Elsevier Editorial System(tm) for Geomorphology
Manuscript Draft

Manuscript Number:

Title: Local and watershed controls on large wood storage in a mountainous stream network

Article Type: Research Paper

Keywords: large wood; wood storage; wood volume; floodplain; in-channel; out-of-channel

Corresponding Author: Mr. Matthew Christopher Vaughan, M.S.

Corresponding Author's Institution: University of California, Davis

First Author: Matthew Christopher Vaughan, M.S.

Order of Authors: Matthew Christopher Vaughan, M.S.; Gregory B Pasternack, PhD; Anne E Senter, MS; Helen E Dahlke, PhD

Abstract: A combination of differing large wood (LW) storage metrics and LW nomenclature used in previous studies has led to the current conceptualization that LW storage generally decreases downstream through a mountainous stream network. This study provides evidence that this conceptual model may be misguided. The goal of this study was to investigate numerous and diverse local and watershed scale variables that might control LW storage as well as to assess downstream trends in LW storage. The testbed catchment was the 2,874 km2 mountainous Yuba River watershed in northern California, USA, which is mostly forested and impacted by flow manipulation and hydraulic gold mining. One hundred fourteen stream sites of drainage areas ranging from < 1 km2 to > 1,000 km2 were inventoried for LW (length > 1 m, diameter > 10 cm), and the LW volume of storage per channel length was calculated. Potential control variables were derived from a 10-m digital elevation model and measured or estimated in the field. Nonparametric Mann-Whitney U tests showed that the total LW volume per channel length did not decrease in the downstream direction based on drainage area, and was highest in 3rd order streams. Using the Akaike Information Criterion for multiple linear regression model selection, bankfull channel width, local shrub cover and percent of contributing stream cells over intrusive igneous geologies were significant positive predictors of total LW volume per channel length. Local side slope and percent contributing stream cells in urban areas were significant negative predictor variables in the model. Models run at smaller spatial scales successfully identified which subbasins and elevation bands were driving controls on LW storage. A higher percentage of LW volume was found outside of baseflow-wetted channels in downstream reaches than in upstream reaches, suggesting that lateral distribution of LW is impacted by channel morphology and drainage area, and that surveying for LW only within the bankfull channel neglects a significant portion of the LW budget available for fluvial transport. In addition, results suggest that LW deposition onto floodplains may have been previously understated when considering LW supply and transport capacities in streams of different drainage areas.

Suggested Reviewers: Samantha Capon PhD
Australian Rivers Institute, Griffith University
s.capon@griffith.edu.au
Riparian and flooplain ecology

Adelaide Johnson PhD

Hydrologist, PNW Research Station, USDA Forest Service
ajohnson03@fs.fed.us
Hydrologist, geomorphologist

Lenka Kuglerova PhD
Ecology and Environmental Sciences, Umea University
lenka.kuglerova@emg.umu.se
Riparian vegetation scientest

Bernadette Blamauer PhD
Institute for Water Management, Hydrology, and Hydraulic Engineering, University of Natural Resources and Life Sciences, Vienna
bernadette.blamauer@boku.ac.at
Riparian vegetation, fluvial geomorphology

Gregory Egger PhD
Karlsruhe Institute for Technology, University of the State of Baden-Wuerttemberg
gregory.egger@umweltbuero.at
Riparian woodlands, large wood

Virginia Garófano-Gómez PhD
Hydraulic Engineering and Environment, Polytechnical University of Valencia
virginiagarofano@gmail.com
Riparian vegetation, fluvial geomorphology

Jung I Seo PhD
Forest Resources, Kongju National University
jiseo.watershed@gmail.com
Hydrology, forest ecosystems, GIS, geomorphology

Martin Doyle PhD
Nicholas School of the Environment, Duke University
martin.doyle@duke.edu
Large wood, fluvial geomorphology

Jeff Opperman PhD
Great Rivers Partnership, The Nature Conservancy
jopperman@tnc.org
Floodplain ecology

John Stella PhD
Forest and Natural Resources Management, SUNY Environmental Science and Forestry
stella.jc@gmail.com
Riparian and stream ecology

UNIVERSITY OF CALIFORNIA, DAVIS

BERKELEY • DAVIS • IRVINE • LOS ANGELES • RIVERSIDE • SAN DIEGO • SAN FRANCISCO | SANTA BARBARA • SANTA CRUZ

LAND, AIR AND WATER RESOURCES
WATERSHED HYDROLOGY & GEOMORPHOLOGY LAB
219 VEIHMEYER HALL
(585) 506-5565

ONE SHIELDS AVENUE
DAVIS, CALIFORNIA 95616

November 20th, 2014

Geomorphology

Dear Editor:

We are writing on behalf of our submission of the research paper, "Local and watershed controls on large wood storage in a mountainous stream network" for publication in Geomorphology.

We previously submitted this manuscript to Ecological Applications. Their reviewers returned the manuscript with many positive reviews, and suggested that we submit to Geomorphology instead. We have addressed all Ecological Application reviews calling for revision and improvement, and have included the details of our revision in our submission.

We believe that this study provides a major step forward in the understanding of large wood distribution at the watershed scale. A combination of large wood storage metrics and nomenclature has led to the current conceptualization that large wood storage generally decreases in the downstream direction throughout a stream network. Our data from the Yuba River watershed along with a robust statistical analysis showed that no such simple trend existed, and a mix of watershed and local controls were able to significantly predict large wood storage. In addition, smaller spatial scales were investigated so that individual control factors could be traced back to the subbasin where the effect was greatest. Changes in lateral distribution were also investigated, since our field surveys included floodplains, while most others have not. These types of analyses have not been done on a mountainous watershed with a similar disturbance history to that of the Yuba River watershed. In addition, our findings are put into context with the existing literature, and a new conceptual model for large wood distribution is outlined.

We understand that the scope of Geomorphology includes the development of scientific principles to support environmental decision-making and management, and that articles on the dynamics of large wood in streams have been included in the journal commonly before. We believe that this manuscript is in line with the goals of the journal to present significant and novel science, and would provide a unique and valuable perspective to the understanding and management of large wood in streams.

In order to obtain high-quality, independent reviews of our manuscript at a time when the response rate of potential reviewers can be low, we are providing a list of ten potential reviewers who are American and international experts on riparian science and large wood. We have never discussed this manuscript with any of those listed or collaborated with any of them on research projects. See below. Meanwhile we have to report two experts whom we have conflicts of interest with regarding this manuscript. Those two are Dr. Herve Piegay whom we are collaborating with on another large wood manuscript and Dr. Ellen Wohl whom we have discussed this manuscript and research with extensively.

This manuscript has not been previously published, nor is it currently under review in any other journal. Each co-author approves of this manuscript in its present form. Thank you for your consideration – we look forward to your response.

Sincerely,

Matthew Vaughan & Professor Greg Pasternack
Hydrologic Sciences Graduate Group

List of suggested reviewers:

Dr. Samantha Capon (s.capon@griffith.edu.au). Australian Rivers Institute, Griffith University.

Dr. Adelaide Johnson (ajohnson03@fs.fed.us). PNW Research Station, USDA Forest Service.

Dr. Lenka Kuglerova (lenka.kuglerova@emg.umu.se). Department of Ecology and Environmental Sciences, Umea University.

Dr. Bernadette Blamauer (bernadette.blamauer@boku.ac.at). Institute for Water Management, Hydrology and Hydraulic Engineering, University of Natural Resources and Life Sciences, Vienna.

Dr. Gregory Egger (gregory.egger@umweltbuero.at). Karlsruhe Institute for Technology, University of the State of Baden-Wuerttemberg.

Dr. Virginia Garófano-Gómez (virginiagarofano@gmail.com). Department of Hydraulic Engineering and Environment, Polytechnical University of Valencia.

Dr. Jung Il Seo (jiseo.watershed@gmail.com). Department of Forest Resources, Kongju National University.

Dr. Martin Doyle (martin.doyle@duke.edu). Nicholas School of the Environment, Duke University.

Dr. Jeff Opperman (jopperman@tnc.org). The Nature Conservancy.

Dr. John Stella (stella.jc@gmail.com). Department of Forest and Natural Resources Management SUNY College of Environmental Science and Forestry.

Title: Local and watershed controls on large wood storage in a mountainous stream network

Running Title: Controls on large wood storage

Authors: Matthew C. Vaughan*, Gregory B. Pasternack, Anne E. Senter, and Helen E. Dahlke

*Corresponding author. mcvaughan@ucdavis.edu

Address: Department of Land, Air, and Water Resources, University of California, One Shields Avenue, Davis, CA 95616-8626, USA

Abstract

A combination of differing large wood (LW) storage metrics and LW nomenclature used in previous studies has led to the current conceptualization that LW storage generally decreases downstream through a mountainous stream network. This study provides evidence that this conceptual model may be misguided. The goal of this study was to investigate numerous and diverse local and watershed scale variables that might control LW storage as well as to assess downstream trends in LW storage. The testbed catchment was the 2,874 km^2 mountainous Yuba River watershed in northern California, USA, which is mostly forested and impacted by flow manipulation and hydraulic gold mining. One hundred fourteen stream sites of drainage areas ranging from < 1 km^2 to > 1,000 km^2 were inventoried for LW (length $\geq$ 1 m, diameter $\geq$ 10 cm), and the LW volume of storage per channel length was calculated. Potential control variables were derived from a 10-m digital elevation model and measured or estimated in the field. Nonparametric Mann-Whitney U tests showed that the total LW volume per channel length did not decrease in the downstream direction based on drainage area, and was highest in 3rd order streams. Using the Akaike Information Criterion for multiple linear regression model selection, bankfull channel width, local shrub cover and percent of contributing stream cells over intrusive igneous geologies were significant positive predictors of total LW volume per channel length. Local side slope and percent contributing stream cells in urban areas were significant negative predictor variables in the model. Models run at smaller spatial scales successfully identified which subbasins and elevation bands were driving controls on LW storage. A higher percentage of LW volume was found outside of baseflow-wetted channels in downstream reaches than in upstream reaches, suggesting that lateral distribution of LW is impacted by channel morphology

and drainage area, and that surveying for LW only within the bankfull channel neglects a significant portion of the LW budget available for fluvial transport. In addition, results suggest that LW deposition onto floodplains may have been previously understated when considering LW supply and transport capacities in streams of different drainage areas.

Key words: large wood; wood storage; wood volume; floodplain; in-channel; out-of-channel

1. Introduction

1.1. Downstream Trends in LW Storage

Large wood (LW) stored in stream channels has substantial influences on stream ecology, stream hydraulics, channel morphology, and sediment dynamics (Keller and Swanson, 1979; Gurnell et al., 2002; Montgomery et al., 2003). The storage of LW in any stream is governed by a variety of processes causing input and output of LW. Input of LW into a stream reach can be caused by debris slide, avalanches, windthrow, bank erosion, and fluvial transport from upstream, while LW output can be caused by physical fragmentation, chemical decomposition, and fluvial transport by flotation (Swanson 2003). If these processes could be predicted reliably, calculating LW storage would be a simple operation. In practice, each of these processes is rather complex and stochastic. A more common approach to understand how LW storage is distributed in a stream network has been to measure LW storage in a stream and attempt to relate this to local and landscape scale variables (Fox and Bolton 2007, Baillie et al. 2008). Many LW studies have investigated longitudinal trends in LW storage throughout a watershed in order to understand how geomorphic processes are affected differently by LW at different spatial locations and scales in a stream network, since more LW volume per channel length or per channel area presumably increases effects on sediment trapping, habitat creation, step-pool creation, and other processes influenced by LW (Wohl and Jaeger 2009).

Several authors have reported that storage volumes of LW per channel area generally decrease downstream through a stream network, where increasing drainage area, stream order, channel width, or a combination of the three are used to define the downstream direction. Table 1 contains a summary of 22 studies that investigated downstream trends in LW storage. Of the eleven studies that calculated LW volume or biomass per channel area, ten showed a downstream decrease, with the exception of Seo and Nakamura (2009), who included the floodplain in surveys. Both studies that reported LW piece count per channel area (Montgomery et al., 1995; Baillie et al., 2008) also showed a downstream decrease.

Calculating LW volume per channel area is useful for aquatic habitat studies (Fausch and Northcote, 1992) or local effects of LW on channel morphology (Beechie and Sibley, 1997). A thought experiment shows that as streams become wider in the downstream direction through a watershed though, LW per channel area will decrease even if the total volume of LW storage in the stream at each cross-section is constant or random. Consider a hypothetical stream network with a constant longitudinal distribution of LW volume per length (e.g. 10 m^3 per 100 m). LW volume per channel area will decrease downstream in this stream network because channel area is explicitly correlated with channel width. It follows that volume per channel area is explicitly inversely correlated with channel width.

To represent LW storage volumes and find longitudinal trends that are statistically distinguishable from those in random data, it is proposed here that calculating and analyzing LW volume per channel length is preferable. This metric represents a cross-sectional sample of LW storage volume at each surveyed stream site for a given channel length, regardless of channel width or location within the stream network. Another advantage of this metric is that it represents the volume of LW that was deposited and is available for transport within the stream's reach. The seven studies listed in Table 1 for which LW volume per channel length was calculated observed an increasing trend, no trend, or an increase followed by a decrease in the downstream direction.

Terminology is problematic in papers investigating trends in LW storage. Studies have used terms such as LW “abundance,” “amount,” or “frequency” when citing works that showed that LW volume per channel area tends to decrease in the downstream direction (Bisson et al., 1987; Fetherston et al., 1995; van der Nat et al., 2003; Atha 2013). These terms could be misleading since they do not reflect the dimensionality of the metric involved. “Wood load,” is often used to represent LW volume per channel area, though the use of “load” in this context could also be misleading, since it is used differently in sediment dynamics, where it typically represents the total mass or volume of sediment passing a point or leaving a basin per unit time. In addition, studies that calculated LW volume per channel length and reported an increasing trend downstream (Martin and Benda, 2001; Fox and Bolton, 2007) have been noted as exceptions to the common trend of decreasing LW volume per channel area downstream without mention that a metric with different dimensionality was calculated (Wohl and Jaeger, 2009; Rigon et al., 2012). An effort was made here to reduce ambiguity by explicitly stating what metric was calculated each time it is discussed.

The combination of differing LW storage metrics and nomenclature has led to the current conceptualization that LW storage decreases downstream throughout a mountainous stream network. However, Table 1 indicates that this conclusion may be distorted by the methods applied to estimate LW storage. In addition to investigating this downstream trend in LW storage, this study aimed to directly test whether diverse topographic, land cover, disturbance history, and geological variables at local and watershed scales yielded a statistically significant effect on LW volume per channel length throughout the stream network. To facilitate that, the study was done for a watershed with a complex disturbance and management history in a region with a scarce record of LW dynamics, and tested the potential controls on multiple spatial scales.

1.2. LW Storage on Floodplains

A recent review of field techniques used in LW studies found that LW storage on floodplains was rarely considered (Macka et al., 2011), though wood on floodplains is known to influence flow resistance, conveyance, and channel-floodplain connectivity (Latterell et al., 2006; Wohl, 2013). Sediment storage on floodplains is a central part of the conceptual model for watershed scale sediment dynamics (Hooke, 2003; Owens, 2005), since sediment is often deposited on floodplains during flood events. Similarly, LW tends to mobilize primarily during high flows, including those that inundate floodplains (Fremier et al., 2010), so considering the LW storage both in the baseflow-wetted channel and outside of the baseflow-wetted channel on active floodplains would be reflective of what is available for downstream fluvial transport, and ultimately deposition in areas that are managed for LW.

When studies have mapped LW on floodplains, the standard practice has been to measure along sample transects within the study reach (O'Connor and Ziemer, 1989; Hering et al., 2000), which can introduce considerable error (Gippel et al., 1996; Warren et al., 2008). To the authors' knowledge, Seo and Nakamura (2009) and Lawrence et al. (2012) are the only prior studies that surveyed the active floodplain extent of each stream site, and the results of Seo and Nakamura (2009) suggested that LW volume per bankfull channel area actually increases downstream when active floodplains are considered in addition to baseflow channels. In this study, the entire active stream corridor, including floodplains and wetted channels were surveyed for LW. Observations were analyzed both in combination with and separately from each other to provide insight into lateral changes in LW distribution throughout a stream network. This approach fills a knowledge gap that exists due to the limited survey extents of previous studies.

1.3. Study Goals

The overall goals of this study were to (i) test for downstream trends in LW storage at the watershed scale, (ii) investigate what local and watershed scale variables might control LW storage, and (iii) investigate downstream trends in lateral LW storage distribution. To do so, a field study was conducted to measure LW storage throughout the Yuba River watershed in California’s northern Sierra Nevada. A stratified random sampling scheme was used at the watershed scale to allow robust statistical analyses. A wide range of physically based terrain indices were calculated in a Geographical Information System (GIS) and combined with field measurements in order to investigate local and watershed controls. Statistical analyses included categorical hypothesis testing and continuous multiple linear regression (MLR) modeling to predict LW storage based on indices and measured variables.

2. Study Area

The Yuba River watershed is located in California, USA. This study considers the watershed that drains to Englebright Dam (39°14'23.91"N, 121°16'9.32"W; WGS1984 datum), which was completed in 1940 to store alluvial deposits from hydraulic mining operations higher in the watershed. Its 2,590 km of streams drain an area of 2,874 km^2 on the western slope of the northern Sierra Nevada Mountain Range (Figure 1). The Yuba River headwaters fall from 2,777 m above mean sea level and meet Englebright Dam at 115 m above mean sea level. The watershed has three major subbasins: the North Yuba (1,271 km^2), Middle Yuba (544 km^2), and South Yuba (912 km^2).

The Northern Sierra Nevada has a Mediterranean-montane climate with hot, dry summers and cool, wet winters. Annual precipitation is generally 50 - 200 cm, depending on elevation. Approximately 70 - 90% of precipitation falls as snow from November to April above 1800 m elevation (Barbour et al., 1991; Mount, 1995). Dry conditions prevail from May to September with occasional summer thunderstorms. In addition to annual snowmelt, rain-on-snow floods driven by atmospheric rivers (Dettinger et al., 2011) have recurred approximately once a decade in the past 30 years, in 1986, 1997, and 2006. These episodically extreme climatic events generate large hydrographic spikes in discharge. Aerial imagery, reservoir management records, and reservoir manager anecdotes suggest that LW transport increases greatly during these events. Approximately six water years had passed since the last hydrologically extreme event at the time of the field surveys reported herein, with regular smaller floods occurring almost annually.

Vegetation patterns are similar across the Sierra, with interwoven bands of oak woodland, ponderosa pine, mixed conifer, white fir, red fir, and Lodgepole pine forests ordered by ascending elevation, and subject to variations in aspect and topography (Barbour et al., 2007). In addition to hillslope vegetation that occupies stream corridors, riparian vegetation can often be found alongside channels. The distribution of riparian species of willows, alder, cottonwood, and a variety of understory vegetation also depends on elevation, aspect, topography, as well as on stream channel geomorphology, geology, and availability of floodplains (Harris, 1989; Barbour et al., 2007).

Like many mountain catchments throughout the world, the one drained by the Yuba River has been subjected to significant anthropogenic impacts; in this case the largest impacts are associated with mining, timber harvesting, and flow regulation. Historic hydraulic gold mining, widespread forest and stream resource extraction, and modern development have combined to dramatically alter the Yuba River watershed. During the California Gold Rush of the mid-to-late 1800's, Yuba River morphology, riparian continuity, and aquatic ecology were impacted by hydraulic mining operations, wherein jets of highly pressurized water were directed onto mountain topsoil to slough lower-grade gold-bearing paleo-sedimentary gravels into gravity-separation sluice boxes. This high rate of landscape change was concentrated on gold-bearing ridge tops as well as in stream channels, where the mining tailings were shunted as a means of disposal. In all, about 522 x 10^6 m^3 of sediment were mobilized, the greatest amount of any basin in the Sacramento River network (Gilbert, 1917; James, 2005). Clear-cut timber harvesting supplied the mines with steam energy and the working population with heating and cooking fuel (McKelvey and Johnston, 1992). Though hydraulic mining was formally ended in 1884, surreptitious practices continued thereafter, many hillside scars have never recovered, and sedimentary debris is still widespread in river segments connected to source areas.

The watershed was also developed for water supply and hydroelectric power; it is now highly managed with impoundments and diversions. The most significant impoundment is New Bullards Bar Reservoir, which is near the outlet of the North Yuba River. Upstream of this reservoir the North Yuba catchment lacks any major impoundment, providing an undammed baseline for comparison with the other two regulated major tributaries. Nearly all LW that is deposited into this facility is removed and burned to ensure safety of recreational watercraft. Other major impoundments are Jackson Meadows Reservoir on the Middle Yuba River and Lake

Spaulding on the South Yuba River, which exports water to the Bear and American River watersheds (Snyder et al., 2004) (Figure 1). LW from these facilities passes over dams only during high flows.

3. Methods

3.1. Field Methods

As a key innovation to advance LW studies at the watershed scale, locations for field measurements were selected by a stratified random sampling scheme using an ArcGIS (v.10) geodatabase and the Microsoft Excel random number generator, so that the population of stream sites with a wide variety of contributing drainage area would be nearly equally sampled. Stratified random sampling and related variants using equal effort in each strata have not been widely applied in LW studies to date to capture watershed-scale relations, but are well known and used in field ecology (Johnson, 1980; Miller and Ambrose, 2000; Manly and Alberto, 2014) and hydrology (Thomas and Lewis, 1995; Yang and Woo, 1999). Drainage area was selected as the key variable upon which to stratify a watershed-scale study. Because it spans orders of magnitude in the Yuba watershed, it was necessary to bin logarithmically. Table 2 shows the half log-scale drainage area bins that were the basis for stratification to yield equal effort sampling spanning all scales and some basic characteristics of streams in each bin. Stream sections backflooded by reservoirs to the point that the effects were visible from satellite imagery were excluded from the selection process. Since the Yuba River watershed is a remote mountainous region, accessibility was included as a factor in site selection in that potential stream sites were restricted to within 1 km of an extensive primitive road network. This constraint removed only approximately 11% of the stream network from the selection process, leaving the vast majority available for stratified random sampling. A total of 150 sites were selected to yield an oversample list, and then based on available time and resources the first 114 random stream sites were visited from July to September 2012 (Figure 1).

The bankfull channel width was measured and recorded at each site, and the entire active stream corridor was searched for any unrooted LW (length $\geq$ 1 m, mean diameter $\geq$ 10 cm) from the stream site location to either 50 or 100 m upstream. Due to the diverse morphology of stream sites, the field indicators used to determine whether a floodplain was active varied. In general, these indicators included slope breaks at the edge of floodplains, fluvial deposition of alluvium or vegetative material, and presence of LW that had been stripped of branches and leaves by high flows. The decision of what upstream length to survey was based on timing and logistics, since some sites took longer to access or survey than others. The total distance surveyed in each contributing area bin was similar (1,050 – 1,300 m for bins 1-7; 800 m for bin 8). To quantifiably characterize each stream site based on factors that could influence LW generation and deposition, three local land cover variables were considered: the percent of the surveyed area that was covered by the canopy of mature living trees (known hereafter as "forest"), the percent covered by shrub foliage (known hereafter as "shrub") and the percent that was exposed bedrock (known hereafter as "bedrock"). Each variable was visually estimated independently by three surveyors, and the means of the estimates were recorded. Estimated percentages did not necessarily sum to 100%, since regions of forest, shrub, and bedrock could overlap.

Attributes of two types of LW were measured and recorded: solitary pieces and jams. Solitary pieces were those not touching any other LW piece and were not functionally connected to any other LW by a significant amount of small woody material. LW jams were defined as accumulations of two or more LW pieces that were either touching each other or were functionally connected by a significant amount of continuously connected small woody material. For all LW, it was recorded whether it was found primarily in the baseflow-wetted channel or outside of the baseflow-wetted channel. Although an initial attempt was made to distinguish locally generated LW from fluvially deposited LW, field indicators were not reliable, so this distinction was not used in any analyses.

For each solitary LW piece, the length from end to end (or base of rootwad) was recorded with a measuring tape, and the diameter at each end and rootwad diameter (if present) were measured with large forester calipers. Volume was calculated by assuming that each piece was a cylinder, with diameter equal to the mean of the diameters measured at each end. Rootwads were included in the LW volume calculation, as they are composed of wood and have been shown to contribute to LW stability (Braudrick and Grant, 2000; Manners and Doyle, 2008), though they have often been left out in many previous LW studies. This means LW volume will be calculated more accurately herein, but it is a source of discrepancy when comparing results to previous studies. If the piece had a rootwad, then the volume of the rootwad was approximated by half of an ellipsoid; its major axis was measured in the field, and a minor axis was set equal to the diameter of the LW piece above the rootwad. An estimated fifteen percent porosity was applied to the volume of the rootwad to account for spaces between roots flaring out of the main stem.

For each LW jam, the following parameters were measured and recorded: the longest dimension of the accumulation, the axis perpendicular to that measurement, the representative depth of the accumulation, and the approximate jam density as three categories: high, medium and low. The density categories were determined based on how easily another piece of LW could be inserted into the accumulation; care was given to keep this assessment consistent throughout the field season and the data was spot-checked using photographs.

Manners and Doyle (2008) measured density for LW jams in the Adirondack Mountains, New York, and developed a conceptual model based on the dynamics of wood jam evolution. Their results provided a framework for the estimates used here of 70%, 40%, and 10% density for high, medium and low density classifications, respectively. Initial LW jam volume was calculated by assuming that each jam could be represented by a shallow elliptical cylinder; porosity values were then applied to calculate a final estimated volume of LW within each jam. If a jam would not be well represented by an elliptical cylinder because of a significantly large-sized LW piece protruding out from the main accumulation, then the volume of that piece was calculated and added to the volume of the rest of the accumulation.

The storage volume of LW per channel length was calculated for each stream site by summing the volume of all LW pieces and jams, dividing by the channel length that was surveyed, then scaling to 100 m for all sites for comparative purposes. This metric represents a 100 m long cross-sectional sample of LW storage volume at each surveyed stream site.

3.2. Derivation of Terrain Indices

A 10-m resolution digital elevation model (DEM) (Gesch, 2007) was used in ArcGIS to calculate a variety of terrain indices to explore potential controls on LW storage and downstream trends (Table 3). Contributing drainage area was a main variable of interest, since it increases in the downstream direction throughout a watershed and is closely tied to the question of how LW storage varies longitudinally. Drainage area was determined by calculating flow direction and flow accumulation rasters by path of steepest descent with ArcHydro Tools 2.0. Cells with a drainage area of 0.5 km^2 or greater were designated to represent the stream network (Tucker and Slingerland, 1997). In order to reflect the fact that no LW in New Bullards Bar Reservoir was able to be fluvially transported to downstream sites, the amount of contributing drainage area upstream of this reservoir was subtracted from stream sites downstream of the reservoir. This affected ten stream sites in the largest drainage area bin, but no others, and the contributing drainage area bin classifications were not changed based on this distinction. This would allow the largest contributing drainage area bin to be analyzed separately from the others on a categorical basis, since it likely has the highest episodic discharges and potential for LW mobility.

Channel slope values estimated from GIS increase in accuracy as channel length over which slope is calculated increases (Neeson et al., 2008). Although this was shown on a slightly larger spatial scale (0.2 – 1 km), the principle was applied herein to calculate the slope for each stream site by using the elevation range extracted from the DEM, then dividing by the survey distance. The side slope of the valley at each stream site was calculated by finding the maximum elevation within a 100 m buffer of the surveyed stream site, subtracting the mean elevation of the reach, then dividing by 100 m. This method calculated the side slope on the steeper side of the valley only. Other local and watershed scale indices calculated using the digital terrain analysis of Wilson and Gallant (2000) are summarized in Table 3.

3.3. Watershed Scale Land Cover, Fire History, and Geology Variables

Geospatial datasets for land cover (2002), fire history (2011), and geology (2000) were used to calculate variables that represent potential watershed scale controls on LW storage. These variables were exploratory to see if patterns existed that had not been searched for by previous LW studies. Land cover shapefiles were classified into agricultural, barren, conifer forest, hardwood forest, herbaceous, shrub, urban and wetland categories. Fire history shapefiles were classified into presence or absence of a burn within the 50 years prior to this study. Primary rock type shapefiles were categorized into extrusive igneous, intrusive igneous, metamorphic, sedimentary, and glacial drift lithologies. The percentage of contributing stream cells that passed through each land cover, fire history, and geological category was calculated for each stream site and incorporated into the analyses (Table 3).

3.4. Statistical Analyses

The analysis framework used in this study was to identify a suite of physical variables that might influence LW storage throughout the Yuba River watershed and then statistically test if the variables did play a role, either individually or in combinations. Local and watershed control variables were analyzed in two different ways – once using categorical comparisons of LW volume per channel length on the basis of several variables, then as combinations of continuous variables to see if they would provide meaningful predictive capability.

In order to assess the lateral distribution of LW throughout the watershed, categorical differences in LW volume per channel length were calculated for three groups of quantities. First, the total LW storage that included all LW found in surveys was considered. This quantity was then partitioned and analyzed in terms of LW storage that was found primarily in the wetted-baseflow channel only (in-channel LW storage), and LW that was found primarily outside the baseflow-wetted channel (out-of-channel LW). Differences were statistically compared using the nonparametric Mann-Whitney U test (Mann and Whitney, 1947) on the basis of drainage area, subbasin, elevation, bankfull channel width, stream order, local slope, and local land cover variables. In all cases, categories were made to yield sufficient sample sizes for statistically robust results. For each variable, every category was tested against every other category for significant differences. In the case of drainage area bins, each bin was tested against each other bin, and bins were combined to compare low drainage area (bins 1-4) to higher drainage area (bins 5-8) stream sites. The null hypothesis for each test was that any difference in the median amount of LW volume per channel length was due to sampling error. Statistical significance for these tests and all others in this study were determined at the $\alpha = 0.05$ level.

The extent to which measured and calculated quantities predicted LW volume per channel length for total, in-channel and out-of-channel storage was tested with multiple linear regression (MLR) using a least squares algorithm. To meet assumptions for the distribution of residuals, all data were either log or square-root transformed, depending on the presence of zeros in the dataset (Table 3). A variable consisting of random numbers between 0 and 1 was created and incorporated into all MLR models. This variable acted as a check to ensure that random data would not contribute significantly to the MLR models (Pinheiro and Bates, 2000; Roche et al., 2013). Multicollinearity among the predictor variables was undesirable since the contribution of each individual variable in the MLR model was of interest for the objectives of this study. It was reduced by eliminating variables that had a Spearman-rank correlation coefficient, R, of 0.8 or greater with two or more other variables (Table 3). An Akaike information criterion (AIC) based stepwise backward-forward selection algorithm was run in the R statistical environment (stepAIC), so that the most parsimonious model would be chosen (Kutner et al., 2005). Collinearity of remaining variables was checked prior to confirm that none had R values greater than 0.8 with any other remaining variables. The remaining variables were then used in an MLR model to predict total LW volume per channel length for the three different subbasins and elevation categories within the watershed to see if controls were consistent across multiple spatial scales.

The significance of each variable and y-intercept in the MLR model was checked with t-tests, using the null hypothesis that the coefficient or the y-intercept was not significantly different from zero. The significance of the MLR model was determined with an ANOVA test, in which the null hypothesis is that no linear combination of the independent variables significantly explains the variance of the dependent variable. Each MLR model was run under three assumptions: (i) observations were randomly chosen, (ii) the residuals were normally distributed about zero, and (iii) the residuals were homoscedastic (Walford, 2011). The first requirement was met by experimental design. Normality of the residuals was checked both visually, and by using a chi-square test to determine whether the distribution was significantly different from normal. Residual homoscedasticity was checked visually, and by using the Breusch-Pagan test (Breusch and Pagan, 1979). It was reasoned that spatial autocorrelation was unlikely to impact results of the MLR models. The data used in this study were not a spatial series and sampling was scale dependent, so the chances for autocorrelation effects were limited. For lower drainage area bins, stream sites were spaced adequately far apart and with random distances, due to the large number of potential stream sites and random site selection. Since channel segments in higher drainage area bins must be close to each other by definition, there was less total channel length to randomly choose sites from. This meant that the sites were closer together, but there was still a high level of heterogeneity in stream characteristics and a high variance of LW volume per channel length at stream sites.

To investigate the lateral distribution of LW in channels throughout areas with different drainage areas, the ratio of out-of-channel LW volume to in-channel LW volume was calculated for each drainage area bin. If drainage area played a significant role in determining the percentage of LW found in the wetted channel or in areas of flood deposition, then differences should be seen between ratios for each contributing drainage area bin.

4. Results

4.1. Total LW Volume per Channel Length

A total of 996 LW pieces and 338 LW jams were measured at the 114 stream sites, including both in-channel and out-of-channel LW. The mean piece volume was 0.3 m^3 and the mean jam volume was 4.9 m^3, both with relatively high standard deviations (0.8 and 16.6 m^3, respectively). LW storage volume per channel length at the stream sites was highly variable, ranging from 0.03 to 283 m^3 per 100 m, with a mean of 23.2 m^3 per 100 m, a median of 6.8 m^3 per 100 m, and a standard deviation of 50.0 m^3 per 100 m (Figure 2). When the data were extrapolated to the entire stream network on the basis of the mean LW volume per channel length, the total estimated LW volume for the Yuba watershed upstream of Englebright Dam was 600,500 m^3. Given the high variation among sampled stream sites, there is significant uncertainty associated with this figure, probably on the order of 10^4 m^3.

Differences in total LW volume per channel length were not significant between stream sites with low drainage areas (bins 1-4 combined), and stream sites with high drainage areas (bins 5-8 combined). When stream sites from each of the eight bins were individually compared to each other (eight choose two), 27 out of the possible 28 combinations yielded statistically insignificant differences, with the lone exception that sites in bin 8 stored less total LW per channel length than sites in bin 4 ($p = 0.03$; Figure 3a). Remarkably, when the contributing drainage area was ~ 1 km^2 (i.e., bin 1) versus ~ 1,800 km^2 (i.e., bin 8), there was no statistically significant difference in total LW volume per channel length.

Differences in total LW volume per channel length by stream order were not statistically significant for 25 out of 28 tests, with the notable exception that 3rd order streams stored significantly more LW volume per channel length than 1st, 4th, and 6th order streams (Figure 3b). There were no significant differences between any one bankfull channel width category and any other (Figure 3c). Stream sites with low ($S < 0.05$ m m^{-1}), medium ($0.05 \leq S < 0.1$ m m^{-1}), and high ($S \geq 0.1$ m m^{-1}) local slope showed no significant differences in total LW volume per channel length when each was compared to the others. Stream sites at high ($E \geq 1600$ m), medium ($800 \leq E < 1600$ m), and low ($E < 800$ m) elevation showed no significant differences when LW volume per channel length values were compared. Stream sites from the three subbasins did not have significantly different LW volume per channel length values from one another.

Total LW volume per channel length compared by different local land cover variables showed significant median differences; reaches with ≥ 50% forest or shrub cover had significantly higher LW volume per channel length (Figures 3d-e) and reaches with ≥ 50% exposed bedrock had significantly less LW volume per channel length (Figure 3f).

Of the variables tested (Table 3), results of the stepwise AIC-based model selection found that five created the most parsimonious model with the highest explanatory power ($AIC = 252.4$). Local side slope, bankfull channel width, local percent shrub cover, percent contributing stream cells in urban areas, and percent contributing stream cells over intrusive igneous rock together significantly predicted LW volume per channel length ($p < 0.0001$) with an adjusted R^2 value of 0.31. All five variables and the y-intercept had highly significant coefficients in the model.

Directionality of impact for the variables was mixed, in that higher local percent shrub cover, bankfull channel width, and upslope percent intrusive igneous rock contributed to higher LW volume per channel length, while higher local side slope and percent contributing stream cells in urban areas contributed to lower LW volume per channel length (Table 4). Note that the artificial random variable was not chosen in the AIC-based algorithm, indicating that the MLR model successfully avoided significant random effects.

The five variables chosen by the stepwise AIC algorithm for the entire watershed also significantly predicted total LW volume per channel length for each of the three subbasins and elevation categories individually, though with differing combinations of individual controls (Table 5). Local percent shrub cover was consistently a significant predictor variable across all models. In addition to local percent shrub cover, model results for the three subbasins showed that bankfull channel width and upslope percent stream cells over intrusive igneous rock were significant in the North Yuba, local side slope was significant in the Middle Yuba, and bankfull channel width and upslope percent of stream cells in urban areas were significant in the South Yuba. Models for the three elevation categories showed that local shrub cover, bankfull channel width and upslope percent urban areas were significant at high elevation stream sites, local shrub cover and upslope intrusive igneous rock were significant at medium elevation stream sites, and only local percent shrub cover was significant for low elevation stream sites.

4.2. In-channel LW Volume per Channel Length

Of all the LW surveyed and characterized above, 146 LW pieces and 57 LW jams were found to be primarily within the baseflow-wetted channel during surveys. The total volume of all these was 258 m^3, accounting for 13.5% of all measured LW. The mean in-channel LW storage volume per channel length for all survey reaches was 4.0 m^3 per 100 m, with a standard deviation of 20.2 m^3 per 100 m. There were 34 sites where no LW was found to be primarily in the baseflow-wetted channel. When the data were extrapolated to the entire stream network by the mean in-channel LW volume per channel length, the in-channel LW storage in the entire watershed upstream of Englebright Dam was found to be 58,700 m^3, with an uncertainty on the order of 10^4 m^3.

In comparing low drainage area stream sites (bins 1-4 combined) to higher drainage area stream sites (bins 5-8 combined), stream sites with lower contributing drainage area had significantly more in-channel LW volume per channel length ($p < 0.001$). This contrasted with results considering total LW volume per channel length, which showed no significant difference. Similarly, sites on 5th and 6th order streams had significantly less in-channel LW volume per channel length than sites on 1st, 2nd, or 3rd order streams. Sites on 4th order streams also had significantly less in-channel LW volume per channel length than sites on 2nd or 3rd order streams but not significantly less than sites on 1st order streams.

The highest elevation ($E \geq 1600$ m) stream sites had significantly higher in-channel LW volume per channel length than medium ($800 < E < 1600$ m) and low elevation ($E < 800$ m) sites, though there was no significant difference between medium and low elevation sites. The narrowest channels (1-10 m) had significantly higher in-channel LW volume per length than all of the other channel width classifications, though no significant differences were found between any two of the other classifications. Results of hypothesis testing of in-channel LW volume per channel length on the basis of subbasin, slope, and land cover variables were identical to that of the total LW volume per channel length, in that subbasins and slope had no significant differences, though differences on the basis of percent forest, shrub and bedrock reach-scale land cover variables were statistically significant.

Even after transformation, the residuals of the MLR model for in-channel LW volume per channel length did not meet the requirements for normality or homoscedasticity, so the results were not valid. Thus, although in-channel LW volume per channel length showed statistically significant categorical connections with local and watershed scale variables, none of the links could be described by a linear model to produce predictive empirical equations.

4.3. Out-of-channel LW Volume per Channel Length

Of all the LW recorded, 850 LW pieces and 281 LW jams were found outside of the baseflow-wetted area. The volume of these totaled 1,654 m^3, accounting for 86.5% of the total LW volume found in the surveys. The mean out-of-channel LW storage volume per channel length for all survey reaches was 19.1 m^3 per 100 m, with a standard deviation of 43.5 m^3 per 100 m. Three out of the 114 stream sites had no LW outside of the baseflow-wetted channel. When the data were extrapolated to the entire stream network by the mean LW volume per channel length, the out-of-channel LW storage in the entire watershed upstream of Englebright Dam was found to be 495,700 m^3, with an uncertainty on the order of 10^4 m^3.

Similar to total LW volume per channel length, out-of-channel LW volume per channel length showed no significant difference between areas of low contributing drainage area (bins 1-4 combined) versus high contributing drainage area (bins 5-8 combined). When stream sites from each of the eight bins were individually compared to each other (eight choose two), 25 out of the possible 28 combinations were not statistically significant; out-of-channel LW volume per channel length in bin 4 was significantly higher than bins 1, 2 and 8.

Sites on 1st order streams had significantly less out-of-channel LW volume per channel length than sites on 2nd or 3rd order streams, and sites on 3rd order streams had significantly more out-of-channel LW volume per channel length than sites on 4th and 5th order streams. Just as with total LW volume per channel length, no significant differences were found between subbasin, elevation, slope, or channel width categories. Categorical differences in out-of-channel LW volume per channel length on the basis of land cover variables were nearly identical to those of total LW volume per channel length, although the difference based on percent forest cover was just above the level of significance ($p = 0.064$).

As with the in-channel LW volume per channel length, the residuals of the MLR model predicting out-of-channel LW volume per channel length were significantly different from normal based on the chi-square test, so the model was rejected.

4.4. Downstream Changes in the Lateral Distribution of LW

The ratio of out-of-channel to in-channel LW volume is shown for each drainage area bin in Table 6. In all drainage area bins, there is more out-of-channel LW volume than in-channel LW volume, though in bin 3, the ratio is nearly 1:1. In general, this ratio was higher in reaches with higher drainage area. This indicates that of the LW that was present in a given reach, one could expect a higher percentage to be deposited out-of-channel in downstream reaches than in reaches with low drainage area, regardless of the downstream trend of total LW volume per channel length.

5. Discussion

5.1. Downstream Trends of LW Storage

Total LW volume in the active stream corridor per channel length was highly variable throughout the watershed across stream sites having contributing drainage areas ranging from < 1 km^2 to > 1,000 km^2. There was no simple decreasing trend for LW volume per channel length in the downstream direction on the basis of contributing drainage area, and there was significantly higher total LW volume per channel length at stream sites on 3rd order streams (Figure 3b). Keller and Swanson (1979) noted that LW biomass per channel area (kg m^{-2}) decreased downstream from small headwater streams (1 m width; 0.2 km^2 drainage area) to the large McKenzie River (40 m width; 1,024 km^2 drainage area). Their results were converted to LW volume per 100 m for comparison to this study (Table 7). The conversion indicates that although biomass per channel area decreased downstream, the LW volume per 100 m of channel length actually increased from 1st to 3rd order streams, and then decreased in the downstream direction, similar to the results of this study. Wohl and Jaeger (2009) reported higher LW aggregation in mid-sized streams in the Front Range of Colorado, USA, while the LW volume per channel area decreased throughout the channel network.

Narrow (1-10 m), high-elevation ($\geq$ 1600 m), and lower contributing drainage area (bins 1-4) stream sites were found to have significantly higher in-channel LW volume per channel length than other stream sites on a categorical basis. These differences were confirmed with two-way hypothesis testing only, since the MLR model violated statistical assumptions and no continuous trend could be determined. Two-way hypothesis testing did not illuminate any downstream trends for out-of-channel LW volume per channel length and the simplest test showed that the difference in the median value of out-of-channel LW volume per channel length for bins 1-4 combined versus bins 5-8 combined was not significant.

Stream sites with higher drainage areas tended to have a higher ratio of out-of-channel to in-channel LW volume than stream sites with lower drainage areas (Table 6). This redistribution is likely due to a combination of (i) fluvial processes that allow for LW deposition onto active floodplains during the floods capable of entraining LW and (ii) the relatively larger area and greater roughness of floodplains compared to baseflow-wetted channels that exist at these reaches.

Previous researchers have offered the interpretation that headwater reaches are transport limited and larger rivers are supply limited for LW based on observations that LW volume or biomass per channel area is higher in headwater streams (Keller and Swanson, 1979; Swanson, 2003; Wohl and Jaeger, 2009; Rigon et al., 2012), LW piece count per channel area is higher in headwater streams (Hassan et al., 2005), LW jam count per channel length is higher in headwater streams (Marcus et al., 2002), and LW export is lower in streams with higher drainage area (Fremier et al., 2010). The results of this study indicate that the importance of LW deposition onto floodplains during high flows may have previously been understated or overlooked. The findings that (i) the total LW volume per channel length was not significantly different between headwater and lower streams and (ii) the ratio of out-of-channel to in-channel LW volume increased in the downstream direction together indicate that lower in-channel LW volume per channel length in streams with higher contributing drainage area is largely due to preferential deposition of LW onto floodplains during floods, rather than an increased transport capacity alone. This mechanism has also been suggested as a possible explanation for decreasing in-channel LW storage in the downstream direction by Gurnell et al. (2002) and Hedman et al. (1996), though without quantification.

5.2. Controls on LW Storage

The stepwise AIC algorithm determined an MLR model with five variables to be the most parsimonious in significantly predicting total LW volume per channel length throughout the entire study area, explaining about a third of the variance (Table 4). This suggests that the approach used here was useful, but also that the distribution of LW volume per channel length in the Yuba River watershed is highly complex. This model included local and watershed scale variables with both positive and negative coefficients. MLR models run at smaller spatial scales with the same remaining variables showed that the effect of these individual controls at the full watershed scale could be traced back to individual subbasins and elevation categories.

Local percentage of shrub cover estimated *in situ* tended to be the most important factor influencing total LW volume per channel length; it was highly significant when combined with the other four variables. It was also the only variable that was consistently significant across all MLR models run at smaller spatial scales in the three subbasins and elevation categories. While they were not significant in the MLR model, differences in local percent forest cover and local percent exposed bedrock had significant or near-significant differences in total, in-channel, and out-of-channel LW volume per channel length based on Mann-Whitney U tests. Fox and Bolton (2007) also observed less LW volume per channel length in bedrock rivers than in alluvial rivers in the Pacific Northwest. The significance of local land cover variables may be attributed to the difference in roughness factors that influence the deposition of LW as it is fluvially transported during high flows. LW may be more likely to be deposited in areas with a higher percentage of shrub or forest cover, since higher roughness reduces flow speeds and may entangle or trap LW pieces, while exposed bedrock is smoother and less likely to permit LW deposition. The differences based on percent forest cover may also reflect higher rates of local tree mortality recruitment in forest dominated streams compared to other types of streams.

Bankfull channel width showed no significant differences on a categorical basis (Figure 3c), but was a highly significant predictor of LW volume per channel length when combined with the other four variables in the final MLR model. This suggests that LW volume per channel length does not simply increase downstream as bankfull channel width increases, but that it can be higher in wider streams if other factors are also at play. Bankfull channel width was a significant predictor in the North and South Yuba subbasins, but not in the Middle subbasin. Among the elevation categories, it was only significant for high elevation stream sites.

The percentage of contributing stream cells that were over intrusive igneous rock was a highly significant predictor of LW volume per channel length with a positive coefficient. The intrusive igneous rocks in the Yuba River watershed are gabbro, granodiorite, and peridotite, which are highly resistant layers. In addition to its significance in the full watershed scale MLR model, this variable was significant in the North Yuba subbasin, and at medium elevations, but not in other subbasins or in other elevation categories. After reviewing field photographs, no qualitative differences could be found between stream morphologies over intrusive igneous rocks versus other geological facies. Underlying geologies are the building blocks for overlying biological and geomorphological systems. It is possible that the percentage of contributing stream cells that were over intrusive igneous rock was a significant variable in the model since it is correlated with separate process-based variables that were not considered in the study.

Local side slope was a significant contributor to the MLR model for total LW volume per channel length, though with surprising directionality (Table 4). One might expect steeper side slopes to recruit more LW onto floodplains due to a higher rate of tree mortality recruitment; to the contrary, side slope had a significantly negative coefficient in the model. A more important effect may be that corridors with less steep side slopes have more width of active floodplains to produce and store wood in conjunction with presence of more saturated and deeper soils as well as more shrubs to capture LW. In addition, corridors with lower side slopes are less constricted, which would cause flood velocities to be lower on floodplains compared to having high velocities impinge on narrower, steeper canyon walls. On a smaller spatial scale, local side slope was only significant for predicting LW volume per channel length in the Middle Yuba subbasin (Table 5). This may be because much of the Middle Yuba River runs through the most constricted canyon in the watershed, where high flood velocities probably provides a strong contrast to flood and floodplain hydraulics in locations in the river with gentle side slopes and a wide valley floor.

The percent of contributing stream cells passing through urban areas was a highly significant predictor variable in the MLR model when combined with the other four variables, presenting with a negative coefficient (Table 4). The simplest explanation for this effect is that streams that pass through more developed areas may have lower LW volume supply rates per channel length than others, since development has disrupted riparian forest continuity. Stream sites with lower upstream LW supply and a similar capacity to transport LW as other streams would have lower volume per channel length at these stream sites. In addition, LW storage may be reduced by modern or historic wood removal for development purposes. The South Yuba is the only subbasin where this variable is a significant predictor, and it is only significant in high elevation stream sites (Table 5). A highway corridor parallels the South Yuba River for ~ 20 km, and the nine stream sites with the highest percent contributing stream cells passing through urban areas were in the South Yuba subbasin. While roads parallel parts of the stream network in many other parts of the watershed, the South Yuba River highway corridor is in an area of substantial mountain community development. Construction of the highway was completed in 1960 in preparation for the Squaw Valley Winter Olympics, so development from this corridor has likely been impacting LW storage in these streams for over five decades.

Local slope was among the several variables that were not chosen by the stepwise AIC algorithm in the final MLR model. It also showed no significant differences based on Mann-Whitney U tests. Iroumé et al. (2010) similarly found no significant correlation between LW piece count per channel length and local slope in southern Chile. Rigon et al. (2012) reported statistically significant, but relatively weak correlation ($R = 0.31$) between local slope and LW volume per channel area in streams of the eastern Italian Alps, but did not report correlations for slope and LW volume per channel length.

5.3. Comparison to Other Regions and Impact of Disturbance

The median total LW volume per channel length in the Yuba watershed (6.8 m^3 per 100 m) is similar to that found by Fox and Bolton (2007) in Douglas Fir – Ponderosa Pine forests (7 m^3 per 100 m) and narrow (0-3 m wide) alpine streams (8 m^3 per 100 m) in “stream basins that are relatively unaffected by anthropogenic disturbance” in western Washington State, USA. The median total LW volume per channel length found in the Yuba watershed is less than that found in relatively pristine Western Washington streams and wider alpine streams considered by Fox and Bolton (2007), which had values of 51 – 93 and 18 m^3 per 100 m, respectively.

The mean total LW volume per channel length in the Yuba watershed (23.2 m^3 per 100 m) is similar to the Whirinaki River in New Zealand (19.5 m^3 per 100 m) (Baillie et al., 2008), and is higher than that found in the Appalachian Mountains (13.3 m^3 per 100 m) (Hedman et al., 1996). The variability in storage in the Yuba watershed was considerably higher than that found in these studies; the range in LW volume per channel length was on the order of 10^2 m^3 per 100 m, rather than 10^1 m^3 per 100 m.

Aside from urban development, it is possible that LW storage in the Yuba River basin may be highly impacted by other recent and historic human disturbance and management, though the directionality of the effect is unclear. Timber harvesting in support of historic mining operations likely decreased the mean tree diameter of forests in the study area, while more recent logging may have increased the abundance of downed LW in the river network. Mobilized sediment as a result of hydraulic gold mining is not known to have a direct effect on LW recruitment, but dams constructed on tributaries certainly affect the movement of LW through the watershed.

In many mountainous watersheds, a significant source of LW recruitment is thought to derive from debris flows (Reeves et al., 2003; Iroumé et al., 2010; Rigon et al., 2012). Curtis et al. (2005) showed that 85% of the Middle and South Yuba subbasins had minor or negligible erosion potential, and that overall, low hillslope erosion rates were found throughout the Yuba River watershed. This result indicates that debris flows are unlikely to be substantial contributors to LW recruitment in the Yuba River.

Comiti et al. (2008) found that in mountain streams of the Southern Andes, the LW piece count per channel area varied widely between adjacent basins with different fire disturbance histories. In the Yuba River watershed, however, the percent contributing stream cells that passed through an area that burned in the past 50 years was not a significant predictor of total LW volume per channel length. While fire has likely been active in the Yuba River watershed and throughout the Sierra Nevada from the late Holocene (Anderson and Smith, 1997) until modern times, fire suppression since the early 1900s may be a more important disturbance to forest dynamics and LW storage volumes than fire itself. Widespread fire suppression began in 1905, and continued as the dominant practice until the 1960s. This management practice has led to an increase in burnable surface debris and higher density of shrubs and understory trees (Sugihara et al., 2006), which may have led to increased LW volumes in the stream network. Though the authors are not aware of LW studies focused on LW response to fire suppression, Lassettre et al. (2008) observed a general increase in LW mass per channel area over a multi-decadal time-scale on the Ain River in Southeastern France, which they attributed in part to afforestation.

6. Conclusion

This study has shown that the total LW volume per channel length in the Yuba River watershed does not show a simple decreasing trend in the downstream direction when active floodplains are considered, and that this quantity tends to be highest in 3rd order streams. The ratio of out-of-channel to in-channel LW volume tended to increase moving downstream, which is likely due to floodplains becoming more prevalent in streams of higher drainage area. The inclusion of floodplains in this study's LW surveys and analyses indicates that LW transport capacities of streams may have been overstated in previous studies. Results herein show that LW is often deposited within the area that is fluvially activated during high flows. Much of this area can be outside of the bankfull channel width, which is the common lateral extent of most previous surveys.

The MLR model predicting total LW volume per channel length indicates that a reasonable portion of the variance in this quantity can be significantly predicted using a combination of local and watershed variables. The model results from the smaller spatial scales showed that effects of each variable could be traced back to specific subbasins and elevation bands. Our MLR models were certainly limited in accounting for the full complexity of LW volume per channel length. Future work could incorporate a higher number of observations and additional process-based predictor variables.

In order to understand the change in storage or flux of LW through a watershed, repeat surveys or long-term monitoring are required. These types of investigations are warranted in order to understand LW dynamics in a watershed such as the Yuba River system, where little is known about how disturbances interact to impact the LW budget.

Acknowledgments

Financial support for this work was provided by (1) a National Science Foundation doctoral dissertation research grant to co-author Anne Senter (Award 1031850) and (2) a Cooperative Ecosystem Studies Unit grant from the United States Army Corps of Engineers co-author Greg Pasternack (Award W912HZ-11-2-0038). The authors thank James Jackson, Jonathon Martindill, Robert Gonzalez, Leah Kammel and Pedro Vaughan for assistance with field work, as well as Mark Grismer, Michael Strom, Rocko Brown, and Rachel Hamm for helpful discussions.

References

2000. GIS Data for the Geologic Map of California. US Geological Survey. http://atlas.ca.gov/.

2002. California Land Cover. California Department of Forestry and Fire Protection. http://atlas.ca.gov/.

2011. California Fire History Dataset. California Department of Forestry and Fire Protection. http://fire.ca.gov/.

Anderson, R. S., and S. Smith. 1997. The sedimentary record of fire in montane meadows, Sierra Nevada, California, USA: A preliminary assessment. Pages 313-327 *in* J. Clark, H. Cachier, J. Goldammer, and B. Stocks, editors. Sediment Records of Biomass Burning and Global Change. Springer Berlin Heidelberg.

Atha, J. B. 2013. Identification of fluvial wood using Google Earth. River Research and Applications.

Baillie, B. R., L. G. Garrett, and A. W. Evanson. 2008. Spatial distribution and influence of large woody debris in an old-growth forest river system, New Zealand. Forest Ecology and Management **256**:20-27.

Barbour, M. G., N. H. Berg, T. G. F. Kittel, and M. E. Kunz. 1991. Snowpack and the distribution of a major vegetation ecotone in the Sierra-Nevada of California. Journal of Biogeography **18**:141-149.

Barbour, M. G., T. Keeler-Wolf, and A. A. Schoenherr. 2007. Terrestrial vegetation of California. University of California Pr.

Beechie, T. J., and T. H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams. Transactions of the American Fisheries Society **126**:217-229.

Benda, L., D. Miller, J. Sias, D. Martin, R. Bilby, C. Veldhuisen, and T. Dunne. 2003. Wood recruitment processes and wood budgeting. Pages 49-73 *in* S. V. Gregory, K. L. Boyer, and A. M. Gurnell, editors. The ecology and management of wood in world rivers.

Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, V. K. Kosko, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: Past, present and future. Pages 143-190.

Braudrick, C.A. and Grant, G.E. When do logs move in rivers? Water Resources Research **36**: 571-583.

Breusch, T. S., and A. R. Pagan. 1979. A Simple test for heteroscedasticity and random coefficient variation. Econometrica **47**:1287-1294.

Comiti, F., A. Andreoli, L. Mao, and M. A. Lenzi. 2008. Wood storage in three mountain streams of the Southern Andes and its hydro-morphological effects. Earth Surface Processes and Landforms **33**:244-262.

Curtis, J. A., L. E. Flint, C. N. Alpers, and S. M. Yarnell. 2005. Conceptual model of sediment processes in the upper Yuba River watershed, Sierra Nevada, CA. Geomorphology **68**:149-166.

Dettinger, M. D., F. M. Ralph, T. Das, P. J. Neiman, and D. R. Cayan. 2011. Atmospheric rivers, floods and the water resources of California. Water **3**:445-478.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British-Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences **49**:682-693.

Fetherston, K. L., R. J. Naiman, and R. E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology **13**:133-144.

Fox, M., and S. Bolton. 2007. A regional and geomorphic reference for quantities and volumes of instream wood in unmanaged forested basins of Washington state. North American Journal of Fisheries Management **27**:342-359.

Fremier, A. K., J. I. Seo, and F. Nakamura. 2010. Watershed controls on the export of large wood from stream corridors. Geomorphology **117**:33-43.

Gesch, D. B. 2007. The National Elevation Dataset.*in* D. E. M. T. a. Applications, editor. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

Gilbert, G. K. 1917. Hydraulic-mining debris in the Sierra Nevada.*in* D. o. t. Interior, editor. United States Geological Survey, Washington, D.C.

Gippel, C. J., B. L. Finlayson, and I. C. Oneill. 1996. Distribution and hydraulic significance of large woody debris in a lowland Australian river. Hydrobiologia **318**:179-194.

Gurnell, A. M., H. Piegay, F. J. Swanson, and S. V. Gregory. 2002. Large wood and fluvial processes. Freshwater Biology **47**:601-619.

Harris, R. R. 1989. Riparian communities of the Sierra Nevada and their environmental relationships. Pages 393-398 *in* DL Abel (tech. coord.), Proceedings of the California riparian systems conference: Protection, management, and restoration for the 1990s. USDA Forest Service General Technical Report PSW-110.

Hassan, M. A., D. L. Hogan, S. A. Bird, C. L. May, T. Gomi, and D. Campbell. 2005. Spatial and temporal dynamics of wood in headwater streams of the Pacific Northwest. JAWRA Journal of the American Water Resources Association **41**:899-919.

Hedman, C. W., D. H. V. Lear, and W. T. Swank. 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. Canadian Journal of Forest Research **26**:1218-1227.

Hering, D., J. Kail, S. Eckert, M. Gerhard, E. I. Meyer, M. Mutz, M. Reich, and I. Weiss. 2000. Coarse woody debris quantity and distribution in central European streams. International Review of Hydrobiology **85**:5-23.

Hooke, J. 2003. Coarse sediment connectivity in river channel systems: a conceptual framework and methodology. Geomorphology **56**:79-94.

Iroumé, A., A. Andreoli, F. Comiti, H. Ulloa, and A. Huber. 2010. Large wood abundance, distribution and mobilization in a third order Coastal mountain range river system, southern Chile. Forest Ecology and Management **260**:480-490.

James, L. A. 2005. Sediment from hydraulic mining detained by Englebright and small dams in the Yuba basin. Geomorphology **71**:202-226.

Johnson, D.H. 1980. The comparison of use and availability measurements for evaluating resource preference. Ecology **71**:61-65.

Keller, E. A., and F. J. Swanson. 1979. Effects of large organic material on channel form and fluvial processes. Earth Surface Processes **4**:361-380.

Kutner, M. H., C. J. Nachtsheim, J. Neter, and W. Li. 2005. Applied linear statistical models. Fifth edition. HcGraw-Hill.

Lassettre, N. S., H. Piégay, S. Dufour, and A.-J. Rollet. 2008. Decadal changes in distribution and frequency of wood in a free meandering river, the Ain River, France. Earth Surface Processes and Landforms **33**:1098-1112.

Latterell, J.J., Scott Bechtold, J., O'Keefe, T.C., Van Pelt, R. and Naiman, R.J. 2006. Dynamic patch mosaics and channel movement in an unconfined river valley of the Olympic Mountains. Freshwater Biology **51**: 523-544.

Lawrence, J. E., V. H. Resh, and M. R. Cover. 2012. Large-wood loading from natural and engineered processes at the watershed scale. River Research and Applications.

Macka, Z., L. Krejci, B. Louckova, and L. Peterkova. 2011. A critical review of field techniques employed in the survey of large woody debris in river corridors: a central European perspective. Environmental Monitoring and Assessment **181**:291-316.

Manly, B.F.J. and Navarro Alberto, J.A. 2014 Introduction to Ecological Sampling. Taylor and Francis Group, LLC, Boca Raton, FL.

Mann, H. B., and D. R. Whitney. 1947. On a test of whether one of two random variables is stochastically larger than the other. The Annals of Mathematical Statistics **18**:50-60.

Manners, R. B., and M. W. Doyle. 2008. A mechanistic model of woody debris jam evolution and its application to wood-based restoration and management. River Research and Applications **24**:1104-1123.

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

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

McKelvey, K. S., and J. D. Johnston. 1992. Historical perspectives on forests of the Sierra Nevada and the transverse ranges of sourthern California: Forest conditions at the turn of the century.*in* U. F. Service, editor.

Miller, A.W. and Ambrose, R. F. 2000. Sampling patchy distributions: comparison of sampling designs in rocky intertidal habitat. Marine Ecology Progress Series **196**: 1-14.

Montgomery, D. R., J. M. Buffington, R. D. Smith, K. M. Schmidt, and G. Pess. 1995. Pool spacing in forest channels. Water Resources Research **31**:1097-1105.

Mount, J. F. 1995. California rivers and streams. University of California Press.

Neeson, T. M., A. M. Gorman, P. J. Whiting, and J. F. Koonce. 2008. Factors affecting accuracy of stream channel slope estimates derived from geographical information systems. North American Journal of Fisheries Management **28**:722-732.

O'Connor, M. D., and R. R. Ziemer. 1989. Coarse woody debris ecology in a second-growth Sequoia sempervirens forest stream. USDA Forest Service Gen. Tech. Rep. PSW-110:165-171.

Owens, P. N. 2005. Conceptual models and budgets for sediment management at the river basin scale. Journal of Soils and Sediments **5**:201-212.

Pinheiro JC, Bates DM. 2000. Mixed-effects models in S and S-PLUS. New York: Springer-Verlag. 528 p.

Reeves, G. H., K. M. Burnett, and E. V. McGarry. 2003. Sources of large wood in the main stem of a fourth-order watershed in coastal Oregon. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **33**:1363-1370.

Rigon, E., F. Comiti, and M. A. Lenzi. 2012. Large wood storage in streams of the Eastern Italian Alps and the relevance of hillslope processes. Water Resources Research **48**:W01518.

Roche, L. M., Kromschroeder, L., Atwill, E. R., Dahlgren, R. a, & Tate, K. W. (2013). Water Quality Conditions Associated with Cattle Grazing and Recreation on National Forest Lands. PloS One, **8(6)**:e68127.

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

Snyder, N. P., D. M. Rubin, C. N. Alpers, J. R. Childs, and J. A. Curtis. 2004. Estimating accumulation rates and physical properties of sediment behind a dam: Enblebright Lake, Yuba River, northern California. USGS Staff - Published Research Paper **489**.

Sugihara, N. G., J. W. Van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode. 2006. Fire in California's ecosystems. University of California Press, Berkeley.

Swanson, F. J. 2003. Wood in rivers: A landscape perspective. Pages 299-313 *in* S. V. Gregory, K. L. Boyer, and A. M. Gurnell, editors. The ecology and management of wood in world rivers.

Thomas, R.B. and Lewis, J. 1995. An evaluation of flow-stratified sampling for estimating suspended sediment loads. Journal of Hydrology **170**:27-45.

Tucker, G. E., and R. Slingerland. 1997. Drainage basin responses to climate change. Water Resources Research **33**:2031-2047.

van der Nat, D., K. Tockner, P. J. Edwards, and J. V. Ward. 2003. Large wood dynamics of complex alpine river floodplains. Journal of the North American Benthological Society **22**:35-50.

Walford, N. 2011. Practical statistics for geographers and earth sciences. John Wiley & Sons Ltd., Singapore.

Warren, D. R., W. S. Keeton, and C. E. Kraft. 2008. A comparison of line-intercept and census techniques for assessing large wood volume in streams. Hydrobiologia **598**:123-130.

Wilson, J. P., and J. C. Gallant. 2000. Digital terrain analysis. Terrain analysis: Principles and applications:1-27.

Wohl, E. 2013. Floodplains and wood. Earth-Science Reviews **123**:194-212.

Wohl, E., and K. Jaeger. 2009. A conceptual model for the longitudinal distribution of wood in mountain streams. Earth Surface Processes and Landforms **34**:329-344.

Wyrick, J. R. and Pasternack, G. B. 2012. Landforms of the Lower Yuba River. Prepared for the Yuba Accord River Management Team. University of California at Davis, Davis, CA, 91pp.

Yang, D., Woo, M-K. 1999. Representativeness of local snow data for large scale hydrologic investigations. Hydrological Processes **13**:1977-1988

Table 1

Table 1. Summary of studies that have investigated downstream trends in LW storage

Study	Lateral extent of channel surveys	Term used to describe metric	Downstream trend	Based on	Statistical reasoning	Region	Drainage area (km^2)
			LW volume per channel area				
Keller and Swanson (1979)*	Unknown	Coarse debris loading	Decreasing	Drainage area, stream order, channel width	Stated general trend	Pacific Northwest	0.2 - 1024
Harmon et al. (1986)	Unknown	Amounts of CWD	Decreasing	Drainage area, channel width	Stated general trend	Temperate ecosystems	Various
Lienkaemper and Swanson (1987)	In-channel only	Amounts of large debris	Decreasing	Drainage area, stream order	Stated general trend	Pacific Northwest	0.1 - 60.5
Robison and Beschta (1990)	In-channel only	-	Decreasing	Stream order	Stated general trend	Southeast Alaska	0.72 - 55.4
Beechie and Sibley (1997)	In-channel only	-	Decreasing	Channel width	Multiple regression	Pacific Northwest	Unknown

Table 2

Table 2. Half-log scale contributing drainage area bins and stream site characteristics

Bin	Drainage area range (km^2)	Mean bankfull channel width (m)	Mean slope ($m\ m^{-1}$)	Total stream distance in study area (km)	Number of sites
1	0.5 − 1.58	5.2	0.14	1013.3	17
2	1.58 − 5	5.1	0.12	591.8	16
3	5 − 15.8	7.9	0.05	354.8	14
4	15.8 − 50	12.1	0.08	214.8	16
5	50 − 158	15.2	0.03	196.8	13
6	158 − 500	21.1	0.04	89.9	15
7	500 − 1,581	28.3	0.03	119.8	13
8	1,581 − 5,000	37.5	0.04	9.4	10
All	-	15.2	0.07	2590.6	114

Notes: Stream sites were chosen at random from these bins.

Table 3

Table 3.Variables derived from GIS or estimated in the field and used in statistical analyses

Watershed scale	Units	Explanation
Drainage area	km^2	Upslope contributing drainage area
Strahler stream order*	-	ArcGIS stream order tool, using the flow direction raster
Elevation	m	Elevation of stream site above mean sea level
Upslope distance*	m	Channel length from stream site to the farthest point in the upslope stream network
Upslope stream density	$km\ km^{-2}$	Number of stream cells divided by number of total cells in upslope watershed, converted for units
Upslope channel slope	$m\ m^{-1}$	Mean slope of all stream cells in drainage area
Upslope terrain slope	$m\ m^{-1}$	Mean slope of all terrain cells in drainage area
Upslope stream power index*	m^2	Mean stream power index ($A \cdot S$) of all stream cells in contributing area
Upslope wetness index*	-	Mean wetness index ($\ln (A / S)$) of all stream cells in contributing area
Upslope channel elevation range*	m	Vertical distance from highest cell in upslope stream network to the stream site

Table 4

Table 4. Summary of results for the MLR model to predict total LW volume per channel length

Adjusted R^2 = 0.31; p < 0.0001; AIC = 252.4				
Variable	*β*	*b*	Std. Error	*p*
Local percent shrub	0.49	0.24	0.04	< 0.0001
Bankfull channel width	0.38	0.83	0.22	< 0.001
Upslope percent intrusive igneous rock	0.22	0.06	0.02	< 0.01
Local side slope	-0.26	-0.76	0.26	< 0.01
Upslope percent urban	-0.31	-0.35	0.10	< 0.01
Intercept	-	-1.51	0.35	< 0.0001

Notes: The *β* coefficient is what would have resulted had all of the variables first been standardized to a mean of 0 and a standard deviation of 1, which allows for comparison of contribution among the variables. The *b* coefficient is the actual value used in the model.

Table 5

Table 5. Summary of results for the MLR models to predict total LW volume per channel length in each subbasin and elevation category

Variable	North Yuba Adj. R^2 = 0.45; p < 0.01		Middle Yuba Adj. R^2 = 0.50; p < 0.001		South Yuba Adj. R^2 = 0.27; p = 0.011	
	β	p	β	p	β	p
Local percent shrub	**0.55**	**< 0.01**	**0.58**	**< 0.001**	**0.57**	**< 0.01**
Bankfull channel width	**0.57**	**< 0.01**	0.18	0.31	**0.59**	**< 0.01**
Upslope percent intrusive igneous rock	**0.46**	**< 0.01**	0.22	0.12	-0.02	0.90
Local side slope	-0.025	0.88	**-0.37**	**0.042**	-0.065	0.69
Upslope percent urban	-0.16	0.37	0.034	0.84	**-0.56**	**< 0.01**
Intercept	-	**< 0.01**	-	**< 0.01**	-	**0.034**

Variable	High elevation Adj. R^2 = 0.42; p < 0.001		Medium elevation Adj. R^2 = 0.22; p = 0.022		Low elevation Adjusted R^2 = 0.24; p = 0.017	
	β	p	β	p	β	p
Local percent shrub	**0.65**	**< 0.001**	**0.43**	**0.015**	**0.46**	**0.012**
Bankfull channel width	**0.58**	**< 0.01**	0.20	0.24	0.28	0.15
Upslope percent intrusive igneous rock	0.19	0.17	**0.36**	**0.032**	0.010	0.95
Local side slope	-0.26	0.080	-0.11	0.44	-0.31	0.12
Upslope percent urban	**-0.60**	**< 0.001**	-0.20	0.31	0.045	0.79
Intercept	-	**< 0.01**	-	**0.021**	-	0.088

Notes: Symbology is the same as Table 4. Elevations were classified as high ($E \geq 1600$ m), medium ($800 \leq E < 1600$ m), and low ($E < 800$ m). Significant values are shown in bold.

Table 6

Table 6. Percent of out-of-channel and in-channel LW volume, and ratio of out-of-channel to in-channel LW volume by drainage area bin

	Drainage area bin								
	1	2	3	4	5	6	7	8	All
Percent out-of-channel LW volume	71.1	60.8	55.2	94.1	85.9	99.9	97.2	99.2	86.5
Percent in-channel LW volume	28.9	39.2	44.8	5.9	14.1	0.1	2.8	0.8	13.5
Ratio of out-of-channel to in-channel LW volu	2.5	1.6	1.2	16.0	6.1	1092.5	34.7	132.2	6.4

Table 7

Table 7. LW storage data from Keller and Swanson (1979)

Stream	Biomass per channel area (kg m^{-2})	LW volume per channel length (m^3 per 100 m)*	Length of sampled section (m)	Channel width (m)	Stream order	Drainage area (km^2)
Devilsclub Creek	43.5	8.7	90	1.0	1	0.2
Watershed 2 Creek	38.0	19.8	135	2.6	2	0.8
Mack Creek	28.5	68.4	300	12.0	3	6.0
Lookout Creek	11.6	55.7	300	24.0	5	60.5
McKenzie River	0.5	4.0	800	40.0	6	1024.0

Notes: LW volume per 100 m (*) was back-calculated from the original data to demonstrate that this quantity increases considerably, and then decreases in the downstream direction.

Figure captions

Figure 1. Map of the Yuba River watershed above Englebright Dam and the 114 stream site locations selected by a stratified random sampling scheme based on drainage area.

Figure 2. Box and whisker plot of LW storage per 100 m for 114 field reaches. The horizontal line represents the median value, the top and bottom of the box represent the 75^{th} and 25^{th} percentile, whiskers represent the 90^{th} and 10^{th} percentiles, and the circles are outliers.

Figure 3. Box and whisker plots of LW storage per 100 m for each (a) drainage area bin, (b) stream order, (c) bankfull channel width category, (d) shrub prevalence, (e) forest prevalence, and (f) exposed bedrock prevalence. Mann-Whitney U tests were performed on all combinations of bins or categories, and only the statistically significant differences are marked with common letters.

Figure 1 (Color)

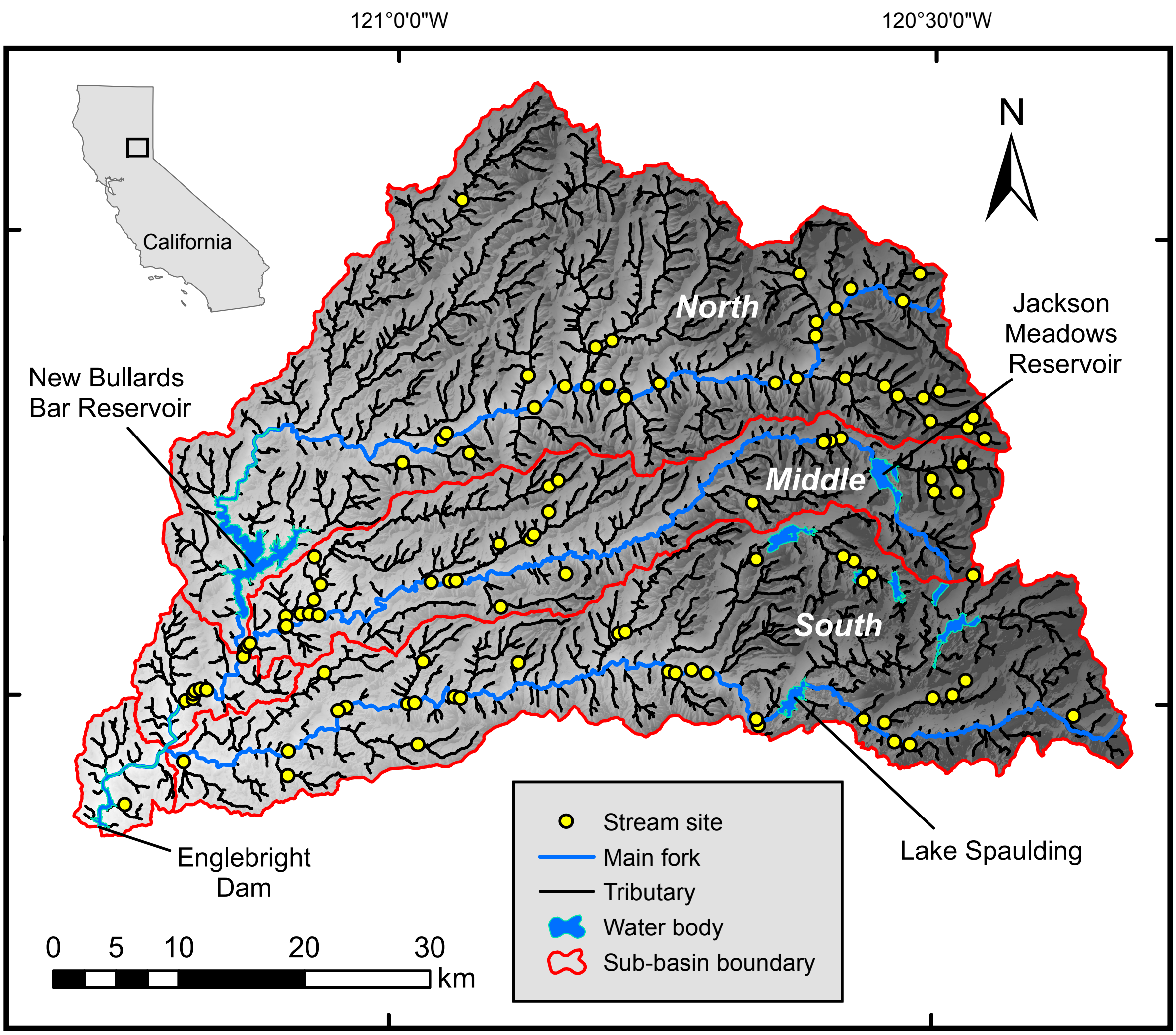


Figure 1 (Greyscale)

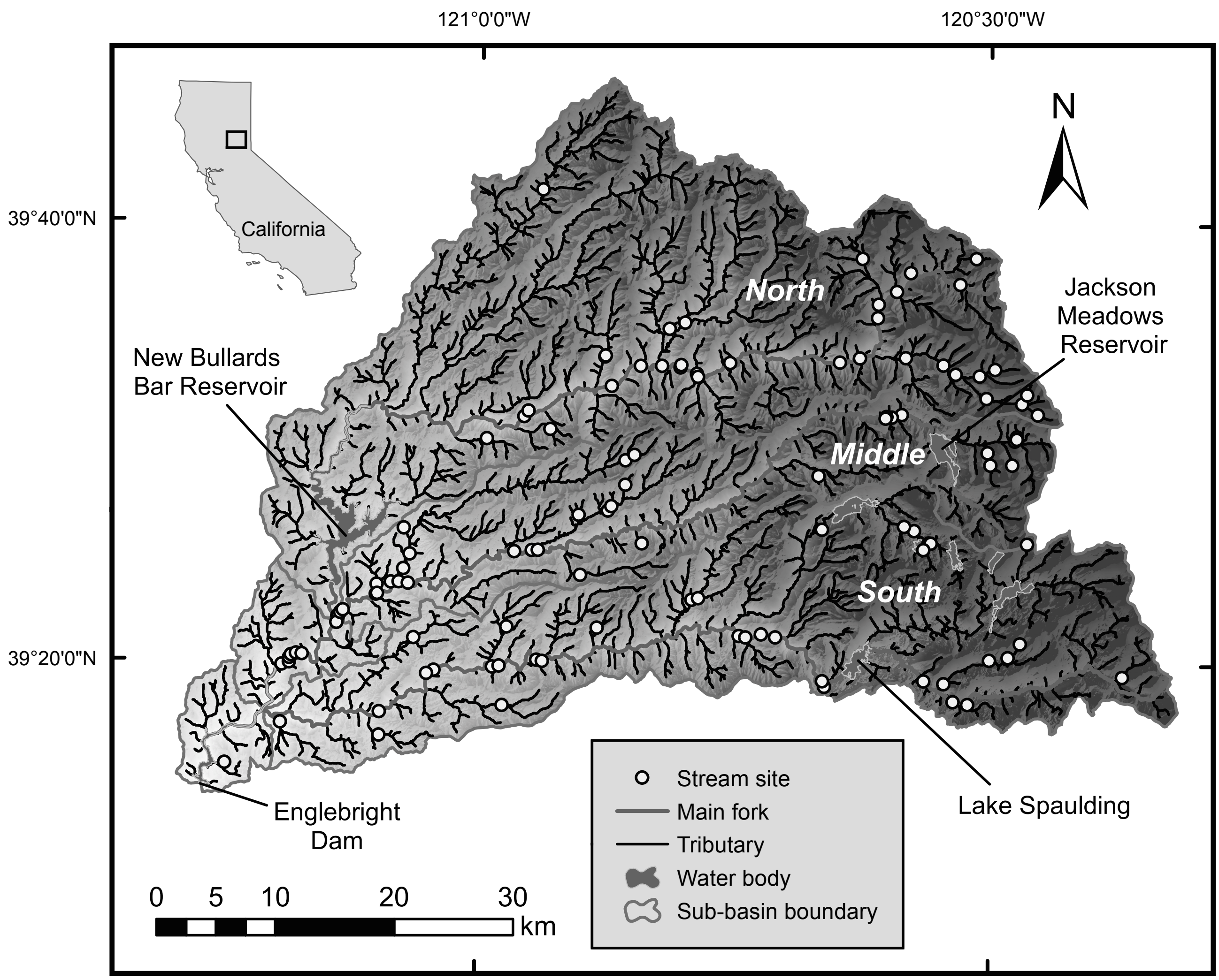


Figure 2 (Greyscale)

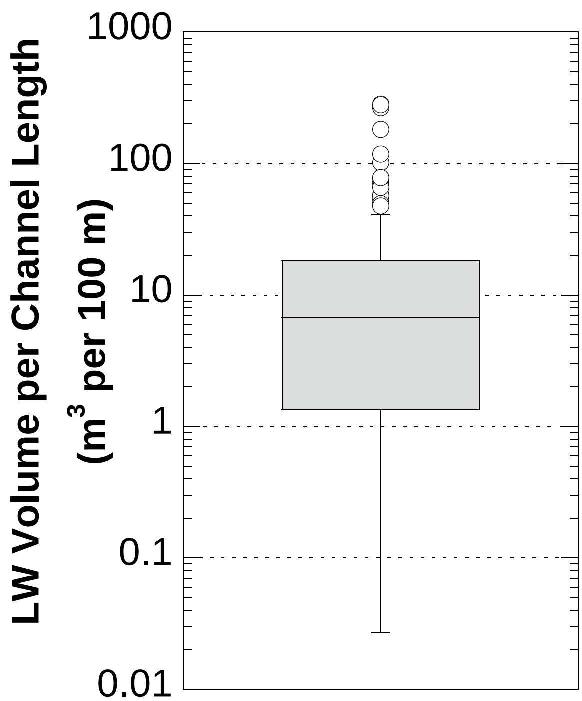
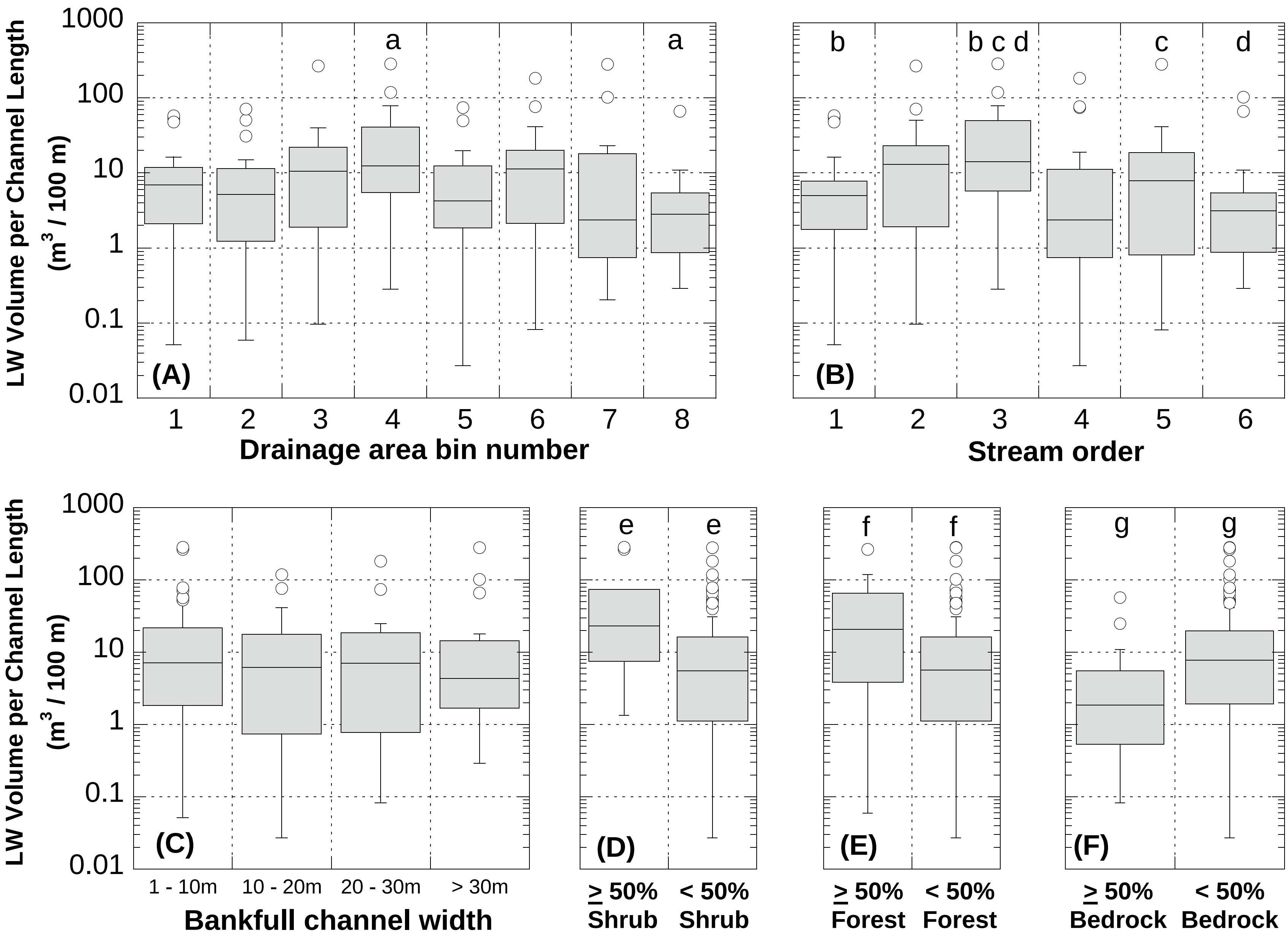


Figure 3 (Greyscale)



Responses to Ecological Applications reviewer comments

Previous version of manuscript submitted to EA

Click here to download Supplementary material for online publication only: YRwoodvol_20140408_EA.doc