the daily cycle, I detrended the baseflow data by subtracting a fitted power function for each baseflow period (Table 6.1).

Because I expect that changes in stream stage relate to ET demand, I explored the correlation between SR, average PAR, maximum PAR, and VPD (as measures of ET demand), and the time derivative of stage (d') during each baseflow period using the Pierson correlation coefficient (r). To identify time lags between ET demand and falling stage, I calculated r between d' and the other variables at temporal offsets that increased by 30 minute increments. I identified lag times between ET demand and stream response as the temporal offset that led to r values closest to -1.

6.3.2 *Modeling ET from Streamflow*

I developed an empirical model to estimate ET from streamflow and applied it to six of the twelve baseflow periods: those starting 11/30/07, 2/3/08, 3/29/08, 5/2/08, 3/28/09, and 5/1/09. As a foundation for the model, I conceptualized the daily cycles as fluctuations in storage of groundwater in the riparian zone, or more precisely the zone adjacent to the stream where forest ET draws on groundwater (i.e., zone of root-groundwater contact), using the equation

$$S_R' = -E_T + G_W + -Q \qquad (6.1)$$

where S_R' is the time derivative of riparian groundwater storage, E_T is the rate of evapotranspiration, G_W is groundwater input from upgradient, and Q is stream discharge (all in units of volume per time). If the riparian water table is closely correlated with stream stage, then

$$d'A_R = -E_T + G_W + -Q \qquad (6.2)$$

where d' is the time derivative of stage, and A_R is the area of the riparian zone. Detrending the stage data eliminates Q and some part of G_W, so that

$$d_d'A_R = -E_T + G_{Wd} \qquad (6.3)$$

where d_d' is the time derivative of detrended stage, and G_{Wd} is the portion of groundwater recharge that varies daily as a result of cyclic changes in hydraulic gradient caused by local lowering of the water table by ET withdrawal. If there were no ET influence, one would expect d_d' and G_{Wd} to be zero. The value of G_{Wd} is controlled by the hydraulic gradient, which in this case is the difference between the riparian water table elevation and the hillslope water table elevation, as well as the subsurface hydraulic properties. If it is assumed that the hillslope water table elevation is nearly constant over daily time scales, and if riparian water table elevation closely matches stage, as I have already assumed, then G_{Wd} will be a function of the riparian water table elevation, which in turn controls stage (d). Therefore I assume that G_{Wd}, an unknown variable, can be estimated as a function of detrended stage (d_d), a known variable. Equation (6.3) can then be rearranged into

$$d_d' = -E_T/A_R + \mathrm{f}(d_d)/A_R \qquad (6.4)$$

where $\mathrm{f}(d_d)$ is an unknown function of stage. The form of the function should reflect groundwater dynamics controlled by subsurface hydraulic properties. Because A_R is expected to be nearly constant over the short time periods and small stage fluctuations encompassed by each baseflow period, it can be incorporated into f(d_d) as a constant, and equation (6.4) can be rearrange so that

$$E_T/A_R = f(d_d) - d_d'. \qquad (6.5)$$

I estimated the unknown function f(d_d) for each baseflow period empirically, by analyzing the variation of stage recovery rates during nocturnal periods (10:00 pm to 7:00 am) when ET effects were presumed to be negligible. I smoothed the d_d data series prior to this analysis by averaging across all days in the period (i.e., found average d_d at 1:00 am, 1:30 am, etc.), plotted nocturnal values of average d_d against average d_d', and fit a curve to these data. This function is not expected to be universal, even within a site, but should vary through time because it is dependent on changing subsurface hydrologic conditions such as soil moisture and the regional water table elevation.

From equation (6.5), I then estimated the area over which ET affects groundwater, after the method described by Bond et al. (2002). For each of the six periods for which E_T/A_R was found, if it is assumed that all ET losses are from saturated groundwater, the average daily volumetric ET (i.e., average of E_T integrated over each day) is expected to equal the water 'lost' in the stream flow each day (Q_{lost}). Lost water was calculated by finding the cumulative difference between the observed cyclic hydrograph and a hydrograph constructed by linking each daily peak discharge with straight lines, and dividing the sum by the number of cycles thus bounded (Figure 6.4). Thus the equation for calculation of A_R is

$$A_R = Q_{lost}/(f(d_d) - d_d') \qquad (6.6)$$

where f(d_d) is again an empirical function for the recovery rate of the riparian water table that must be found independently for each period of analysis.

To test the validity of the model, I attempted to find alternate ways to estimate ET rates. I explored modeling ET flux as a function of average SR, average PAR, maximum PAR, and VPD. Granier et al. (1996), working in French Guyana, found a linear relationship between sap flow (a surrogate for forest ET) and VPD up to 1.5 kPa, at which point sap flow started to plateau due to stomatal closure. This value of VPD was exceeded only 4% of the time during the baseflow study periods, so VPD was the preferred predictor or ET. I also observed that VPD had the best correlation to d_d' of the four variables tested, supporting this preference. The maximum correlation between VPD and d_d' occurred at various lag times (Figure 6.5), apparently depending on the average stage of the period being analyzed (Figure 6.6). Therefore, I modified equation (6.5) to enable consideration of lags, and substituted a linear function of VPD for ET rate

$$kV_{PD(t=i-l)} + b = f(d_{(t=i)}) - d_d'_{(t=i)} \qquad (6.7)$$

where k and b are constants, V_{PD} is VPD, the time step, t, is denoted in the subscripts, and l is the lag. I found k and b empirically by plotting $V_{PD(t=i+l)}$ against $f(d_{(t=i)}) - d_d'_{(t=i)}$ for all values of i, and fitting a regression using least square errors. A range of values of l were tested and the one resulting in the highest regression R^2 was used.

6.4 Results

The estimates of the water table recovery rate (i.e., the empirical function $f(d_d)$) showed great variability, and even changes in the sign of the slope, depending on the average stage of the baseflow period (Table 6.2). At relatively high stream stages, d_d' decreased at a nearly constant rate between 10:00 pm and 7:00 am (Figure 6.7a). During the 12-day period that began on March 28, 2009, with an average stage of 0.4 m, the relationship between the nocturnal values of d_d' and d_d had the form of a curve that was well fit by a quadratic function and a rational function within the range of observed values (Figure 6.7b). I used the quadratic function, but a reanalysis using the rational function resulted in negligible differences in ET estimates. The trend during this baseflow period was for the rate of groundwater recharge to decrease throughout the night. At the lowest stream stages, however, the relationship between d_d' and d_d was nearly reversed. During the 7-day period that began March 29, 2008, with an average stage of 0.27 m, as water level rose from 10:00 pm to 7:00 am, the rate of rise increased (Figure 6.7c). The relationship between the nocturnal values of d_d' and d_d had a linear form (Figure 6.7d).

Average ET in the riparian zone calculated with equation (6.5) ranged from 5.6 to 12.1 mm/day, while the discharge lost to the stream ranged from 320-570 m^3/day (Table 6.3). These values of Q_{loss} represent 1-4% of the daily discharge. The estimated riparian area (Table 6.3), calculated with equation (6.6), varied systematically with the average stage of the period being considered (Figure 6.8). The range of values of A_R, 0.03-0.07 km^2, represent about 1-2% of the total drainage basin area. Average VPD (Table 6.3) correlated well with E_T/A_R, but not with Q_{loss} (Figure 6.9). ET appears to initially rise as VPD rises, but to reach a limit of approximately12 mm/day.

Temporal variation in ET within each baseflow period was matched to a linear function of VPD according to equation (6.7). The best-fit values of k (Table 6.3) ranged from 0.75-1.24. The two sides of equation (6.7), when plotted separately against time, match well (Figure 6.10), with Nash-Suttcliffe coefficients of efficiency ranging from 0.75 to 0.89 (Table 6.3). In general, the greatest deviation of the two methods occurs at night, when ET is expected to be negligible. The ET estimated with equation (6.5) occasionally goes negative at night, which probably reflects weaknesses in the assumptions made in deriving the equation. The lags found for equation (6.7) commonly differed from those presented in Figure 6.6 (Table 6.3).

6.5 Discussion

The nocturnal relationship between d_d and d_d' at our site varies widely with time and stage (Figure 6.7), with the rate of recovery sometimes increasing as stage rises through the night, sometimes decreasing, and sometimes staying nearly constant. The variation in trends of the d_d-d_d' relationship may reflect variation in substrate hydrologic properties. In the higher flow periods, when the rate of groundwater recharge decreased throughout the night, the trend may be a result of the steady decrease of relative head gradient between the regional groundwater and the riparian groundwater, as the riparian water table depression caused by ET gradually recovers. The trend of the lower flow periods, when the rate of groundwater recharge increased throughout the night, is more difficult to explain, although it has some features in common with the transmissivity feedback reported elsewhere during rainfall events (Bishop et al., 1990) and snowmelt (Kendall et al., 1999). In these cases, the researchers observed increased subsurface flow rates close to the surface as the saturation level rose because of hydraulic conductivity values that decreased with depth. It is possible that the active bioturbation at La Selva, with numerous shallow root casts and large subterranean insect nests and burrows (Clark, 1990), contributes to higher conductivity rates nearer to the surface. If groundwater movement is limited by tighter soils at low stages, the flow rate might be expected to increase as the water table rises into horizons with more macropores or looser sediment, thereby increasing the rate of stage rise.

Considering the d_d-d_d' trends from the standpoint of Darcy's law for groundwater flow, $Q = Tw(\mathrm{d}h/\mathrm{d}l)$, where Q is flow of groundwater into the stream, T is transmissivity, w is the width of flow, and $\mathrm{d}h/\mathrm{d}l$ is hydraulic gradient, suggests that at this study site different terms of the equation may dominate the flow of groundwater into the channel at different stages. T is equal to Kb, where K is hydraulic conductivity and b is saturated thickness (which is analogous to stage in the model), and appears to dominate groundwater flow into the channel during low stage periods. So at low flows, increases in b lead to higher Q in spite of the concurrent reduction in $\mathrm{d}h/\mathrm{d}l$. At higher stages, however, $\mathrm{d}h/\mathrm{d}l$ appears to dominate flow into the stream, with Q decreasing through the night as stage recovers. The variable w is somewhat nebulous in the case of this study, but one could assume that it relates to the width of riparian zone contact with the stream, which is likely related to bank length, although it is unclear how much of the stream network should be included.

ET rates (E_T/A_R) calculated with equation (6.5), which ranged from 5.6 to 12.1 mm/day, were 2-3 times higher than the 3.8 mm/day maximum reported by Granier et al. (1996) for stands in French Guyana. This difference is likely explained by differences in forest composition related to the fact that the French Guyana sites receive about half to three-quarters of the annual precipitation at La Selva. Additionally, the ET measured for the baseflow periods is likely to be higher than annual averages of ET, because by nature my method is only applicable during rainless periods, which should correlate to less cloud cover, higher net radiation, lower humidity, and higher VPD than average. I attempted to estimate long term ET and VPD averages at La Selva for comparison with the data. I calculated average VPD for the period for which I have detailed meteorological data (11/12/07-11/19/09) to be 0.34 kPa. Assuming the annual ET measurements of Loescher et al. (2005) are representative of more recent conditions as well, the average daily ET is approximately 6 mm/day. These values are plotted in Figure 6.9a, and closely match the observed VPD and estimated ET for the baseflow period beginning 11/30/07. More generally, they fit with the trend of initially rising ET with rising VPD, eventually reaching an ET limit as VPD continues to rise. This limit may reflect the maximum rate at which trunk tissue can transmit water upward, stomatal closing in high VPD conditions invoked by Granier et al. (1996), or energy limitation inhibiting higher ET loss.

The estimates of ET water loss for El Surà calculated with the method in Figure 6.4 represent 1-4% of total baseflow in the 12 study periods. This is similar to the loss of 1-6% of flow that Bond et al. (2002) observed at their study site in western Oregon. The values of riparian area that I calculated represent 1-2% of the drainage basin of El Surà. In contrast, Bond et al. (2002) found that only 0.1-0.3% of their 1-km^2 study basin contributed to ET losses to the stream. The order of magnitude difference in the portion of the basin contributing to water withdrawal could reflect differences in riparian zone characteristics such as width, or possibly shallower rooting depths by the 40-year old second-growth trees and shrubs in Oregon. In general, tropical trees have slightly deeper roots than temperate conifers (Canadell et al., 1996), although data from tropical sites are very scarce and highly variable. I do not have data on average root depth of riparian trees at La Selva, although observations of the root wads of toppled trees lead me to suppose that many large individuals have relatively shallow roots in spite of heights that can exceed 50 m (Hartshorn and Hammel, 1994). The observed decrease in riparian area with declining stage is also consistent with the findings of Bond et al. (2002). As water table drops, I expect that some plants that were marginally connected to the groundwater will lose contact. This does not suggest that these plants will cease to transpire, but rather that they will obtain their water from sources other than the groundwater that affects streamflow on a daily time scale (Ehleringer and Dawson, 1992; Meinzer et al., 1999).

The progressive increase of lag time with decreasing stage that I observed (Figure 6.5) is very similar to that observed by Bond et al. (2002). They calculated lag between sap flow maxima and stream discharge minima, rather than d_d' minima, and thus found longer lag times, in the range of 4-8 hours. When I analyze the La Selva data for lag to discharge minima, I find a similar range of lags (4.5-8.5 hours). Bond et al. (2002) suggest the increasing lag may be caused by the vegetation accessing deeper water sources that have slower flow rates. This would appear to agree with the observation of increased transmissivity at higher stages, in that flow through shallow pathways will be faster than deeper pathways, leading to increased signal travel times as the shallow pathways become inactive. The meaning of the lag times are complicated, however, by inconsistencies among the two primary methods of measuring them. The lags found by selecting the best correlation of VPD with d_d' (Figure 6.6) vary with average stage. The lags found by optimizing equation (6.7), however, are all close to 1.5 hours regardless of stage (Table 6.3). This discrepancy may be a result of simplifications made during the process of deriving equation (6.7), or the trend in lags in Figure 6.6 may simply be an artifact of the more steeply declining flow trend for the higher flow periods (Figure 6.3). In the latter case, assuming the true lag is constant across stream stages, the uniform lag could potentially represent physiological characteristics of water use by trees, or some other factor.

The similarity of the values of ET through time in Figure 6.8 estimated through independent lines of reasoning (VPD and stream stage) support the hypothesis that the flow cycles are driven by forest water use. The agreement also supports the assumptions made in deriving equation (6.5). Other support for the supposition that stage and riparian water table elevation are tightly coupled comes from limited groundwater field data. I simultaneously monitored water level in a well in the small floodplain near the study site and stage in the stream adjacent to the well for 10 days in November 2009. During rainfall events there was a slight gradient sloping from the well to the stream, but between rainfall events the stage and water table elevation were within the measurement error of one another.

6.6 Conclusions

The model provides a starting point for estimating ET rates and some features of groundwater dynamics using only stream flow cycles as measured with an easily emplaced pressure transducer. I checked the validity of the method using widely available meteorological data, finding that variation in VPD, which has been shown to vary linearly with sap flow up to values of 1.5 kPa, matches the modeled ET with high efficiency. True validation will require direct measurements of sapflow in combination with stream gaging and analysis of baseflow cycles, but the method appears promising and demonstrates a direct forest-stream link that may have significance to stream ecosystem function and physical processes. The calculated ET values tend to be higher than estimates of long term averages, but this is likely because baseflow occurs when rain and cloud cover is minimal, resulting in higher than average forest ET.

The dynamics of the nightly flow recovery derived from the empirical model give some indication of subsurface characteristics. At high stages, when the upper portion of the subsurface is active, recovery rates decrease with rising stage. This suggests that as the near-stream water table, which had been lowered by ET during the day, approaches the regional water table, flow rates are reduced by the decreasing head differential. In contrast, at low stages, when only the lower portion of the subsurface is active, recovery rates increase with rising stage until ET commences, stopping the recovery process. This suggests a decrease in hydraulic conductivity with depth resulting in an increase in transmissivity with rising water levels.

6.7 Tables

Table 6.1. Baseflow period flow trend power function parameters

Start Date	11/30 /2007	1/9 /2008	2/3 /2008	2/28 /2008	3/29 /2008	5/2 /2008	9/12 /2008	10/25 /2008	2/17 /2009	3/19 /2009	3/28 /2009	5/1 /2009
Days	7	12	7	17	7	7	2	2	3	7	12	6
y_o[1]	0.475	0.541	0.368	0.325	0.285	0.294	0.396	0.417	0.501	0.490	0.433	0.330
a[1]	-0.0559	-0.0796	-0.0217	-0.0106	-0.0275	-0.0236	-0.0417	-0.0402	-0.0597	-0.0482	-0.0403	-0.0196
b[1]	0.827	0.722	0.822	0.456	0.931	0.559	1.093	0.684	1.041	1.010	0.695	0.901

[1]Best fit power function parameters ($y=y_o+ax^b$) with x in units of weeks and y in meters.

Table 6.2. Groundwater recovery functions, f(d_d)

Start Date	Function Form	Slope	Equation f(d_d) [1]
11/30/2007	Quadratic	Negative	$y = -35x^2 - 0.14x + 0.00028$
2/3/2008	Quadratic	Negative	$y = -17x^2 - 0.12x + 0.0005$
3/29/2008	Linear	Positive	$y = 0.0817x + 0.0005$
5/2/2008	Quadratic	Positive	$y = 18.2x^2 + 0.12x + 0.00042$
3/28/2009	Quadratic	Negative	$y = -25x^2 - 0.11x + 0.00058$
5/1/2009	Linear	Horizontal	$y = -0.0217x + 0.0004$

[1] x is detrended depth (d_d) in units of m, and y is water table recovery rate (G_{Wd}) in units of m/hr

Table 6.3. Baseflow period flow and ET characteristics

Start Date	11/30 /2007	1/9 /2008	2/3 /2008	2/28 /2008	3/29 /2008	5/2 /2008	9/12 /2008	10/25 /2008	2/17 /2009	3/19 /2009	3/28 /2009	5/1 /2009
Days	7	12	7	17	7	7	2	2	3	7	12	6
Ave Q_{loss} (m^3/day)	395	570	438	414	320	371	499	371	428	473	545	353
Ave Q (m^3/day)	35670	42830	19170	13450	8890	9700	24950	27870	46690	40940	26280	14310
Proportion of Q 'lost'	0.011	0.013	0.023	0.031	0.036	0.038	0.020	0.013	0.009	0.012	0.021	0.025
Ave stage, d (m)	0.44	0.47	0.36	0.31	0.27	0.28	0.39	0.41	0.49	0.47	0.40	0.32
Cycle amplit. (mm)	4.6	6.2	6.2	7.1	7.5	7.4	5.9	5.7	4.5	5.3	6.4	6.2
Ave SR (μmol/s/m^2)	380	406	473	499	541	476	441	425	507	430	486	394
Ave VPD (kPa)	0.36	0.39	0.51	0.53	0.57	0.50	0.48	0.40	0.50	0.43	0.57	0.40
Proportion of VPD [1]	1.05	1.15	1.50	1.57	1.68	1.47	1.40	1.18	1.48	1.26	1.67	1.18
VPD-d_d' lag (hrs)	0.5		1.5		3	3					0	1.5
model lag, l (hrs)	1.5		2.5		1.5	1					1.5	1.5
ET rate (mm/day) [2]	5.6		10.9		12.1	11.8					11.9	9.2
VPD vs ET slope, k [3]	0.75		0.82		1.04	1.09					0.98	1.22
Riparian area (km^2)	0.070		0.040		0.027	0.032					0.046	0.038
Nash-Sutcliffe C.E.	0.751		0.877		0.890	0.782					0.857	0.805

[1] Period average VPD as a proportion of the long term (11/2007-11/2009) average VPD, 0.34 kPa.
[2] This is a period average of E_T/A_R from equation (6.5)
[3] VPD used to find this slope is in kPa, and ET is in mm/hr; this is the k parameter in equation (6.7)

6.8 Figures

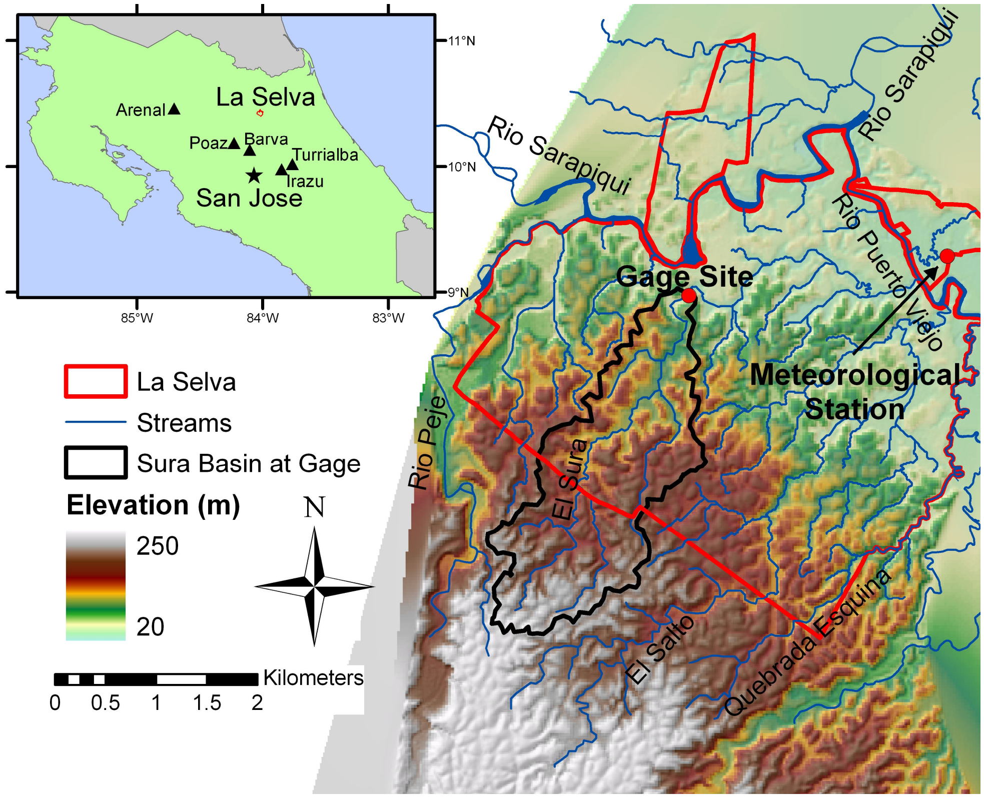

Figure 6.1. Location of study site in Costa Rica. Contributing basin at study site is outlined in black.

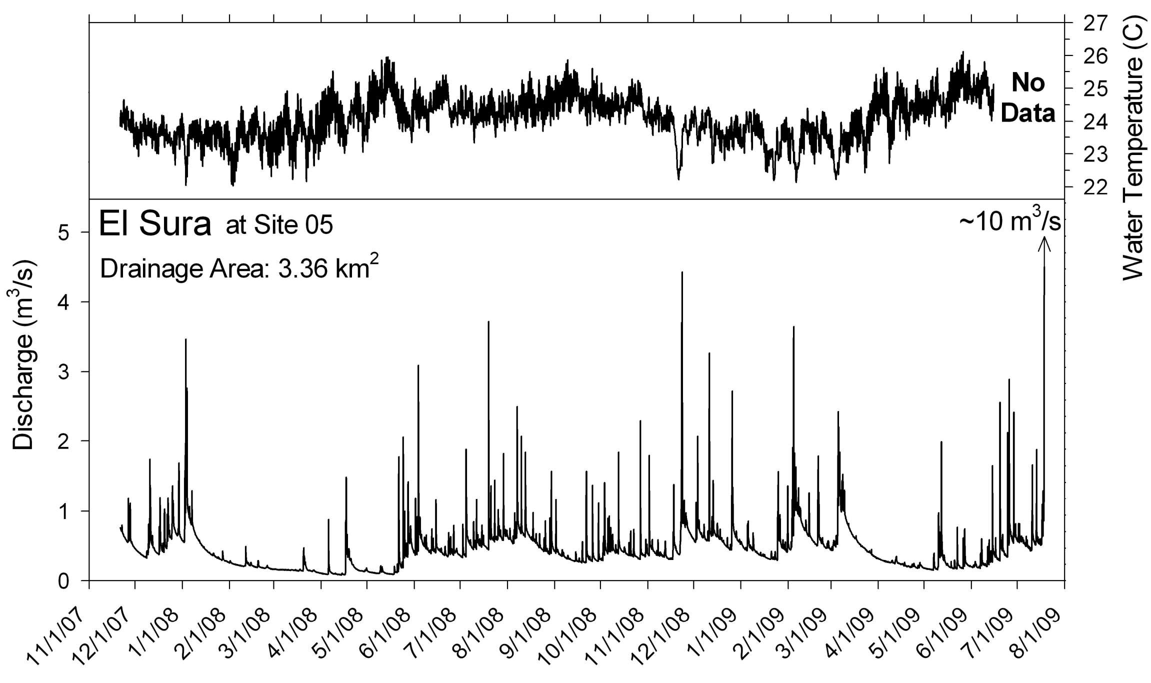

Figure 6.2. Stream discharge and water temperature in El Surà. The highest directly measured flows were 1 m^3/s, so the rating curve (power function) with which I calculate discharge is only well constrained at low flows. Discharge values over 1 m^3/s are extrapolations of the rating curve.

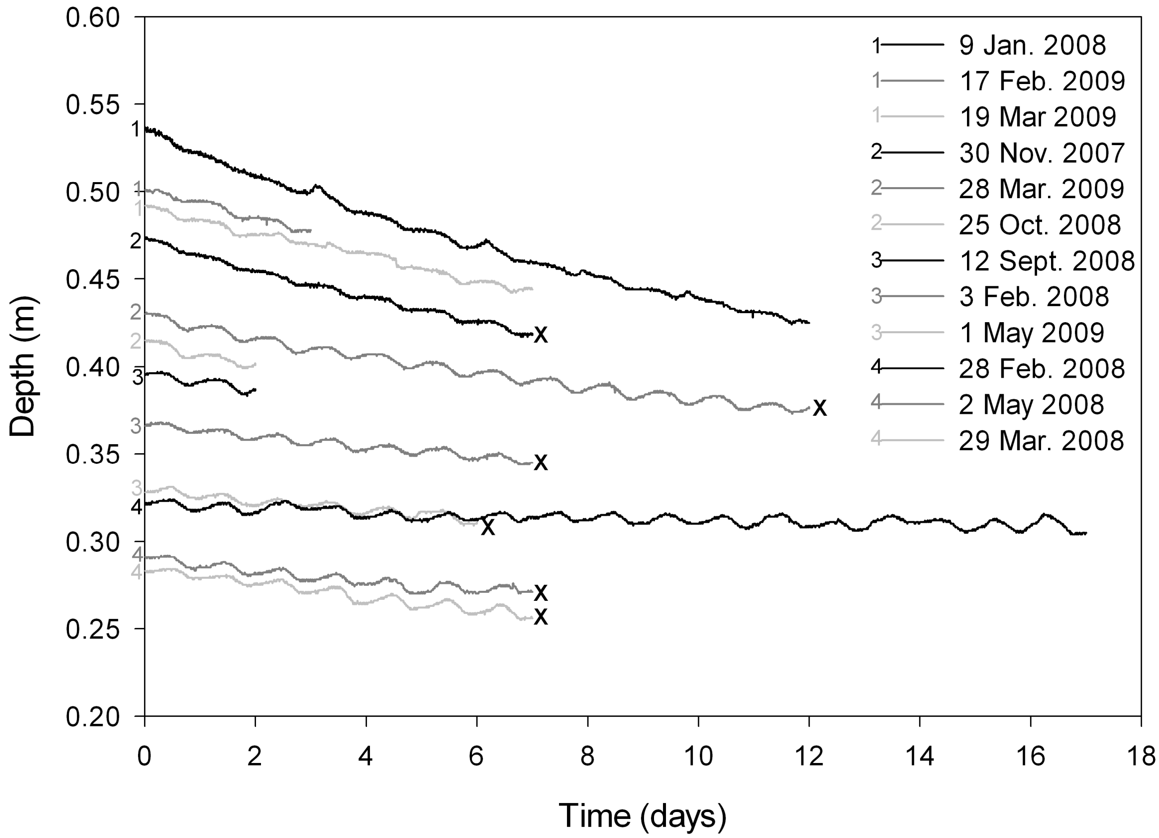

Figure 6.3. Stream stage during baseflow periods analyzed. Dates in the legend indicate start date for each period. ET and groundwater flow were modeled for the six periods marked with an 'X'.

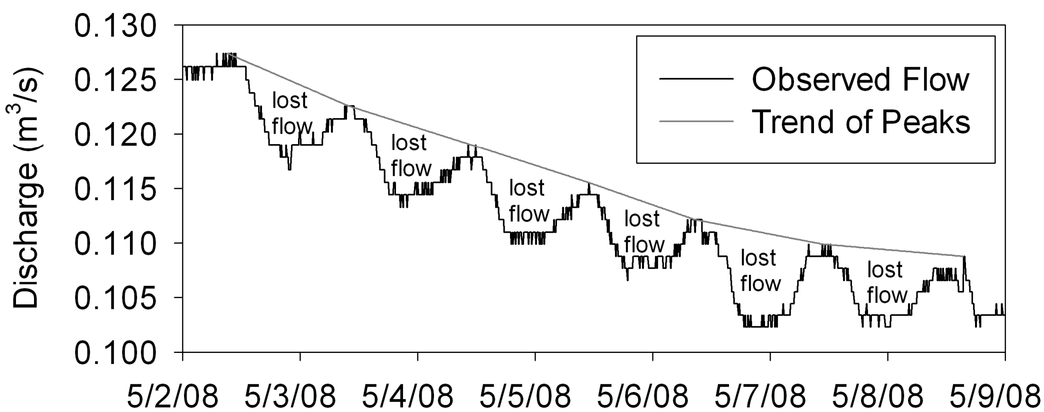

Figure 6.4. Calculation of discharge 'lost' to the stream due to ET. Lost stream flow is the area between the curves.

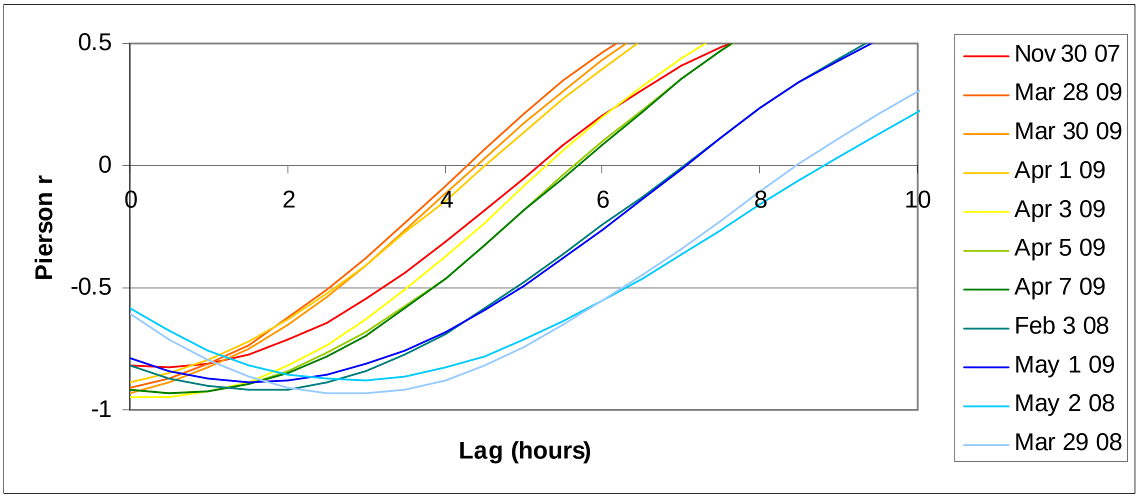

Figure 6.5. Variation of VPD to d_d' correlation (r) with lag time between the two variables. The six modeled study periods are presented, with the 12-day period beginning on 3/28/09 broken into 2-day segments to demonstrate lag variation within a study period. Periods are arranged in order of descending average stage.

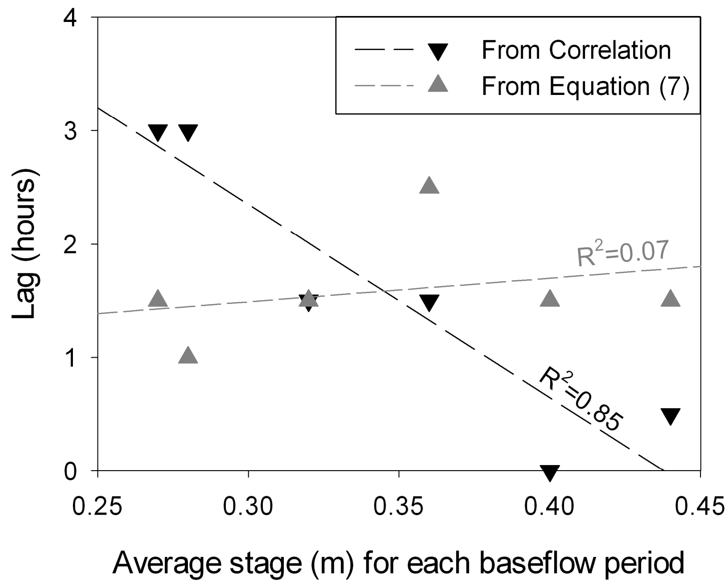

Figure 6.6. Estimated lag values versus average stage for the six modeled baseflow periods. Lag for optimal VPD- d_d' correlation is shown in black, and lag that optimizes equation (7) is shown in gray.

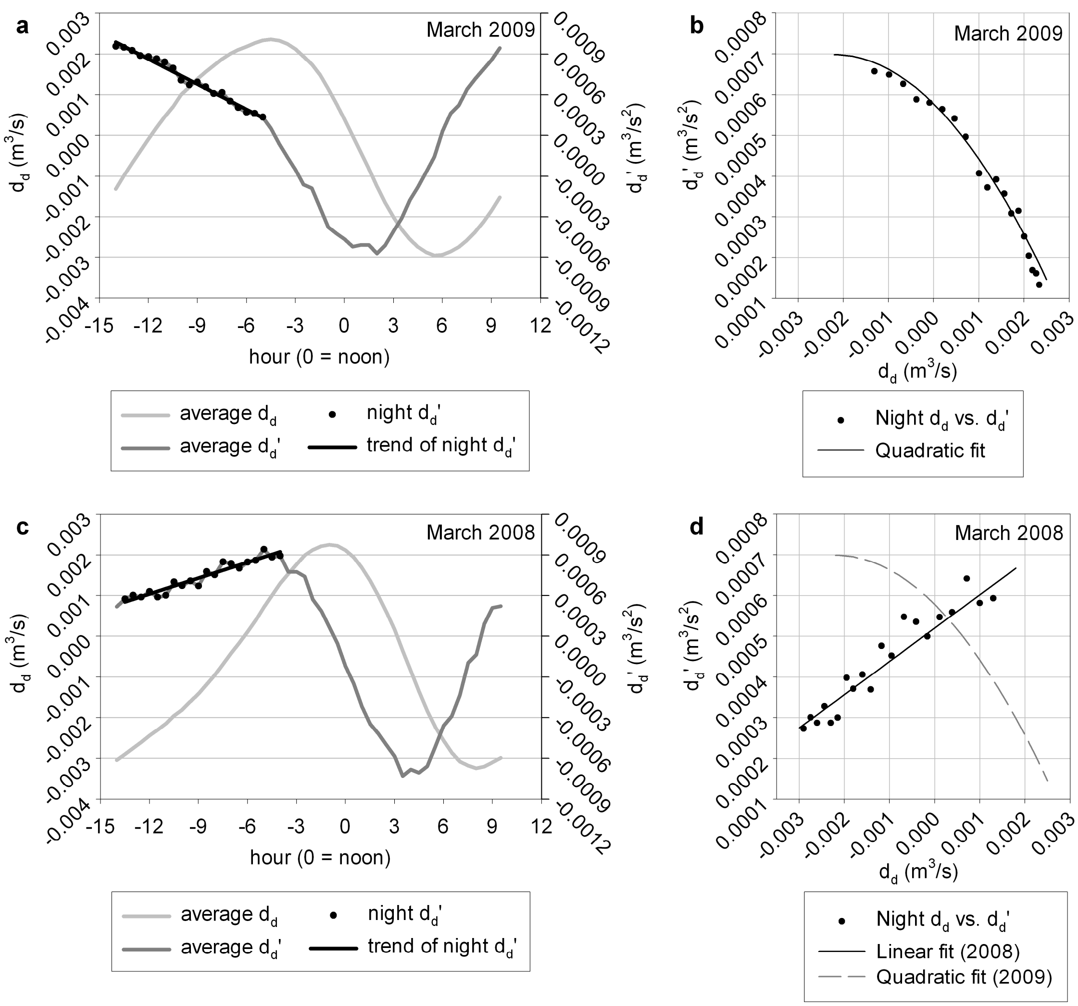

Figure 6.7. a) March 28-April 8, 2009 daily average trend in d_d and d_d', showing linear drop in d_d' at night (10:00pm to 7:00am) when VPD is negligible. b) Quadratic equation fit of d_d' as a function of d_d at night. c) March 29-April 4, 2008 daily average trend in d_d and d_d', showing linear rise in d_d' at night (10:00pm to 7:00am) when VPD is negligible. d) March 2008 data trend compared to part b.

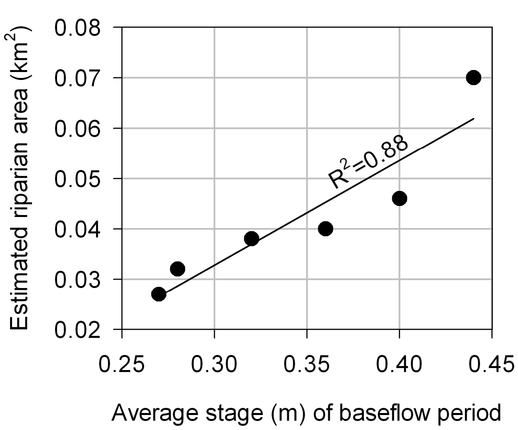

Figure 6.8. Increase in estimated area of forest-groundwater interaction (riparian area) with increasing stage. Data points are from the six modeled baseflow periods.

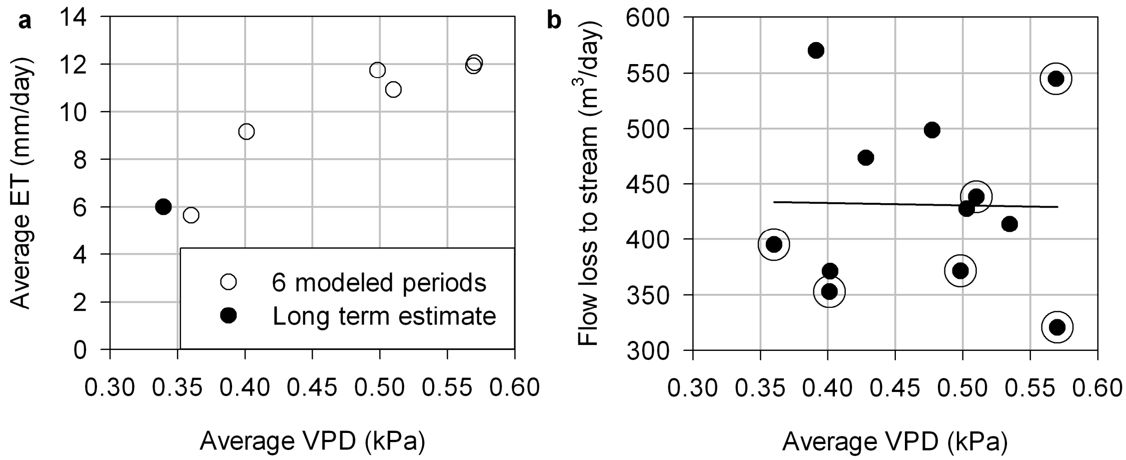

Figure 6.9. a) Daily mean VPD (kPa) vs. average rate of saturated-groundwater-sourced ET within the riparian zone (mm/day). White points are from the six baseflow periods modeled in this study. Black point is the estimated long term average for all of La Selva. b) Daily mean VPD (kPa) versus estimated daily water lost to the stream through ET use (m^3) for all baseflow periods identified in this study. Modeled study periods are circled. Black line is simple regression of all twelve data points.

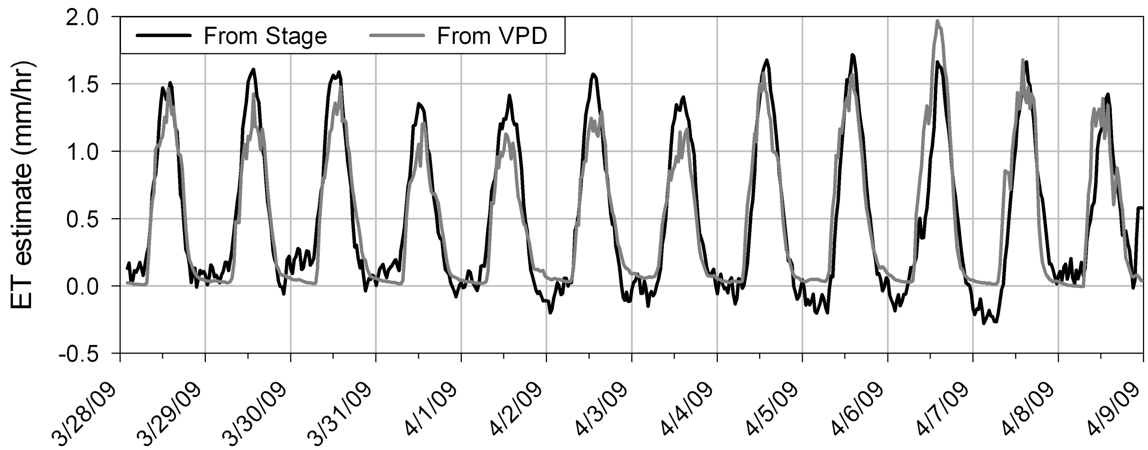

Figure 6.10. Daily cycles in ET as estimated using equation (5) (black) and a linear function of VPD (gray).

7 CONCLUSIONS

7.1 Summary of findings

This dissertation research has found that average wood load in the headwater streams (drainage area less than 8.5 km^2) of La Selva Biological Station is approximately 12.3 m^3/100 m, or 189 m^3/ha. These are the first systematically collected instream wood data reported for a tropical region. Values within individual 50-m-long reaches, of which there were 30, ranged from 3 to 34.7 m^3/100 m and 41 to 612 m^3/ha. These values fall within the lower range reported for global temperate zone wood loads (see Table in Chapter 1). Limiting the comparison to a generalization of the temperate but rainy Pacific Northwest region, La Selva has wood loads that are smaller by a factor of ~4.

Lateral distribution of wood in the streams of La Selva appears to be controlled by hydraulics, but the longitudinal distribution has a much stronger stochastic component. Approximately 50% of the variability of wood load among the 30 sites could be explained by channel and instream wood characteristics. Nonetheless, because average recruitment rates of wood into the streams is expected to be nearly uniform (there is no landslide influence on recruitment), and because variables that might alter recruitment such as valley side slope had no predictive power for wood load, I suggest that fluvial transport of wood has more influence on wood distribution than recruitment processes.

The wood in the study streams is highly transient, with mean residence times estimated between 5 and 7 years. Wood is much more transient at La Selva than in studied temperate streams of the Pacific Northwest region (Keller and Tally, 1979b;

Lienkaemper and Swanson, 1987; Murphy and Koski, 1989; Hyatt and Naiman, 2001) and the Canadian Rocky Mountains (Powell et al., 2009), but has similar residence times to small streams in the semi-arid Colorado Rocky Mountains (Wohl and Goode, 2008). The relatively low residence time for wood at La Selva may be explained by flashier tropical floods, deeper flow depths, higher tropical decay rates, or any combination of these. Short residence times for the wood may prevent it from being as geomorphically effective as wood in temperate streams, but the high volume of wood cycling through the system has the potential to be an important nutrient source for the aquatic ecosystem and a significant component of the landscape-scale carbon budget (Lyons et al., 2002).

Potentially as a result of the transience of wood in the study streams, wood load has little influence on flow resistance. This is in stark contrast to studies in temperate streams that have found wood to be a primary influence on flow resistance, contributing as much as half of the resistance in spite of only covering 2% of the channel bed in one case (Manga and Kirchner, 2000). Although other explanations are not excluded, it seems plausible that the frequent transport of wood in this fluvial system has resulted in a configuration that has less influence on flow hydraulics than in comparable temperate zone streams. Because the tropical streams are adjusted to higher, more competent flows, the roughness contributed by bed material characteristics appears to overwhelm any contribution from instream wood.

Likewise, the intensely studied jam on Quebrada Esquina did not significantly influence the transport of tracer clasts, in spite of a temporary gravel wedge that developed behind the jam during a time of particularly effective flow impoundment. This finding is not as unexpected, since tracer clast transport has not been interrupted by jams in temperate streams, either (Haschenburger and Rice, 2004). However, wood removal has been shown to cause large increases in sediment yield in temperate-zone streams (Smith et al., 1993a; Assani and Petit, 1995). The evacuation of the temporary gravel wedge from behind the study jam indicates that there is the potential for increased yield from the Esquina as well, but it is less clear if this increase will be significant compared to the unimpeded sediment yield.

An additional forest-stream interaction that I document in this study is a link between daily evapotranspiration demand on the forest and discharge in the stream. By tracking the diel cycles in stream stage at the gaging site on El Surà, I demonstrate that changes in flow can be predicted by changes in vapor pressure differential. Some hydraulic properties of the subsurface were inferred in the changing rates of nightly stream stage recovery, suggesting that at high stages and high groundwater levels hydraulic gradient controls the flow of groundwater into the stream, but at low stages transmissivity becomes the dominant control. Hydraulic conductivity appears to increase toward the soil surface, potentially as a result of bioturbation.

This research indicates that 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 equally important for ecosystem function, particularly in lower gradient reaches where it is the primary stable substrate. If managers determine that wood is necessary for tropical stream function, then the transience of the wood may become a challenging issue. Engineered wood structures will be more difficult to maintain than in temperate streams. Likely the best solution would be to preserve riparian buffer forests in logged or managed watersheds, so that the natural supply of wood to the stream system may be maintained.

La Selva is not likely to be representative of all wet tropical fluvial systems. For example, wood dynamics are dramatically different on the Rìo Chagres, Panama, where landslides control wood delivery to the stream (Wohl et al., 2009). This suggests my interpretations of input controls are limited to low relief watersheds. Transport controls, however, could be more universal within the wet tropics. Because I expect tropical floods to quickly break apart landslide-induced jams, I predict that the wood residence times found for La Selva will be applicable at sites with similar ranges of gradient, flow, and bed material size, regardless of the prevalence of debris flows and landslides.

7.2 Synthesis: Relative importance of individual variables in a wood budget

Wood can enter a reach laterally, from the banks and connected hillslopes, or be fluvially transported into the reach from upstream sources. Wood can exit a reach laterally, by deposition onto the floodplain or incorporation into laterally accreted sediment, or be fluvially transported downstream. These processes have been summarized as a wood budget by Benda and Sias (2003). They propose that changes in wood storage ΔS_c (m^3/m) in a channel reach of length x (m) over time t (yrs) can be calculated as:

$$\Delta S_c = [L_i - L_o + Q_i/\Delta x - Q_o/\Delta x - D]\Delta t \qquad (7.1)$$

where L_i is lateral wood recruitment rate (m^3/m/yr), L_o is loss of wood to overbank deposition and channel movement (m^3/m/yr), Q_i is fluvial transport of wood into the channel segment (m^3/yr), Q_o is fluvial transport out of the segment (m^3/yr), and D is decay (m^3/m/yr). I suggest a slight rearrangement of terms in order to emphasize the parallels between the wood budget equation and the continuity equation for water within a channel segment of unit width, yielding:

$$\frac{\partial V_{\mathrm{w}}}{\partial t} = \left[L_{\mathrm{i}}x - L_{\mathrm{o}}x + Q_{\mathrm{i}} - Q_{\mathrm{o}} - Dx\right] \qquad (7.2)$$

where V_{w} is the volume (m^3) of wood stored within the reach of length x. In this equation Q_{i} and Q_{o} are still the flux of wood across the upstream and downstream boundaries, respectively, and all variables have the same units as in equation (7.1).

Equation (7.2) provides a framework for understanding the dynamics of instream wood. But evaluating the various components of the equation is very difficult in most cases. Evaluating the changing contribution of each variable across climate zones is one way to quantify these difficult-to-measure characteristics. For example, if it can be established that decay rate correlates with mean annual temperature, then temperature can be used as a surrogate for decay, rather than expending effort in directly measuring this highly heterogeneous process. As a starting point, I present a generalized comparison of the relative importance and the controls on each variable at La Selva.

The lateral inputs component of this equation comes from a range of sources. Benda and Sias (2003) parameterized lateral inputs with the equation:

$$L_{\mathrm{i}} = I_{\mathrm{m}} + I_{\mathrm{f}} + I_{\mathrm{be}} + I_{\mathrm{s}} + I_{\mathrm{e}} \qquad (7.3)$$

where I_{m} is chronic 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. At La Selva I_{m} is dominant, with secondary contributions from I_{be}. Both I_{f} and I_{s} were not observed, while a single log was observed being exhumed from the bank in a low gradient reach. The relative importance of these components is not representative of all tropical headwater streams. For example, wood inputs to the Rìo Chagres in Panama are dominated by landslide inputs triggered during tropical storms (Wohl et al., 2009).

The other components of the wood budget were not parameterized by Benda and Sias (2003). In order to further extend this concept, I here propose equations for the other components of equation (7.2). For the lateral outputs:

$$L_o = O_f + O_a + O_m \qquad (7.4)$$

where O_f is overbank flood deposition outputs, O_a is abandonment of wood by avulsion or meander cutoff, and O_m is incorporation of wood in point bar sedimentation by meander migration. In the course of the study, I observed at least 5 pieces exported onto the floodplain. No avulsions were observed. O_m is difficult to evaluate, because although I did observe wood buried in silt, it is very likely that it would be remobilized in a flood before the channel migrated sufficiently to allow stabilization of the deposit. In any case, the floodplains of the study streams were very limited and no scroll topography was observed. Thus, O_f appears to dominate the L_o term at La Selva.

Equations for the fluvial transport components are more complex, in that terms are not simply additive and mobility will depend on the frequency distribution of wood size as well as flow magnitude. I recommend that fluvial transport of wood be considered on a per-flow-event basis, and suggest the following equations for each event:

$$Q_i = (S_u)M_u(1-J_u)J \qquad (7.5)$$

$$Q_o = S_c M(1-J) \qquad (7.6)$$

where S_u is upstream wood storage at the beginning of the transport event, S_c is wood storage within the reach, M_u is the proportion of the wood upstream of the reach that is mobilized, M is the proportion of wood within the reach that is mobilized, J_u is the upstream trapping efficiency of jams, boulders, bank irregularities, and other obstructions, and J is the trapping efficiency within the reach. M_u and M will be functions of wood transportability (T), stream competence (C), and possibly J_u or J as well. T will be a function of wood length relative to the channel width, wood diameter relative to the flow depth, and wood density. C will be a function of event discharge, channel slope, and channel roughness. Because wood commonly floats, it could be argued that competence only depends on flow depth, regardless of stream power. But as wood becomes waterlogged or buried, stream power will become increasingly important. Trapping efficiency will be a function of wood mobility (basically T, above), transport capacity of the stream (basically C, above), key piece abundance, sinuosity, the degree to which jams completely span the channel, and the frequency and abruptness of channel constrictions.

Because these two functions are so complex, and the value of M is so difficult to calculate, the relative importance of each component can only be roughly estimated. Channel-spanning jams are rare at La Selva, with seven observed in the 1.5 km of channel surveyed. If jams are defined as groups of at least three wood pieces in contact with one another, 42% of the pieces are in jams. Therefore, jamming is probably a minor component, although the other factors that affect J, such as boulder or constriction trapping, could be important. Large floods and the low retention rates and mean residence times of the wood suggest that C will be very important.

If equation (7.6) is accurate, there is the potential for self-enhancing feedback with equation (7.2), because of the dependence of fluvial transport out of the reach on wood storage within the reach and the dependence of wood storage in the reach on fluvial transport out of the reach. Essentially this is saying that jams trap wood, creating larger jams and trapping more wood.

Finally, the decay component can be calculated as:

$$D = S_c F_s R_d \quad (7.7)$$

Where S_c is the reach wood storage, F_s is a wood surface area conversion factor (m^2/m^3, i.e., the average surface area per unit volume of wood), and R_d is the decay rate of wood (m/yr, i.e., the rate at which the wood surface retreats). The spatial variability of R_d is expected to be very high, and the value will depend on temperature, microbial or fungal diversity, wood characteristics, frequency of wetting or drying, and degree of abrasion by sediment transport (Aumen et al., 1983; Melillo et al., 1983; Bilby et al., 1999; Bucher et al., 2004). As with Q_o, decay will be a function of the wood volume in the reach, the very quantity it is being used to estimate. This will lead to an interaction between the two, and likely make equation (7.2) indefinite except in environments where D is negligible relative to L and Q. Because the terms are multiplicative, they will all have equal influence on the value of D; a doubling of any of the three will lead to doubling D.

Comparing the relative importance of all the major components of the wood budget is somewhat qualitative. At La Selva, wood input is dominated by L_i, with secondary influence from Q_i. This statement may at first appear to contradict a primary conclusion of Chapter 2, that fluvial transport differences between the study sites is a greater influence on site-to-site wood load variation than is lateral input differences between the sites. However, the results of Chapter 2 more precisely show that Q_o has a greater influence on wood load at a site than L_i, leaving open the possibility that L_i may be more influential than Q_i. Wood introduction appears to be rather constant from reach to reach; it is the preferential removal of wood from high energy reaches that leads to spatial variation in wood load. The ratio of L_i / Q_i is difficult to estimate since sourcing wood was not attempted in this study, and could be considered either in terms of pieces or volume. But because of the high discharges observed in the study streams, and the relative scarcity of jams that might trap passing wood, I suspect the ratio may be higher than in similar temperate streams. This supposition is based on the reasoning that once wood is mobilized it is more likely to break apart than come to rest again because of the high energy of the floods and the predominance of highly decayed pieces in the stream which are unlikely to survive transport.

Wood output is dominated by Q_o, with very few instances of export onto the floodplain being observed. Larger rivers, with well developed floodplains, will likely have higher ratios of L_o / Q_o regardless of the climatic setting. Furthermore, many tropical streams, including those at La Selva, have multiple floods each year with magnitudes similar to the annual flood, as opposed to temperate streams where the annual maximum flow series is a good indicator of formative flows. Thus there are more transport events to which equations (7.5) and (7.6) should be applied.

Although each of the terms so far discussed was difficult to measure in the field, the most difficult term to quantify was decay. An estimate of the D/Q_o ratio is limited by the short duration of the wood decay study, but I suspect it is quite low. Wood that was frequently exposed to the air rotted quickly, but the submerged wood stayed quite sound for 2.3 years, and fluvial outputs were so high that they should dominate. An effect of decay that is not incorporated into equation (7.7) is the weakening of otherwise immobile wood, and its subsequent breakage and transport. It is not clear if this specific process of removal should be considered decay or fluvial export. Because of the high tropical decay rates, one might assume that D/Q_o is higher than similar temperate streams, yet in temperate streams with very low flows and low wood mobility, decay may dominate the wood export, even if the absolute value of decay is much lower than at La Selva.

This study enables simplification of equations (7.2) through (7.7) by elimination of the components which are negligible at La Selva. In the reduced equations below, the most influential components are shown in bold font.

$$\frac{\partial V_w}{\partial t} = \boldsymbol{L_i}\,x - L_o\,x + Q_i - \boldsymbol{Q_o} - \boldsymbol{D}x \qquad (7.8)$$

$$L_i = \boldsymbol{I_m} + I_{be} \qquad (7.9)$$

$$L_o = O_f \qquad (7.10)$$

$$Q_i = (S_u)\boldsymbol{M_u}(1\text{-}J_u)J \qquad (7.11)$$

$$Q_o = S_c\boldsymbol{M}(1\text{-}J) \qquad (7.12)$$

$$D = S_cF_s\boldsymbol{R_d} \qquad (7.13)$$

The variables are wood volume in the reach (V_w), reach length (x), lateral inputs (L_i), mortality input (I_m), bank erosion input (I_{be}), lateral outputs (L_o), floodplain deposition output (O_f), fluvial inputs (Q_i), upstream storage (S_u), proportion mobilized upstream (M_u), trapping efficiency upstream (J_u), trapping efficiency in the reach (J), fluvial outputs (Q_o), storage in the reach (S_c), proportion mobilized in the reach (M), decay (D), surface area conversion factor (F_s), and wood surface retreat rate or decay rate (R_d). The variable J may also merit bold font in equations (7.11) and (7.12), for the reason that it appears to have a very small value rather than a large value. Low values of J would contribute to the low Q_i and high Q_o. As a comparison for La Selva, a landslide-dominated wet tropical stream, such as the Rio Chagres, Panama, would likely have similar relative importance of controls on the total budget in equation (7.8), with the possible exception that decay may not merit the bold font. But the lateral inputs equation would be dominated by landslide inputs (I_s), with a relatively minor role played by I_m.

7.3 Future work

As can be deduced from the synthesis, there are many productive lines of future research: essentially, working to quantify each component of the wood budget in a diversity of environments. Intensive monitoring efforts such as this research will likely continue to yield useful results. Determining the source of wood entering the study reaches will greatly enhance such studies, helping to determine the relative importance of L_i and Q_i. This has already been attempted (May and Gresswell, 2003a), but except when the source of lateral wood is obvious, such as a debris flow, such differentiation has proved to be very difficult. A more frequent monitoring regime than that employed in this study should solve this issue. Surveys timed immediately following floods should reveal the Q_i component, while inter-flood surveys should be able to identify lateral inputs.

Long-term decay studies have the potential to resolve the rate and importance of *D*. The six logs attached to bridge piers over the course of this study provide useful information, but longer and better planned efforts are highly recommended.

Determining mean residence time from observed retention rates over 3 years, as was done in this study, requires the assumption of steady-state conditions. Although this appears valid at La Selva, it is far from certain if this assumption is sound at other sites. Dendrochronology is a very promising approach to estimating long-term residence times, and I highly recommend the acquisition of this kind of data in the temperate zone to expand the number of sites among which comparisons can be made, but it is useless in the tropics where annual tree rings do not form. Thus, longer studies with similar design to this project may be necessary to quantify wood residence time in tropical streams with episodic wood loading. The lack of mass movement at La Selva is likely to be something of an anomaly among tropical forest streams, so I recommend focusing future tropical wood monitoring efforts on catchments where debris flows have been observed.

Broadening the diversity of environments in which instream wood is studied is key to differentiating the influence of environmental factors such as precipitation and temperature. Climate is not a binary variable, temperate and tropical, although this dissertation has emphasized this dichotomy. Rather, subtropical, dry tropical, and seasonal tropical environments are intermediaries, and have the potential to reveal climatic thresholds in wood dynamics. Similarly, a systematic analysis of wood across the gradient of humid temperate to semi-arid temperate streams may increase our understanding of the influence of precipitation.

Finally, stochastic computer models of wood transport, considering individual wood pieces and a sequence of discrete flow events, would provide a means of testing the relative importance of the various components of the wood budget. They could also help identify interactions among the factors that vary across climates, by enabling analysis of factor combinations that are not found in nature. Parameterization of such models would greatly benefit from the field data acquisition described above, but they also have the potential to help narrow the focus of the field data acquisition efforts in advance.

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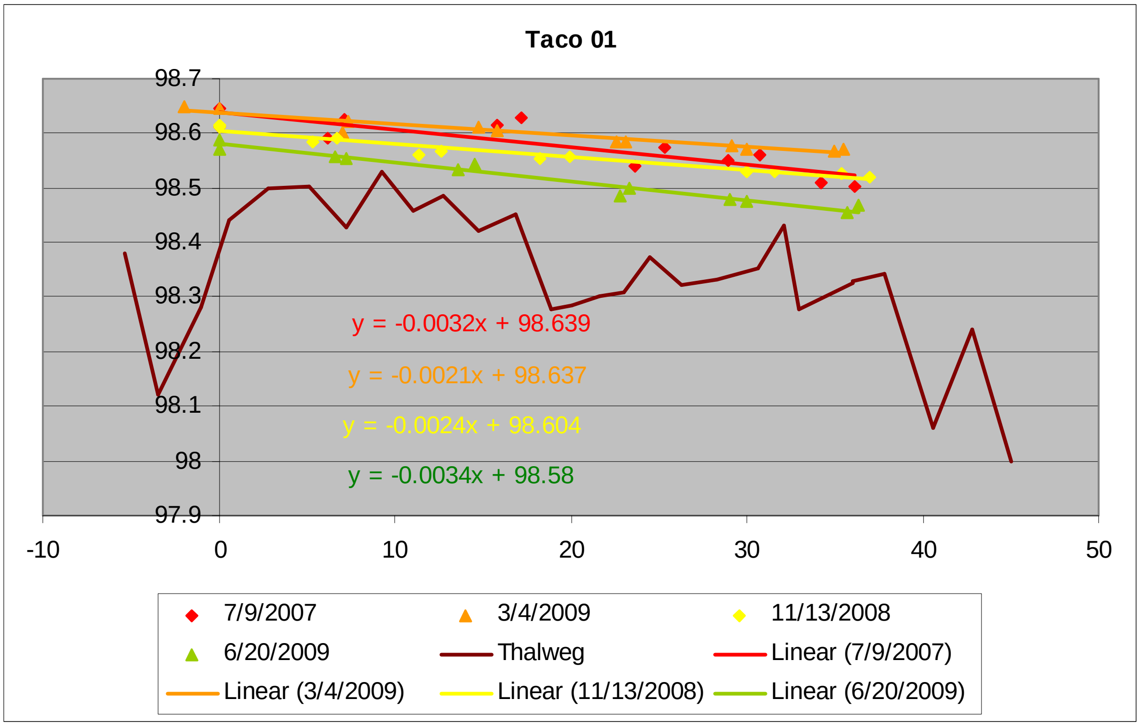
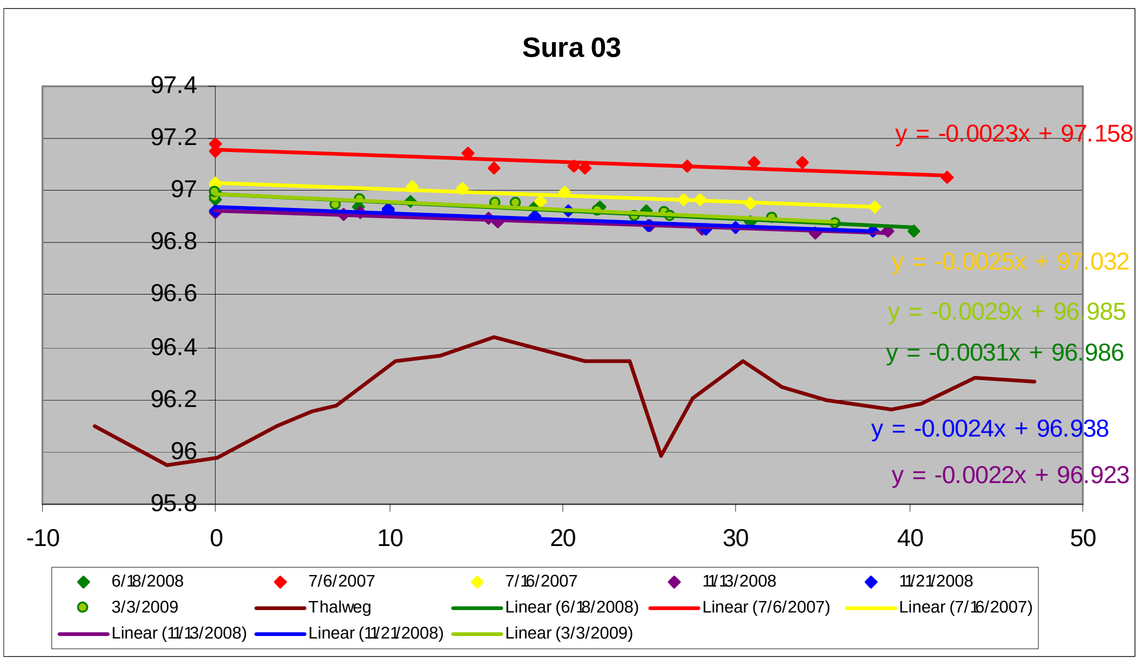
APPENDIX A

Flow resistance study reach profiles. A.1) Taconazo 01, A.2) Sura 03, A.3) Sura 05, A.4)Esquina 17, A.5) Esquina 20, A.6) Esquina 21. Downstream distance on x-axis and elevation above arbitrary datum on y-axis, both in meters. Each site has a unique elevation datum.

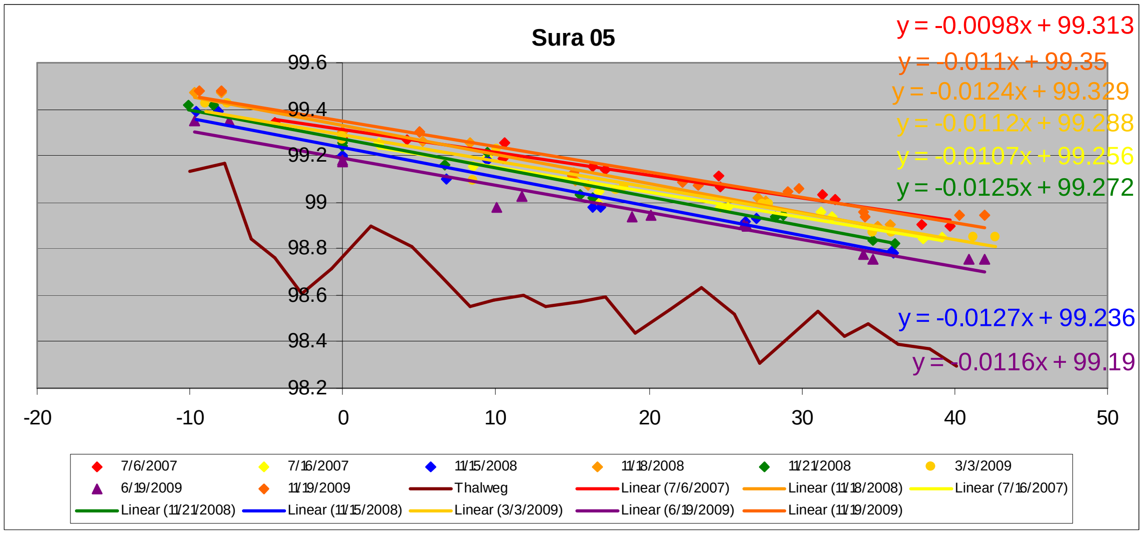
A.1.



A.2.

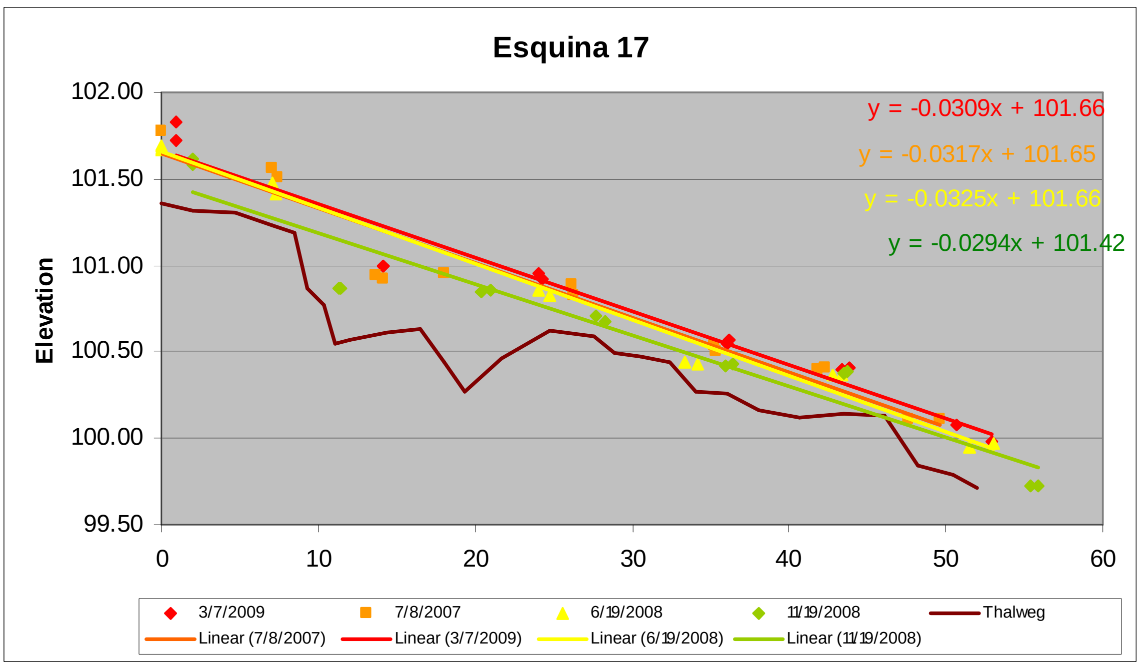


A.3.



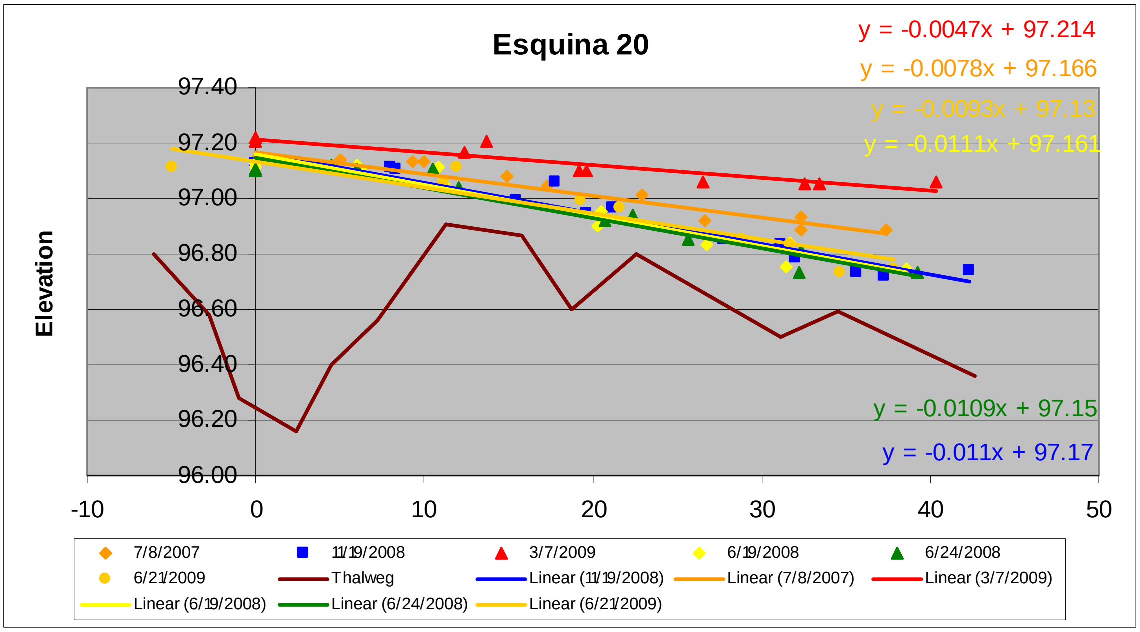
Sura 05
y = -0.0098x + 99.313
y = -0.011x + 99.35
y = -0.0124x + 99.329
y = -0.0112x + 99.288
y = -0.0107x + 99.256
y = -0.0125x + 99.272
y = -0.0127x + 99.236
y = -0.0116x + 99.19
99.6
99.4
99.2
99
98.8
98.6
98.4
98.2
-20
-10
0
10
20
30
40
50
7/6/2007
7/16/2007
11/15/2008
11/18/2008
11/21/2008
3/3/2009
6/19/2009
11/19/2009
Thalweg
Linear (7/6/2007)
Linear (11/18/2008)
Linear (7/16/2007)
Linear (11/21/2008)
Linear (11/15/2008)
Linear (3/3/2009)
Linear (6/19/2009)
Linear (11/19/2009)

A.4.

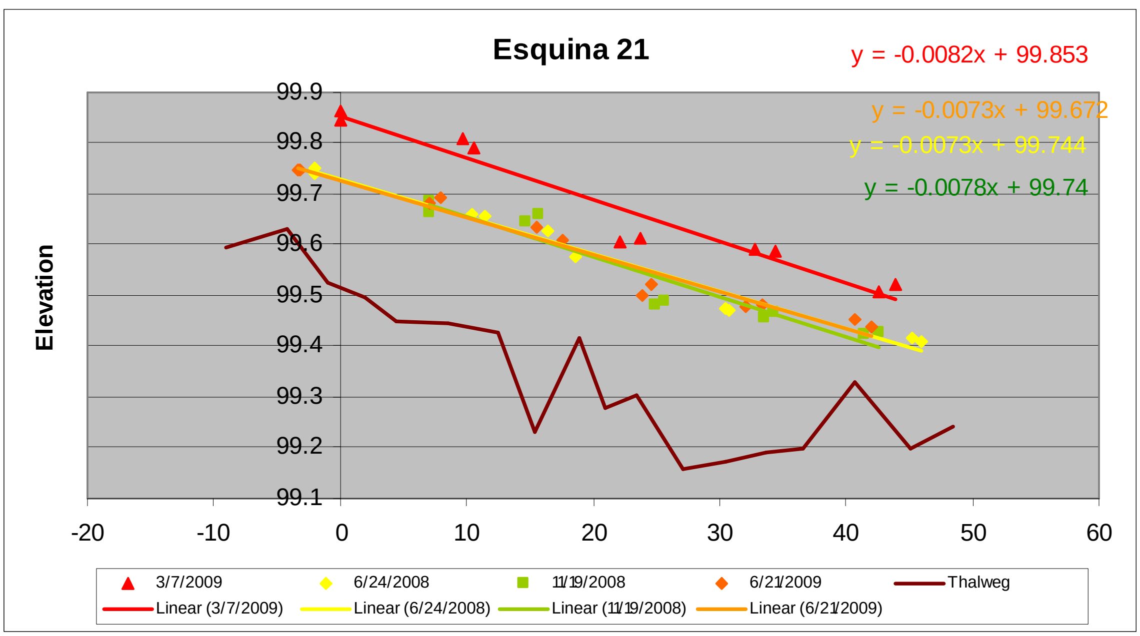


Esquina 17
y = -0.0309x + 101.66
y = -0.0317x + 101.65
y = -0.0325x + 101.66
y = -0.0294x + 101.42
Elevation
102.00
101.50
101.00
100.50
100.00
99.50
0
10
20
30
40
50
60
3/7/2009
7/8/2007
6/19/2008
11/19/2008
Thalweg
Linear (7/8/2007)
Linear (3/7/2009)
Linear (6/19/2008)
Linear (11/19/2008)

A.5.


Esquina 20
y = -0.0047x + 97.214
y = -0.0078x + 97.166
y = -0.0093x + 97.13
y = -0.0111x + 97.161
y = -0.0109x + 97.15
y = -0.011x + 97.17
Elevation
97.40
97.20
97.00
96.80
96.60
96.40
96.20
96.00
-10
0
10
20
30
40
50
7/8/2007
11/19/2008
3/7/2009
6/19/2008
6/24/2008
6/21/2009
Thalweg
Linear (11/19/2008)
Linear (7/8/2007)
Linear (3/7/2009)
Linear (6/19/2008)
Linear (6/24/2008)
Linear (6/21/2009)

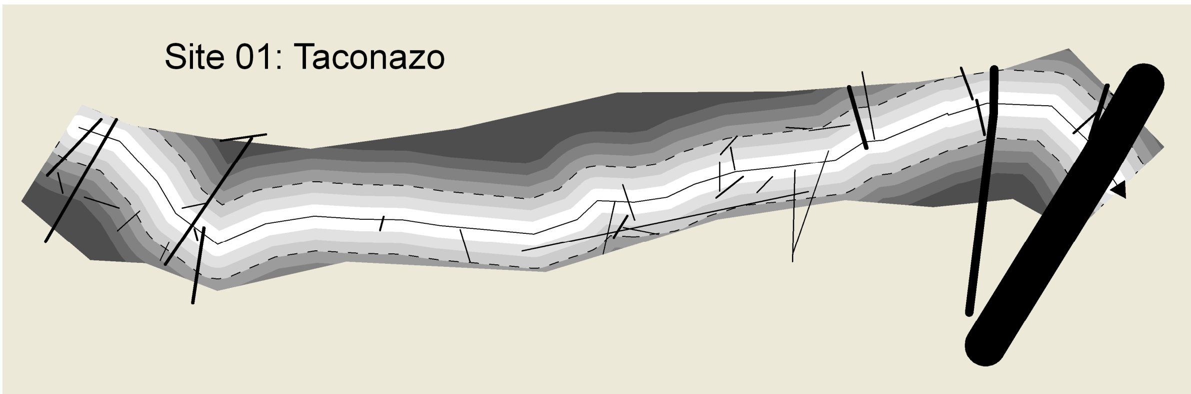
A.6.


Esquina 21
y = -0.0082x + 99.853
y = -0.0073x + 99.672
y = -0.0073x + 99.744
y = -0.0078x + 99.74
Elevation
99.9
99.8
99.7
99.6
99.5
99.4
99.3
99.2
99.1
-20
-10
0
10
20
30
40
50
60
3/7/2009
6/24/2008
11/19/2008
6/21/2009
Thalweg
Linear (3/7/2009)
Linear (6/24/2008)
Linear (11/19/2008)
Linear (6/21/2009)

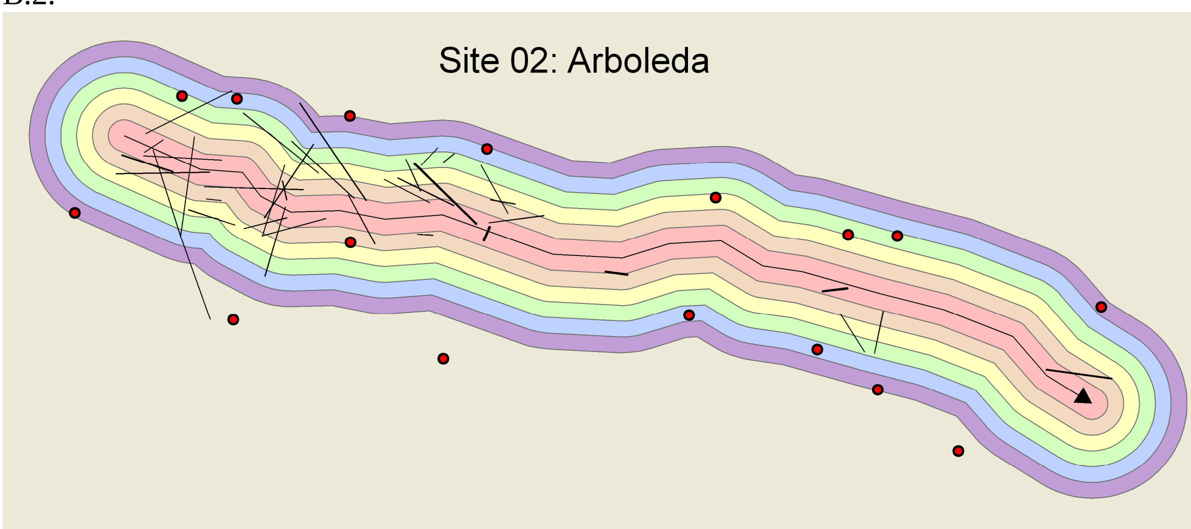
APPENDIX B

Maps of wood distribution in March 2007 within the 10 long-term study reaches. Thick black lines indicate wood pieces, with thickness of line proportional to the cross sectional area of the piece. Thalweg is indicated with thin black line with arrow. Shades of gray or color represent increasing distance from the thalweg. Gray scale figures have thalweg distance zones trimmed to match the surveyed active channel. Red dots in the color figures indicate surveyed active channel margin points.

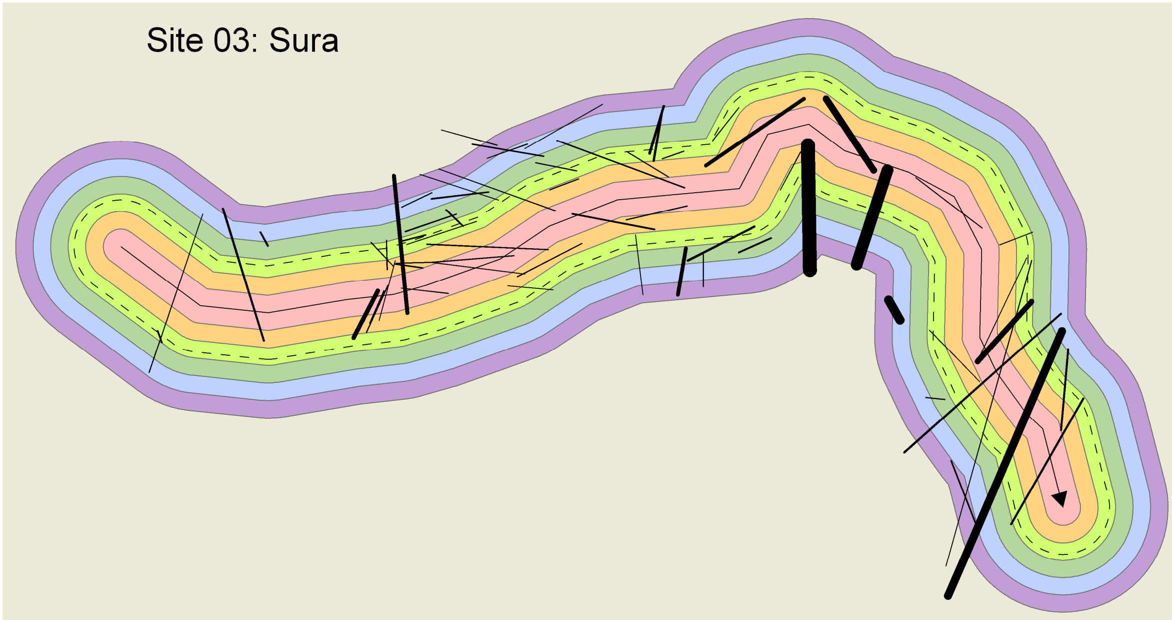
B.1.



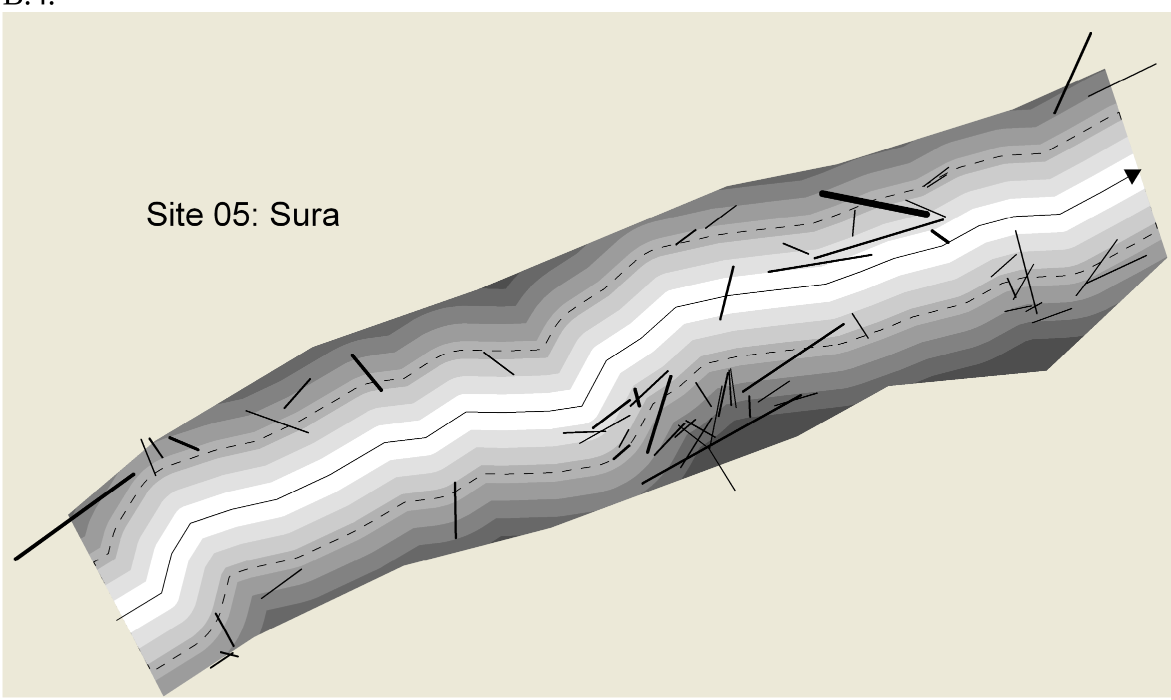
B.2.



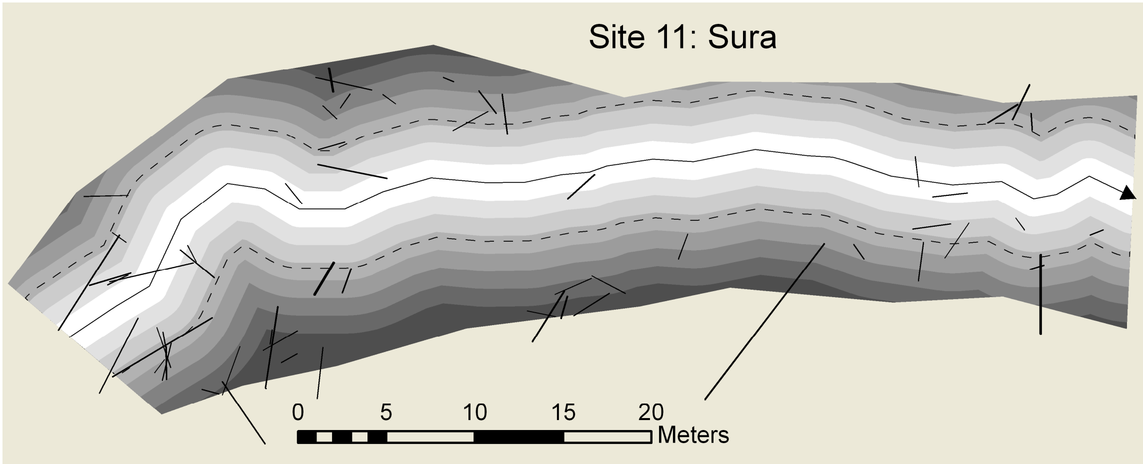
B.3.



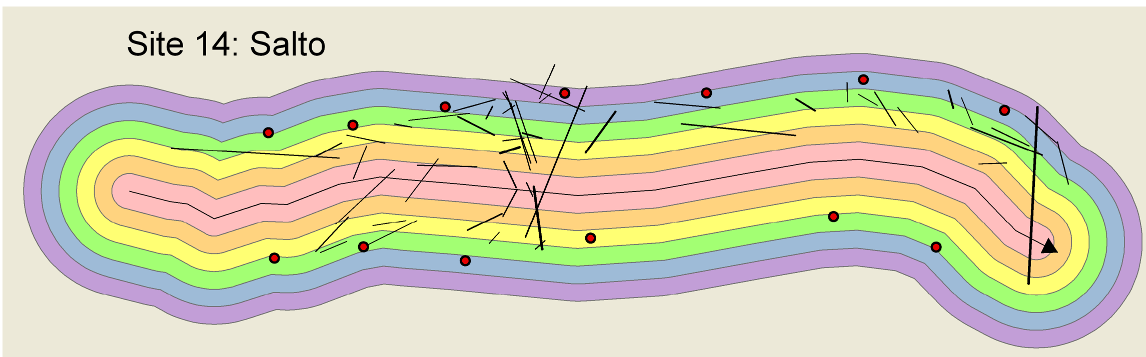
B.4.



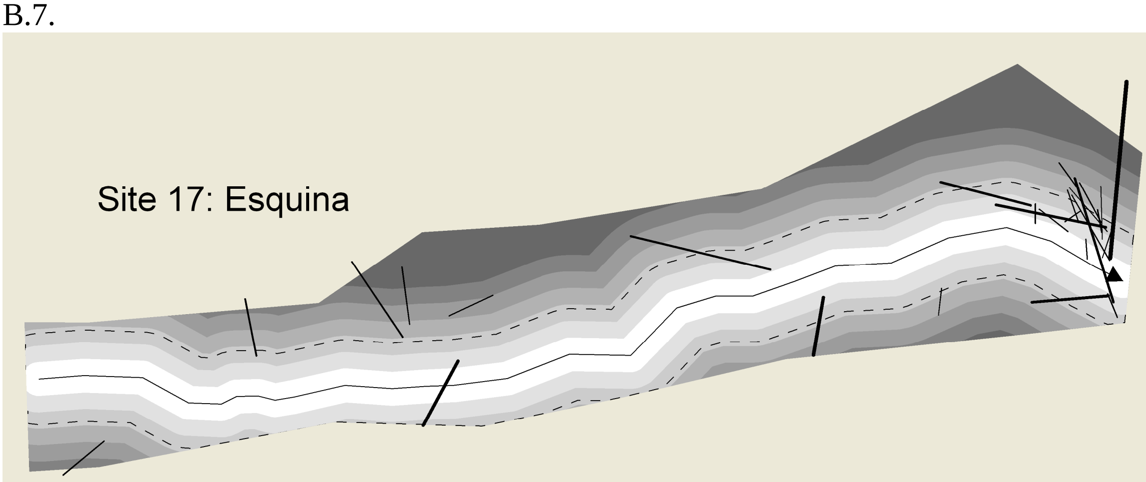
B.5.



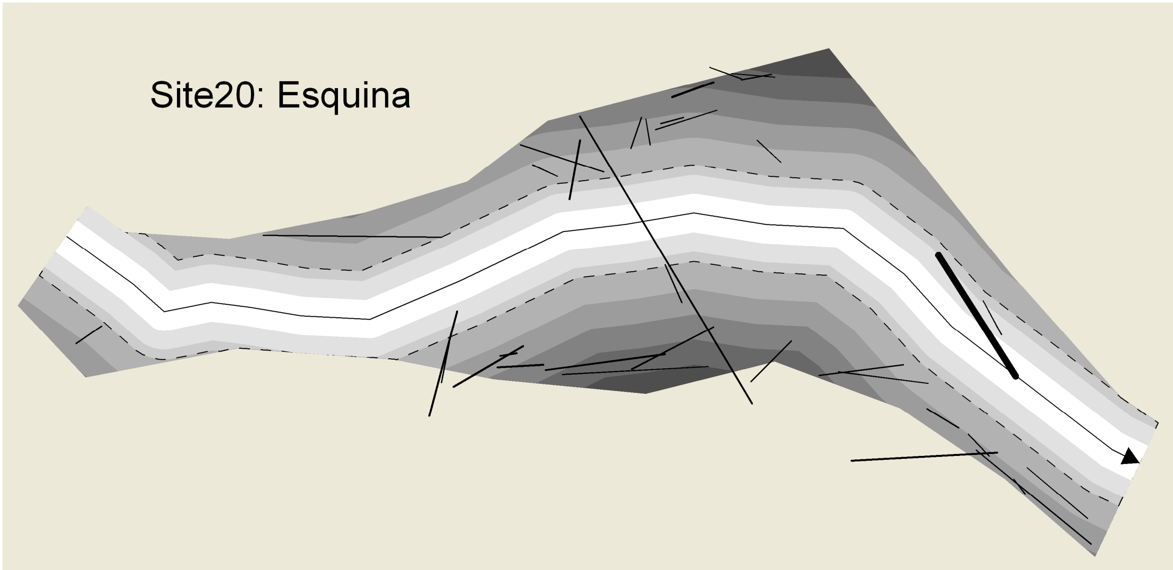
B.6.



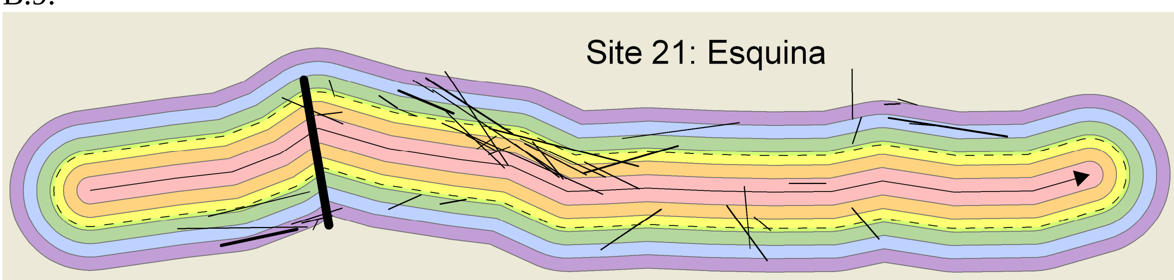
B.7.



B.8.



B.9.



B.10.