

Floodplain downed wood volumes: a comparison across three biomes

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ABSTRACT: Downed large wood (LW) in floodplains provides habitat and nutrients for diverse organisms, influences hydraulics and sedimentation during overbank flows, and affects channel form and lateral migration. Very few studies, however, have quantified LW volumes in floodplains that are unaltered by human disturbance. We compare LW volumes in relatively unaltered floodplains of semiarid boreal lowland, subtropical lowland, and semiarid temperate mountain rivers in the United States. Average volumes of downed LW are $42.3 \text{ m}^3 \text{ ha}^{-1}$, $50.4 \text{ m}^3 \text{ ha}^{-1}$, and $116.3 \text{ m}^3 \text{ ha}^{-1}$ in the semiarid boreal, subtropical, and semiarid temperate sites, respectively. Observed patterns support the hypothesis that the largest downed LW volumes occur in the semiarid temperate mountain sites, which is likely linked to a combination of moderate-to-high net primary productivity, temperature-limited decomposition rates, and resulting slow wood turnover time. Floodplain LW volumes differ among vegetation types within the semiarid boreal and semiarid temperate mountain regions, reflecting differences in species composition. Lateral channel migration and flooding influence vegetation communities in the semiarid boreal sites, which in turn influences floodplain LW loads. Other forms of disturbance such as fires, insect infestations, and blowdowns can increase LW volumes in the semiarid boreal and semiarid temperate mountain sites, where rates of wood decay are relatively slow compared with the subtropical lowland sites. Although sediment is the largest floodplain carbon reservoir, floodplain LW stores substantial amounts of organic carbon and can influence floodplain sediment storage. In our study sites, floodplain LW volumes are lower than those in adjacent channels, but are higher than those in upland (i.e. non-floodplain) forests. Given the important ecological and physical effects of floodplain LW, efforts to add LW to river corridors as part of restoration activities, and the need to quantify carbon stocks within river corridors, we urge others to quantify floodplain and instream LW volumes in diverse environments. Copyright © 2016 John Wiley & Sons, Ltd.

KEYWORDS: floodplain; coarse woody debris; large wood; mountains; subtropical; boreal

Introduction

Downed large wood (>10 cm in width and >1 m in length) within river corridors, which we define as channels and floodplains, is geomorphically and ecologically important (Harmon *et al.*, 1986; Jeffries *et al.*, 2003; Pettit and Naiman, 2006; Collins *et al.*, 2012). Downed floodplain large wood (LW) exerts controls on physical process and form in river corridors. Floodplain LW can be a source of wood to the channel as channels migrate, erode banks, and transport wood from the floodplain (Benda and Sias, 2003; Latterell and Naiman, 2007). Dispersed and jammed (i.e. accumulated in piles) LW on floodplains can influence floodplain inundation and sedimentation patterns by increasing hydraulic resistance during overbank flow (Jeffries *et al.*, 2003; Sear *et al.*, 2010), and can influence channel planform and lateral migration rates (Collins *et al.*, 2012; Polvi and Wohl, 2012). Numerous studies document reciprocal interactions among in-channel LW, floodplain LW, floodplain vegetation, floodplain turnover time, and channel form and process

(Piégay and Gurnell, 1997; Gurnell *et al.*, 2000, 2002; O'Connor *et al.*, 2003; Gurnell and Petts, 2006; Wohl, 2013a). Few studies, however, document floodplain downed LW loads along unmanaged rivers. Our primary objective is to provide such documentation in three regions (semiarid boreal lowland, subtropical lowland, and semiarid temperate mountain) and to examine potential controls on wood loads.

In addition to geomorphic effects, downed floodplain LW provides habitat for riparian and terrestrial biota by providing shelter and food to birds, mammals, amphibians, and aquatic and terrestrial invertebrates (Harmon *et al.*, 1986; Braccia and Batzer, 2001; Bull, 2002; Mac Nally *et al.*, 2002; Ballinger *et al.*, 2010). LW creates sites of nutrient hotspots as the wood decomposes (Schowalter *et al.*, 1998), and accumulations of LW within the floodplain are associated with sites of seedling establishment and the regrowth of riparian vegetation (Pettit and Naiman, 2006). Floodplain LW is also a significant organic carbon (OC) stock within river–floodplain systems (Wohl *et al.*, 2012; Sutfin *et al.*, 2016). Globally, dead LW can be 10–20% of

the above-ground biomass of forests, resulting in a stock estimated at 36–72 Pg C (1 Pg = 10^{15} g = 1 Gigaton) (Cornwell *et al.*, 2009).

Although there is a great deal of literature within the forest ecology discipline on downed and dead LW in upland forests (Russell *et al.*, 2015), which we define as forests located outside of floodplains, very little attention has been given to downed LW within floodplains. The geomorphic and ecological importance of floodplain LW, as well as the unique character of riparian zones, indicates that further attention should be paid to LW loads and patterns in LW loads across different biomes. Riparian ecosystems have high spatial heterogeneity, displaying mosaics of landforms and vegetation, and they are dynamic transition zones between the aquatic and terrestrial realms (Gregory *et al.*, 1991; Naiman and Décamps, 1997). Riparian vegetation commonly differs from upland vegetation, with riparian species undergoing fluvial disturbances (lateral channel migration) as well as upland disturbances (e.g. landslides, debris flows), and riparian forests are more productive compared with upland forests (Naiman and Décamps, 1997). Recent efforts to restore LW to river corridors for ecological and geomorphic benefits (Abbe and Brooks, 2011) also provide motivation for exploring LW loads in unaltered floodplain environments across diverse environments.

Dynamics of floodplain LW

The sources of downed LW in the floodplain include lateral inputs from upland areas, lateral inputs of wood from the channel via flooding and deposition, and mortality and breakage of standing trees within floodplain forests or adjacent terraces and uplands (Harmon *et al.*, 1986). Inputs from upland areas likely dominate in high-relief catchments and valley segments closely coupled to unstable hillslopes on which landslides and debris flows introduce substantial volumes of LW to the floodplain and channel (May and Gresswell, 2003). In contrast, lateral inputs of wood from the active channel to the floodplain likely dominate where overbank flows transport substantial quantities of wood onto the floodplain or where channel avulsion and lateral accretion allow in-channel logjams to be incorporated into the floodplain (Collins *et al.*, 2012). LW floated onto the floodplain during overbank flows is likely to be concentrated along the floodplain margin close to the channel or at the upstream end of secondary channels near island heads (Piégay and Gurnell, 1997), rather than being evenly distributed across the floodplain.

We focus on LW on the floodplain surface and not in the subsurface, within the active channel, or on the channel margins. Consequently, we expect wood recruitment from floodplain forests via breakage and mortality to dominate floodplain wood loads on most river segments, particularly those with relatively low gradients and in low-relief terrains along which laterally and longitudinally extensive floodplains are most likely to be present.

The relative importance of the causes of LW recruitment is likely to vary both spatially and temporally. Lateral channel inputs can create concentrations of LW along the channel–floodplain boundary. Floodplain forest mortality can dominate LW loads in the floodplain interior, and valley side slope inputs can dominate LW loads at the floodplain margins. Disturbances, such as fire, wind storms, and hurricanes, can greatly increase LW loads by causing mortality and breakage of riparian trees (Moroni, 2006; Harmon, 2009). For example, mass mortality of floodplain forests during hurricanes can create a pulsed and episodic input of downed LW to the floodplain

(Phillips and Park, 2009), whereas individual mortality provides a much smaller, continuous input of downed LW.

Reduction of LW loads on the surface of the floodplain can occur through removal by river transport, burial, and through decay (Harmon *et al.*, 1986). Decay involves fragmentation of wood pieces, leaching dissolved materials and resulting weight loss, and microbial metabolism (Harmon *et al.*, 1986). Size reduction via fragmentation could result in the wood piece no longer belonging in the large wood class and could make resulting smaller wood pieces more susceptible to floating and removal during overbank flows. Rates of wood decay vary among tree species at a site and among sites as a function of moisture, temperature, piece size, abrasion, breakage, and microbial decomposition (Harmon *et al.*, 1986; Harmon, 2009). Decay rates are usually investigated for specific species within relatively small study areas (Kueppers *et al.*, 2004; Ricker *et al.*, 2016) and are only generally constrained for ecosystem types at a global scale (Harmon *et al.*, 2001). There are multiple metrics used to report the speed at which large wood or organic matter decays. Most studies use the single exponential model of decay described by Olson (1963), in the form of $Y_t = Y_0 e^{-kt}$, where Y_0 is the initial quantity of wood, Y_t is the quantity left at time t , and k is the decay constant. Wood decomposition can then be described by the decay constant k , the half-life of the wood ($0.693/k$), or the turnover time of the wood ($1/k$) (Olson, 1963; Harmon *et al.*, 1986). In this paper, we report wood turnover times from the literature for the purpose of comparing biomes.

Patterns in upland downed LW loads can be related to broad-scale climatic factors. As latitude increases, forest biomass and net primary productivity generally decrease, leading to a smaller source pool for downed LW (Harmon *et al.*, 1986; Krainka and Harmon, 1995; Saugier *et al.*, 2001). However, decomposition generally decreases with colder climates at higher latitudes, potentially offsetting the effect of decreased productivity (Harmon *et al.*, 1995; Harmon, 2009). Similarly, decreasing temperature with increasing elevation limits decomposition at higher elevations. Mountainous regions that experience orographic precipitation and significant snow accumulation can provide the moisture necessary for increased productivity relative to surrounding lowlands (Schimel *et al.*, 2002), and differences in disturbance regimes in mountainous environments compared with lowland environments can also influence downed LW loads.

Objectives and hypothesis

The objectives of this paper are to: examine patterns in downed LW volumes across three biomes in floodplains unaltered by human modifications; determine the quantity of organic carbon stored in floodplain LW; infer primary influences on floodplain LW volumes, including investigating the influence of vegetation types and disturbance; and compare floodplain LW loads with upland LW loads and in-channel LW loads. Patterns here refer to differences between regions and differences within a region as a result of difference in vegetation community and disturbance. In this context, human modifications include timber harvest, log floating for timber delivery to mills, flow regulation, channelization, construction of artificial levees, road construction in riparian zones, riparian forest management, and floodplain drainage. Floodplains unaltered by human activities can provide a baseline for natural floodplain LW loads, facilitating quantification of human alteration of wood loads through reduced wood recruitment and transport or direct wood removal.

Field sites include the central Yukon River Basin in interior Alaska (semiarid boreal lowlands), Congaree National Park in South Carolina (subtropical lowlands), and subalpine and

montane conifer forests in the Rocky Mountains of Colorado (semiarid temperate mountains). In each of these regions we focus on naturally disturbed sites, rather than on managed forests or sites impacted by human disturbance, and we assume that floodplain vegetation is the dominant source of floodplain LW. We posit that biomes with high forest productivity along with slow decay rates will have the largest downed wood volume (Harmon, 2009; Sutfin et al., 2016). Because these conditions are met in the semiarid temperate mountain sites, we hypothesize that these sites will have the highest LW volume.

Study areas

Semiarid boreal lowlands: the Yukon Flats region, Alaska, USA

The Yukon Flats is a large alluvial basin located in the central Yukon River basin in the dry boreal zone of interior Alaska (Figure 1, Figure 2, Table I). The climate is continental subarctic (Gallant et al., 1995) with discontinuous to continuous permafrost underlying the more than 30 000 km² of the floodplains of the Yukon River and multiple tributaries (Jorgenson et al., 2008). Floodplain vegetation types include herbaceous vegetation, shrubs (willows (*Salix* spp.) and alders (*Alnus* spp.)), deciduous tree species (balsam poplar (*Populus balsamifera*), aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*)), spruce forest (white (*Picea glauca*) and black spruce (*Picea mariana*)), and mixed forests (spruce and deciduous). Wildfire return interval ranges from 37 to 166 years, with a mean recurrence interval of c. 90 years (Drury and Grissom, 2008). Other disturbances include blowdowns and movement of river ice that damages and topples vegetation. High flows occur in the

spring due to snowmelt, with infrequent ice jam floods causing more intense flooding. Decay rates of downed wood for a variety of tree species in this location are unknown, but are likely to be extremely slow given the cold temperatures and low mean annual precipitation (Harmon et al., 1986; Gallant et al., 1995) (Table I).

Subtropical lowlands: Congaree National Park, South Carolina, USA

The subtropical lowland study sites are located within Congaree National Park in South Carolina (Figure 1, Figure 2, Table I). Common tree species include baldcypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), loblolly pine (*Pinus taeda*), sweetgum (*Liquidambar styraciflua*), green ash (*Fraxinus pennsylvanica*), and red maple (*Acer rubrum*). Disturbances include blowdowns and flooding. Although blowdowns associated with hurricanes are the major disturbance on longer time scales, the study sites have not been influenced recently by a hurricane. Rainfall-generated flooding is most frequent during winter and early spring, but can occur at any time during the year. Invertebrate activity contributes to extremely fast wood turnover time (4–5 years) for downed wood on the floodplain (Ricker et al., 2016) (Table I).

Semiarid temperate mountains: Rocky Mountains, Colorado, USA

Sites in the Rocky Mountains are located on the eastern side of the continental divide in a semiarid climate (Figure 1, Figure 2,

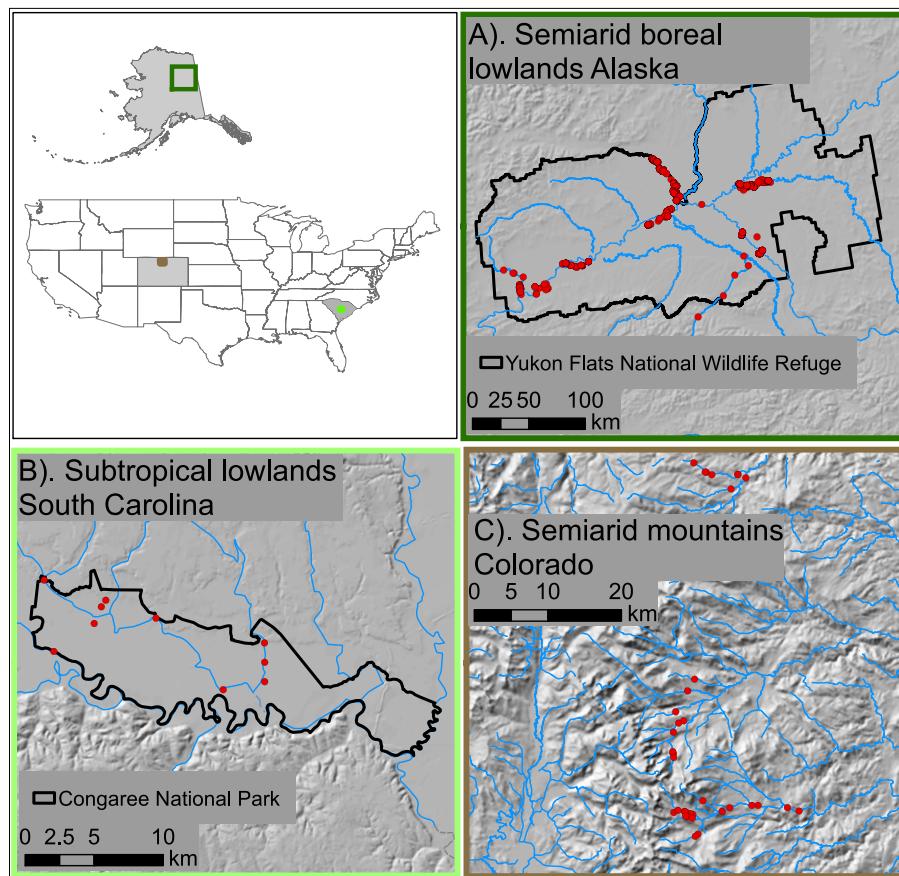


Figure 1. Map showing location of the three study regions. Locations of measurements are shown as red dots for each of the locations. [Colour figure can be viewed at wileyonlinelibrary.com]



Figure 2. Photos of the study regions, showing floodplains in the boreal lowlands in Alaska (A), the subtropical lowland floodplain in South Carolina (B), and the semiarid mountains in Colorado (C). In (A), the two main channels of the Yukon River are approximately 500–700 m wide. In (B), the fallen log at the center of the photo on the Congaree floodplain is approximately 6 m in length. In (C), the distance between the two standing trees in the center of the photo is approximately 3 m. Photo of the semiarid mountains by Lina Polvi Sjöberg. [Colour figure can be viewed at wileyonlinelibrary.com]

Table I. Characteristics of the study sites

Region	Mean annual precipitation (mm)	Mean annual temperature (°C)	Drainage areas of study sites (km ²)	Wood turnover time (years)
Boreal lowlands, Alaska	170	−1	4000–510 000	Unknown
Southern Rockies subalpine	800–1000	4	3–96	600–900 ^a
Southern Rockies montane	400	7	<40	300–400 ^a
Subtropical lowlands, South Carolina	1220	17.6	110–8100	4–5 ^b

^a(Kueppers *et al.*, 2004)

^b(Ricker *et al.*, 2016)

Table I). One group of sites lies within subalpine forest (3500–2850 m elevation) dominated by Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), and limber pine (*Pinus flexilis*) (Veblen and Donnegan, 2005). Snowmelt dominates the hydrograph (Jarrett, 1989), and disturbances include wildfire and blowdowns. Stand-killing fires in the uplands recur at intervals greater than 100 years and

commonly greater than 400 years (Veblen and Donnegan, 2005), although estimated fire return intervals may be different in floodplain valley bottoms with wetter ground conditions. Blowdowns have irregular recurrence intervals and typically only affect isolated trees within small stands (<30 ha), but can recur at intervals of one to two decades (Wohl, 2013b). Wood turnover time in the subalpine zone ranges from 600–900 years (Kueppers *et al.*, 2004) (Table I).

A second group of sites lies within the montane forest (2850–1750 m elevation), which is dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), with blue spruce (*Picea pungens*), aspen, willow (*Salix* spp.), river birch (*Betula fontinalis*), and grasses in riparian areas (Veblen and Donnegan, 2005). Low-severity wildfires recur at intervals of 5 to 30 years and stand-replacing fires recur at intervals of 40–100 years (Veblen and Donnegan, 2005), although again this may differ in the valley bottoms. Blowdowns occur, but are less common than in the subalpine zone. In the montane zone, snowmelt creates annual peak flows, but rainfall convective storms can produce peak flows through the summer (Jarrett, 1989). Wood turnover time in the montane zone is 300–400 years, which is slightly faster than in the subalpine zone (Kueppers et al., 2004) (Table I).

Methods

Field methods

At the semiarid boreal lowland site, we measured the diameter and length of downed LW along transects within the floodplain ($n = 122$). We used the line-intersect method to convert diameters of the wood pieces along the transects into wood volume in $\text{m}^3 \text{ ha}^{-1}$ (Van Wagner, 1968), with the form $V = \frac{\pi^2 * \sum d^2}{8L}$, where V is the volume of wood per unit area, d is the piece diameter, and L is the length of the transect line. We classified the floodplain transects by vegetation type and by presence or absence of recent natural disturbance. We determined that the location experienced recent disturbance if there was clear and widespread evidence of that disturbance. For example, if there were a significant number of charred standing dead trees and downed LW, we determined that fire was a recent disturbance at the location. Vegetation types include herbaceous vegetation, deciduous/shrub, mixed forest with deciduous and conifer species, white spruce forest, and black spruce forest. We also measured basal area using a Panama angle gauge at each transect location. Basal area is an expression of the cross-sectional area of tree trunks as a fraction of the total ground area, and it is a measure of biomass in the riparian forest.

Measurements were taken in the floodplains of five rivers within the Yukon Flats (Dall River, Preacher Creek, Yukon River, Draanjik (Black) River, and Teedrinjik (Chandalar) River). On two of the five rivers, diameter along the tape (tape diameter) and the diameter measured in the plane perpendicular to the long axis of the piece that best represents the downed wood piece as a cylinder (off-tape diameter) are available. On three of the five rivers, only the off-tape diameter of the downed wood is available for each piece. Because the line-intersect method uses the tape diameter, we performed regression analysis for the two rivers with both tape diameter and off-tape diameter to correct LW volumes for the three rivers where only off-tape diameters are available (see Supplementary material). We regressed log LW volumes calculated with off-tape diameter vs. log LW volumes using tape diameter, forcing the intercept to zero. We then inverted and back-transformed the regression, getting an equation to predict LW volumes for those locations where only LW volumes using off-tape diameter was available (see Supplementary information for further discussion of this process). We believe this adjustment is appropriate, and the same results for the comparisons among biomes were found when using LW volumes from the two rivers with diameter along the tape as when using LW volumes for all five rivers with adjusted values for three of the rivers.

Downed LW in the floodplains of the study rivers (Congaree River, Cedar Creek, and Toms Creek) within Congaree National Park in the subtropical lowland site was measured using strip sampling, in which all LW was measured in a transect within the floodplain that was 10 m wide (see Wohl et al., 2011 for an extensive description of methods; $n = 34$). For each piece, the length and diameter that best represented the downed wood piece as a cylinder was measured, resulting in an estimate of wood volume per area. The vegetation type was noted, as was evidence of disturbance (in this case, transects that experienced recent flooding or no evidence of recent flooding). Similarly to the sites in Alaska, widespread evidence was used as an indicator of recent disturbance. Vegetation was classified as tupelo, riverbank/levy forest, or mixed bottomland hardwoods. The basal area of the surrounding forest was also measured using a Panama angle gauge. In addition to floodplain LW, all LW within the stream channel at each study reach was measured.

Downed LW within floodplains of the Rocky Mountains in the semiarid temperate site was measured using fixed-area sampling, in which the length and end diameters for all LW was measured within a specific area of the floodplain along a study reach ($n = 40$), which was the length of approximately 10 bankfull widths. We used the average of the end diameters, along with piece length, to get wood volume. As with the other study areas, we noted the vegetation type and whether the reach was recently disturbed. Vegetation types included montane, subalpine, or non-coniferous vegetation (i.e. sedges and grasses, aspen, willow). We used additional data on downed LW volumes from the montane zone from Jackson and Wohl (2015). Basal areas for floodplain forest adjacent to the channel were measured with a Panama angle gauge in some of the reaches in which downed wood was measured and are available from Jackson and Wohl (2015) and Livers and Wohl (2016). In-stream LW volumes, also available for some of the reaches where floodplain LW measurements were taken, are from Livers and Wohl (2016).

Comparisons between census methods of measuring downed wood (measuring every piece of LW within a specified area) and the line-intersect method show that the line-intersect method can slightly overestimate LW volume (Marsh et al., 1999; Warren et al., 2007), but systematic bias due to surveyor error is not a problem with the method (Ringvall and Ståhl, 1999). Overestimation of LW volumes using the line-intersect method is not an issue for our analyses and comparative results, because we expect the region in which the line-intersect method was used (the semiarid boreal sites) to be the one with the lowest LW volume. Thus, if differences among biomes are present within our data, we can assume that differences would also be present if LW volume measurements had been taken using census methods in the boreal biome.

Analyses

LW volume per hectare was multiplied by an average value of wood density for each site (representative values taken from Forest Products Laboratory, 2010) to get LW mass per hectare. We assumed 400 kg m^{-3} for the semiarid boreal lowland and semiarid temperate mountain sites and 530 kg m^{-3} for the subtropical lowland site. We then multiplied the mass of wood per hectare (Mg ha^{-1}) by 0.5 to get mass of organic carbon per hectare (Mg C ha^{-1}), as approximately half of wood mass is organic carbon (Russell et al., 2015).

In order to determine statistically significant differences in LW volumes ($\text{m}^3 \text{ ha}^{-1}$) and mass of organic carbon (Mg C ha^{-1}) among biomes and among vegetation types and

disturbance groups within biomes, we used non-parametric Kruskal–Wallis and Wilcoxon rank-sum pairwise comparisons (due to non-normality in the data), with a Bonferroni correction for multiple comparisons if needed. We used a 95% confidence interval to determine significance. We also used the Kruskal–Wallis and Wilcoxon rank-sum pairwise comparisons to determine statistically significant differences among biomes in downed LW length, diameter, and basal area of the surrounding vegetation. We used Spearman's correlation coefficient (ρ), which tests for a monotonic relationship between two variables, to determine correlation between basal area and LW volume. All statistical analyses were completed using the R statistical package (R Core Team, 2014).

Results

Significant differences exist among biomes with respect to downed LW volumes, organic carbon mass in LW, LW diameter, and LW length (Figure 3). The mean value of LW volume is the lowest in the semiarid boreal biome ($42.3 \text{ m}^3 \text{ ha}^{-1}$) and highest in the semiarid temperate biome ($116.3 \text{ m}^3 \text{ ha}^{-1}$). There are significant differences in LW volumes between the semiarid boreal biome and the subtropical biome ($P < 0.0001$) and between the semiarid boreal biome and the semiarid temperate biome ($P = 0.025$). When not adjusting

for multiple comparisons with the Bonferroni method, there are significant differences among all three biomes. For organic carbon mass in wood, the pattern is similar for that of LW volume, with the boreal biome being significantly different from the subtropical biome ($P < 0.001$) and the semiarid temperate biome ($P < 0.0001$). We completed the analyses of determining differences in downed LW volume and carbon mass among groups with the subalpine and the montane as separate groups, resulting in four different groups. However, there were no significant differences between the subalpine and montane; the comparisons with the two sub-groups in the semiarid mountains and the boreal lowlands and subtropical lowlands did not change with subdivision of the semiarid mountain biome; and the semiarid mountain sites are geographically close together despite the division between subalpine and montane. Thus, we will present only the comparison among the three main biomes.

The mean diameter of downed LW is lowest in the boreal and highest in the semiarid temperate, with significant differences among each pairwise comparison (boreal–subtropical $P < 0.0001$; boreal–temperate $P < 0.0001$; subtropical–temperate $P = 0.0095$). The mean length of downed LW was the lowest in the subtropical region and highest in the boreal region, with significant differences in length between the subtropical and boreal ($P < 0.0001$) and between the subtropical and semiarid temperate ($P < 0.001$).

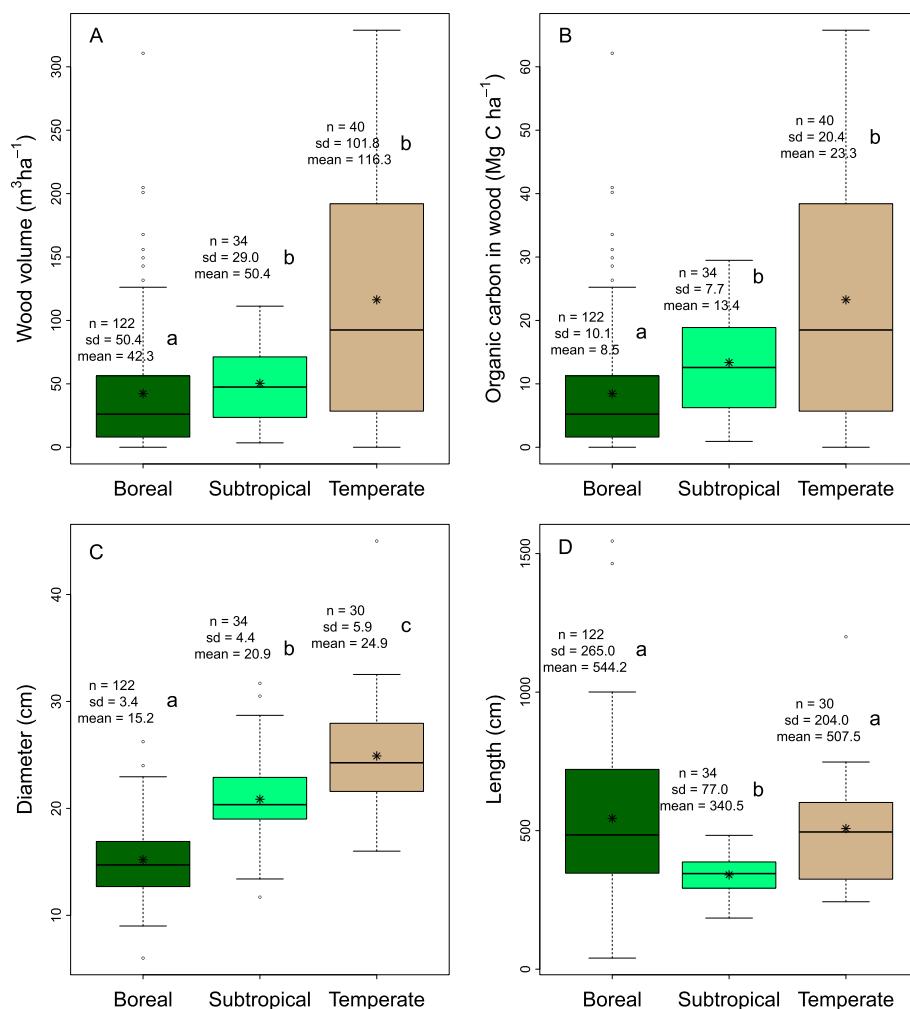


Figure 3. Comparisons among the three study regions in wood volume (A), organic carbon in wood (B), downed wood length (C), and downed wood diameter (D). For boxplots, the star within the box indicates the mean value, the solid line within the box indicates the median value, the box ends are the upper and lower quartile, and the whiskers are the 10th and 90th percentile. Significant differences between pairwise comparisons are indicated with contrasting letters (a, b, c). [Colour figure can be viewed at wileyonlinelibrary.com]

There are also significant differences in basal area between the semiarid boreal and the subtropical biomes ($P < 0.0001$) and the boreal and semiarid temperate biomes ($P < 0.0001$) (Figure 4(A)). For reaches in which disturbances have not modified the standing forest in recent years (undisturbed reaches), there is a weak significant relationship between LW volumes and basal area within the semiarid boreal biome ($p = 0.33$, $P = 0.0008$) and no relationship in the subtropical biome ($p = -0.098$, $P = 0.6004$; Figure 3(B)). However, in the semiarid temperate biome, as basal area increases, LW volumes also increase ($p = 0.73$, $P = 0.001$) (Figure 4(B)).

Intra-region comparisons of LW volumes between recently disturbed and undisturbed sites also show significant differences in the semiarid boreal region ($P < 0.0001$) and the semiarid temperate region ($P = 0.041$), but not in the subtropical region ($P = 0.45$) (Figure 5). LW volumes among vegetation types are also different within the semiarid boreal and semiarid temperate regions (Figure 6). In the boreal region, significant differences occur between the herbaceous vegetation type and: (1) white spruce forest ($P < 0.0001$); (2) deciduous forest ($P < 0.0001$); and (3) mixed forest ($P = 0.0032$), and also between black spruce and white spruce ($P = 0.0014$) and black

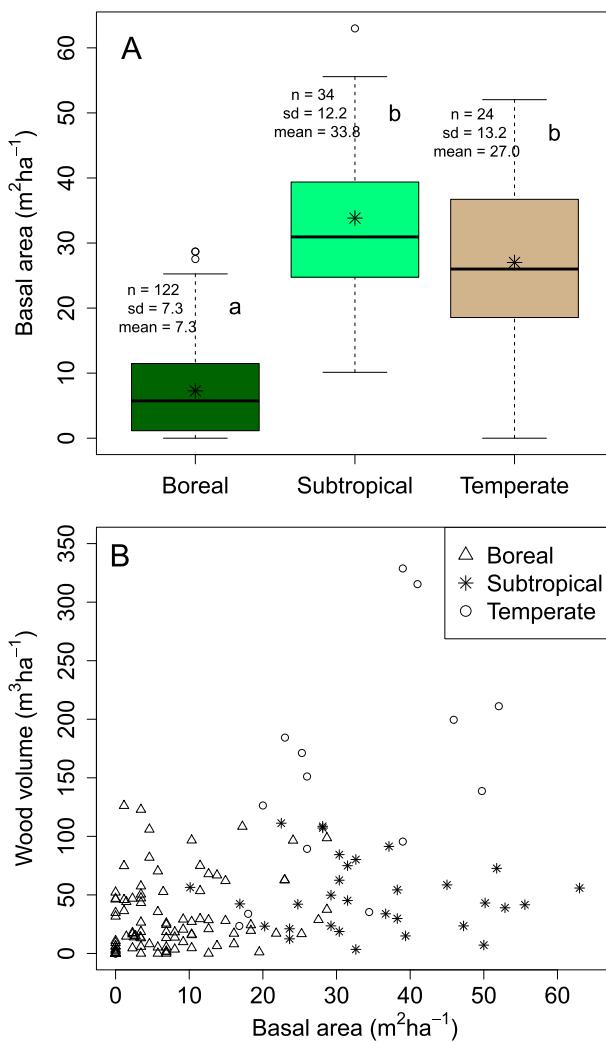


Figure 4. Basal area measurements for each region (A), showing significant differences, and scatterplot of wood volume vs. basal area for reaches that are undisturbed (B). For boxplots, the star within the box indicates the mean value, the solid line within the box indicates the median value, the box ends are the upper and lower quartile, and the whiskers are the 10th and 90th percentile. Significant differences between pairwise comparisons in (A) are indicated with contrasting letters (a, b, c). [Colour figure can be viewed at wileyonlinelibrary.com]

spruce and deciduous forest ($P = 0.023$). In the semiarid temperate region, significant differences occurred between LW volumes in the non-coniferous vegetation and the subalpine vegetation ($P = 0.002$). However, there is a significant difference between all three pairwise comparisons in the semiarid temperate region when no Bonferroni correction for multiple comparisons is made. In-stream LW volume measurements are significantly larger than floodplain LW volumes in the subtropical ($P = 0.044$) and the semiarid temperate ($P = 0.002$) biomes (Figure 7), but measurements of in-stream LW volumes are not available for the boreal lowland site.

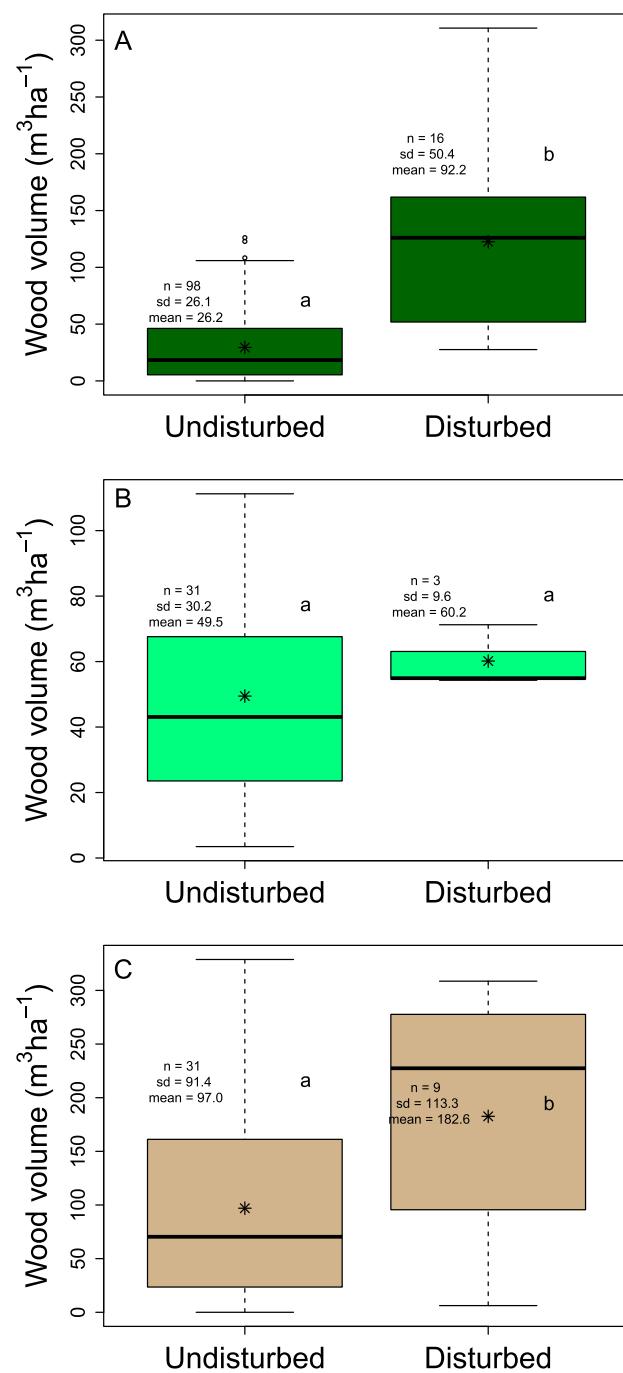


Figure 5. LW volume in undisturbed and disturbed sites in the boreal (A), subtropical (B), and temperate (C) biomes. For boxplots, the star within the box indicates the mean value, the solid line within the box indicates the median value, the box ends are the upper and lower quartile, and the whiskers are the 10th and 90th percentile. Significant differences between groups are indicated with contrasting letters (a, b). [Colour figure can be viewed at wileyonlinelibrary.com]

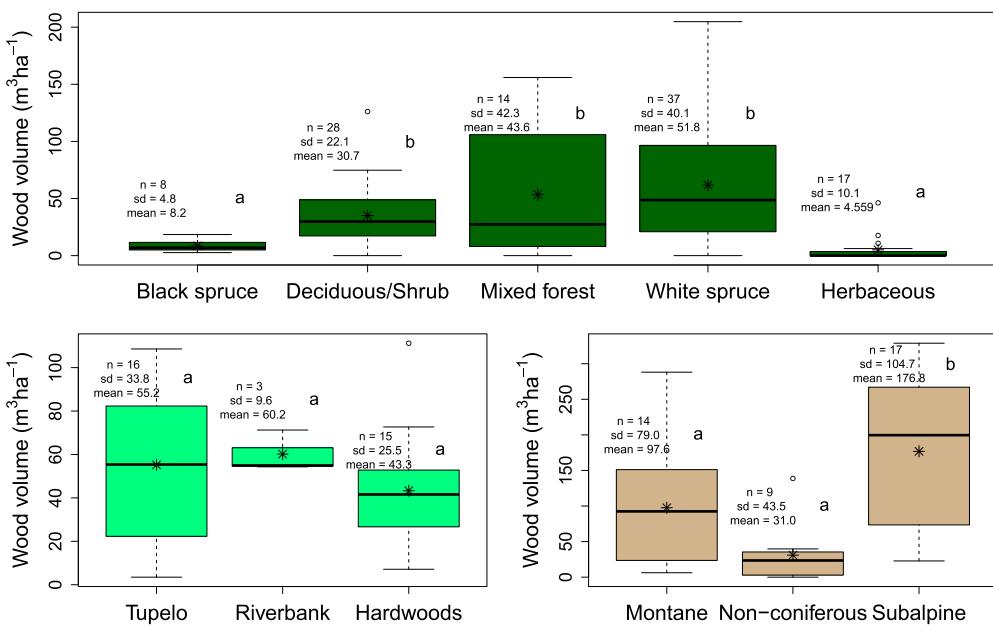


Figure 6. Differences in wood volume among vegetation type within each biome. For boxplots, the star within the box indicates the mean value, the solid line within the box indicates the median value, the box ends are the upper and lower quartile, and the whiskers are the 10th and 90th percentile. Significant differences between groups are indicated with contrasting letters (a, b, c). [Colour figure can be viewed at wileyonlinelibrary.com]

Discussion

Patterns in floodplain LW loads and inferred influences

We hypothesized that the semiarid temperate mountain sites, which have relatively high forest net primary productivity (NPP) and slow wood turnover time, have the largest downed wood volumes. The general trend of high LW loads in regions with high NPP and slow wood turnover time is observed for downed LW in upland environments (Harmon *et al.*, 1986; Krainka and Harmon, 1995; Harmon, 2009). This hypothesis assumes that floodplain LW is primarily recruited from floodplain forest, so that variables such as basal area, which can be used as a proxy for NPP within a particular floodplain forest stand, and regional values of NPP and downed wood turnover time, are likely to strongly influence floodplain LW volumes. Sites in the semiarid temperate mountains, the region of highest relief in our study, have no evidence of LW inputs from hill-slope mass movements. At the semiarid boreal and subtropical sites, we did not directly observe concentrated inputs of LW from the channel to the floodplain surface, with a few exceptions at the upstream end of secondary channels or along the margins of the floodplain.

Variations in diameter and length of downed LW pieces among biomes demonstrate some of the differences in forest productivity and wood turnover time (Figure 3(C) and (D)). The smallest average diameter of downed wood occurs in the semiarid boreal biome, reflecting the smaller amount of forest biomass due to smaller trees. The length of downed LW pieces was smallest in the subtropical biome, which could be attributed to the fast wood turnover time at this site (4–5 years) (Ricker *et al.*, 2016). Because the wood pieces decay so quickly, commonly the downed wood appears shortened and is not preserved in its entire length. However, breakage of LW during transport and/or delivery to the floodplain surface and decay of LW over time complicates piece length and diameter differences or similarities among regions (Merten *et al.*, 2013).

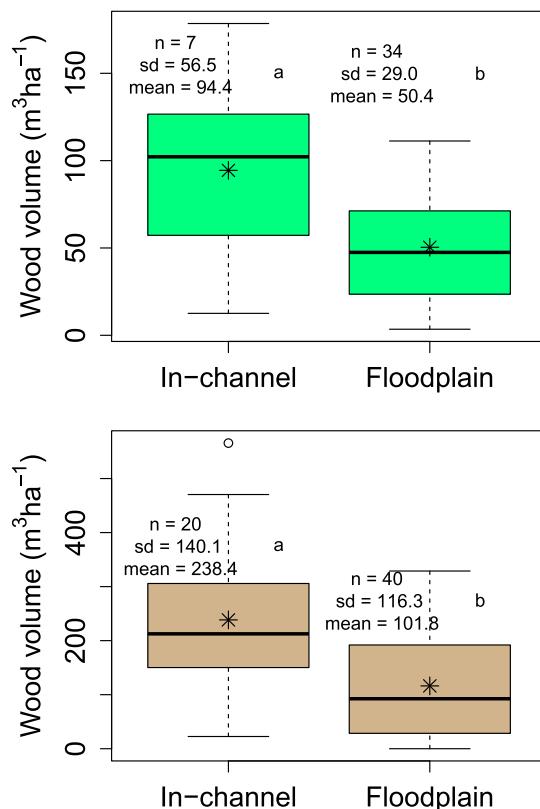


Figure 7. Comparison of instream wood volume with floodplain wood volume for the subtropical lowlands (top) and the semiarid mountains (bottom). For boxplots, the star within the box indicates the mean value, the solid line within the box indicates the median value, the box ends are the upper and lower quartile, and the whiskers are the 10th and 90th percentile. Significant differences between groups are indicated with contrasting letters (a, b). [Colour figure can be viewed at wileyonlinelibrary.com]

The significant correlation between basal area and floodplain LW volumes in undisturbed areas in the semiarid temperate region lends support to our assumption that forest stand biomass influences floodplain LW volumes (Figure 4(B)). The lack of observed correlation in the subtropical biome may reflect the fast wood turnover rate; floodplain LW decays so quickly in the subtropical biome that the standing stock of trees may not accurately reflect the downed LW volume. In the semiarid boreal region, a weak significant correlation between basal area and floodplain LW volumes indicates that as standing biomass increases, downed LW loads also increase. The relationship may be weak in part due to legacies of disturbance undetected by observations in the field or due to the fact that the boreal trees are smaller in diameter and may have not been adequately characterized by the Panama angle gauge. Additional support for the inference that most of the floodplain downed LW results from floodplain forest mortality comes from the low LW volumes in the non-coniferous vegetation in the semiarid temperate mountains and the herbaceous vegetation in the semiarid boreal lowlands (Figure 6). The low LW volumes in the non-forest vegetation types indicate that river deposition may not be important for total LW volumes in these study regions. However, the presence of some LW in the herbaceous vegetation (boreal) and non-coniferous vegetation (semiarid temperate) types demonstrates that deposition of LW via flooding and/or channel migration does contribute to floodplain LW volume. As described previously, trees on the floodplain may result in more blockage of floating LW, reducing deposition of LW from the channel to the floodplain. However, on floodplain surfaces with shorter and less dense vegetation (e.g. the herbaceous type in the boreal and the non-coniferous vegetation in the semiarid mountains), it is possible that LW could move more easily onto the floodplain and be deposited by high flows.

Globally, forest biomass and NPP decrease from the tropics to the high-latitudes due to reductions in growing season length and colder climates (Kucharik *et al.*, 2000; Saugier *et al.*, 2001). NPP in a Louisiana swamp, which is similar in climate and characteristics to the subtropical site, has been estimated to be approximately $550 \text{ g C m}^{-2} \text{ year}^{-1}$ (Conner and Day, 1976). In comparison, estimates for NPP in the semiarid temperate region range from $268\text{--}506 \text{ g C m}^{-2} \text{ year}^{-1}$ in undisturbed sites in the montane zone and $230\text{--}310 \text{ g C m}^{-2} \text{ year}^{-1}$ in the subalpine zone (Bradford *et al.*, 2008; Dore *et al.*, 2010). Average observed NPP in boreal evergreen forests range from around $300\text{--}400 \text{ g C m}^{-2} \text{ year}^{-1}$ (Kucharik *et al.*, 2000; Saugier *et al.*, 2001), although this estimate is not specific to the Yukon Flats region in interior Alaska, which is the location of the semiarid boreal sites. Although the ranges of NPP values overlap, the general trend is that NPP is lowest in the boreal biome and highest in the subtropical biome, which aligns with global trends in forest productivity. Basal area measurements among biomes also show this trend, with basal area in the boreal region significantly smaller than basal area measurements in the semiarid temperate and subtropical regions (Figure 4(A)). However, basal area values do not differ significantly between the subtropical and semiarid temperate sites, which may reflect the diversity of stand ages in both populations and the fact that the high estimates of NPP in the semiarid temperate biome are relatively close to the NPP estimate in the subtropical region.

Our hypothesis that the highest floodplain LW volumes occur in the semiarid temperate mountains, which has a slow wood turnover time and relatively high forest productivity (indicated by high basal area measurements and values of NPP), is supported by the comparison of LW volumes among the three biomes presented in this study. The semiarid boreal

and semiarid temperate sites have much longer wood turnover times than the subtropical site, but the semiarid site also has relatively high forest productivity and large basal area. This results in the semiarid temperate region having the optimal conditions for the largest floodplain LW volumes among biomes. However, there is not a statistically significant difference in medians between the subtropical lowland and semiarid temperate sites when correcting for multiple comparisons. But, due to the small number of multiple comparisons (3), not correcting for multiple comparisons could be considered appropriate, and statistically significant differences in medians among all biomes were present without using the Bonferroni correction. Although the results showing the semiarid temperate mountains with the highest LW volume support the optimal conditions for carbon storage posited by Sutin *et al.* (2016), we stress that this is a preliminary conclusion because of the limited number of sites assessed here.

There are few studies that quantify floodplain LW volume in either managed floodplains or those without human alteration. In a more humid boreal region in northern Sweden, mean floodplain LW volume in old-growth riparian forests unmanaged by humans is $67.8 \text{ m}^3 \text{ ha}^{-1}$ (Dahlström and Nilsson, 2006), which is higher than the mean in the semiarid boreal site in Alaska ($42.3 \text{ m}^3 \text{ ha}^{-1}$) and the subtropical site in South Carolina ($50.4 \text{ m}^3 \text{ ha}^{-1}$). The basal area in the Swedish sites is much greater than the basal area in the Alaskan sites (means of 27.7 vs $7.3 \text{ m}^2 \text{ ha}^{-1}$), reflecting that the boreal sites in Alaska represent floodplain downed LW across all vegetation types (not solely old-growth forests as in the Swedish sites) and that the wetter climate in Sweden probably results in larger trees. Busing and Fujimori (2005) measured downed LW in a stand of old-growth redwood trees in northern California within the riparian zone of Bull Creek and found LW volumes of $743 \text{ m}^3 \text{ ha}^{-1}$ (262 Mg ha^{-1}). This amount of downed LW far exceeds LW in other locations due to the large size of coastal redwoods. Mean downed floodplain LW (in this case, LW $> 7.6 \text{ cm}$ in diameter) in mass per area in an unaltered tropical dry floodplain forest is 14.8 Mg ha^{-1} , which is a volume per area of $28.4 \text{ m}^3 \text{ ha}^{-1}$ (Jaramillo *et al.*, 2003). Average LW volume per area in a seasonally flooded lowland forest in the Peruvian Amazon has been reported to be $42.8 \text{ m}^3 \text{ ha}^{-1}$ (10.3 Mg ha^{-1}) (Chao *et al.*, 2008). The low LW volumes in the dry and wet tropical floodplain forests further indicate that tropical/subtropical regions, despite high forest productivity, may have lower floodplain LW volumes due to fast wood turnover times. Figure 8 shows mean floodplain downed LW mass (in Mg ha^{-1}) across climate types in floodplains that have not been altered by human activities using values from this study and additional references. Each climate type in Figure 8 is represented by only one study, and data are missing for human unaltered floodplains for subtropical dry climates. However, a general trend can be seen in floodplain LW mass that supports our inference that LW loads peak in areas with high forest productivity combined with slower wood turnover times.

Patterns in LW loads due to vegetation type and disturbance

In the semiarid boreal lowlands, the significant differences in LW volume among vegetation types are broadly reflective of the size and spatial density of trees within each vegetation type. The lowest LW volumes occur in herbaceous and black spruce vegetation types. Herbaceous areas of the floodplain do not have trees for a source of downed LW, and most of the black spruce forests in our study area overlie shallow permafrost

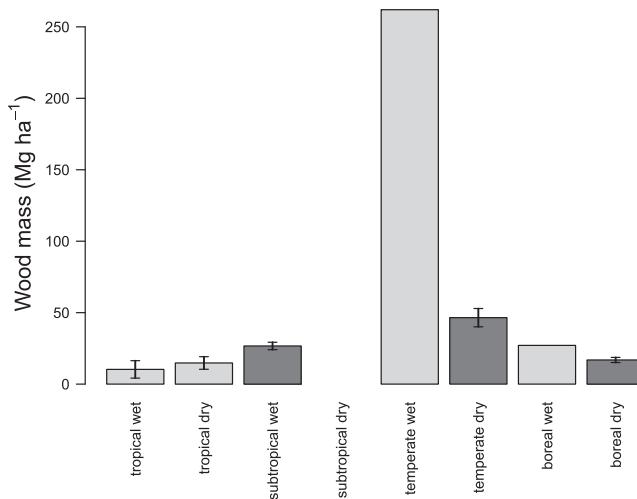


Figure 8. Patterns of floodplain LW mass per area across multiple climates, showing mean value with error bars representing \pm one standard error (when available). Dark gray bars are the study regions presented in this paper. LW mass from floodplains that have not been altered by human activities are not available for subtropical dry environments. References for values are: tropical wet (Chao *et al.*, 2008), tropical dry (Jaramillo *et al.*, 2003), subtropical wet (this study), temperate wet from old-growth redwood stands in northern California (Busing and Fujimori, 2005), temperate dry (this study), boreal wet (Dahlström and Nilsson, 2006), and boreal dry (this study).

and generally have much smaller trees than white spruce forests and some deciduous forests. The other vegetation types (deciduous/shrub, mixed forest, and white spruce) have similar LW volumes.

Fluvial migration and flooding exert controls on floodplain succession and vegetation type in Alaskan boreal forests (Van Cleve *et al.*, 1993; Yarie *et al.*, 1998), and thus fluvial migration, flooding, and the deposition of new floodplain areas control downed LW volumes. Floodplain successional stages include bare surfaces (with potentially herbaceous vegetation) that can be characterized as \sim 0–5 years in age, shrubs that can develop after \sim 5–40 years, deciduous forests that usually develop after \sim 40–100 years, white spruce stands that develop after \sim 100–500 years, and black spruce stands that may develop after centuries to millennia (Walker *et al.*, 1986; Van Cleve *et al.*, 1993; Chapin *et al.*, 2006). These differences in successional development correspond to substantial differences in type of vegetation, tree size, and recruitment potential for downed floodplain LW. Thus, although fluvial dynamics may not directly affect floodplain LW volume by transporting large amounts of LW into or out of the floodplain, river processes indirectly affect floodplain LW via the disturbance caused by channel migration. Channel migration can ‘reset’ the process of vegetation succession by eroding floodplain land at any stage of successional development and by creating new floodplain land for vegetation to colonize.

In the semiarid temperate mountains region, forested vegetation types (subalpine and montane) have higher downed LW volumes compared with non-coniferous vegetation, although the difference between montane and non-coniferous vegetation is not significant when correcting for multiple comparisons (Figure 6). The semiarid temperate sites have channels with much lower lateral mobility and much smaller floodplains. Stand-killing wildfires and blowdowns appear to be the primary mechanisms that reset forest succession in this environment.

We infer that natural disturbances increase floodplain LW volumes at the boreal and semiarid temperate sites because wood recruited to the floodplain during these disturbances

does not decay as quickly as in the subtropical sites (Figure 5). Although hurricanes can create substantial wood loads at the subtropical site, this wood decays so rapidly (4–5 year turnover time (Ricker *et al.*, 2016)) that higher floodplain LW volumes probably do not persist for decades or longer following this type of disturbance. The disturbed sites in the subtropical region are sites that were recently subjected to flooding, which probably does not transport LW into as well as out of the floodplain due to living trees blocking LW transport. In contrast, disturbances such as fire and blowdowns, which occur in the semiarid boreal and semiarid temperate sites and cause breakage and mortality, directly deliver LW to the floodplain surface.

Floodplain LW volumes in regions with relatively slow wood turnover times may increase where warming climate creates greater wood recruitment as a result of increase in disturbances such as wildfire. In the boreal lowlands region, warming climate may result in more frequent fires (Rupp and Springsteen, 2009), and may also result in less geomorphically stable floodplains if permafrost thaw permits greater bank erosion and faster lateral channel migration. The net effect on floodplain LW of more frequent fires versus greater channel migration is difficult to predict. Climate change may also result in shifts in vegetation composition and the advance of treeline to higher latitudes and elevations (Tape *et al.*, 2006; Harsch *et al.*, 2009; Shuman *et al.*, 2014). Net primary productivity could increase due to CO₂ fertilization, increasing forest biomass and affecting LW loads, but this increased growth may be limited by nitrogen availability (Norby *et al.*, 2010). In the western USA, fire frequency may increase with climate change (Liu and Wimberly, 2016), potentially altering floodplain wood loads in the semiarid temperate mountain region. However, the net effects of changing fire frequency and severity on downed LW loads in the boreal lowlands and the western USA are difficult to predict, as more intense and frequent fires may reduce downed LW load through increased combustion and through a reduction in time available for tree growth if fire return intervals are reduced (Harmon, 2009).

Organic carbon storage in floodplain LW

Although floodplain LW can be an important reservoir of organic carbon along river corridors, it is typically not the largest reservoir. In a summary of OC storage along floodplains in various biomes, Sutfin *et al.* (2016) emphasize that floodplain sediment is a much larger reservoir for OC than downed LW. In diverse river corridors (channels and floodplains), OC mass per area measurements range from 1.7 to 2500 Mg C ha⁻¹ in LW and 1.4 to 7735 Mg C ha⁻¹ in floodplain sediment (Sutfin *et al.*, 2016). Values for OC in sediment for sites in Congaree National Park range from 148 to 1118 Mg C ha⁻¹ (Ricker and Lockaby, 2015), which is much larger than the 0.9–29.5 Mg C ha⁻¹ found in LW in the subtropical biome in this study. Similarly, OC mass per area in sediment is larger across multiple sites in the subalpine zone in the Colorado Rockies (Wohl *et al.*, 2012). There is very little information about OC in floodplain sediment for boreal regions, but the high latitudes store a large amount of OC in the subsurface (Hugelius *et al.*, 2014), indicating that there are likely large amounts of OC in floodplain sediment in the boreal region discussed in this study. In addition to being an OC stock within river corridors, LW can promote sedimentation within floodplains and channels (Jeffries *et al.*, 2003; Sear *et al.*, 2010), further enhancing the stock of OC in sediment.

Floodplain versus upland and instream LW loads

We did not measure upland LW loads in the study areas, but representative values are reported in the forest ecology literature (Table II). We found only one other study that provided data for explicit comparisons of instream and floodplain LW mass in old-growth forests, which is an examination of 13 streams (average bankfull width 2.4 m) in old-growth boreal conifer forest of northern Sweden (Dahlström and Nilsson, 2006). An additional study in the tropical dry forest provided LW mass for floodplain and upland environments (Jaramillo et al., 2003). Based on these limited data, river transport appears to concentrate LW within the active channel, creating greater wood loads than in adjacent floodplain environments. This may not be the case for higher-order floodplain rivers with large drainage areas, such as those in the boreal lowlands biome, but the lack of data for floodplain LW loads prevents comparisons of instream and floodplain LW as drainage area increases.

Floodplains appear to have greater LW loads per area relative to nearby uplands in most regions (Table II), but these comparisons are limited by the lack of data on floodplain LW loads and the fact that the upland wood loads are generalized across broad regions, whereas the floodplain data are for specific sites (Table II). Table II gives values for LW loads in uplands compared with floodplain LW loads. An exception to floodplain LW loads being greater than upland forest LW loads may occur in wet tropical environments, where frequent flooding in riparian forests accelerates decomposition rates (Chao et al., 2008). For example, Chao et al. (2008) found that floodplain forests in the western Amazon had lower mean LW loads (10.3 Mg ha^{-1}) compared with non-floodplain forests ($30.9\text{--}45.8 \text{ Mg ha}^{-1}$) in part due to faster decomposition rates and the floodplain forest containing tree species that are less dense than the tree species in non-floodplain forests. Nevertheless, larger LW loads in

floodplain environments relative to uplands seem reasonable, as riparian forests tend to be more productive than upland forests (Naiman and Décamps, 1997).

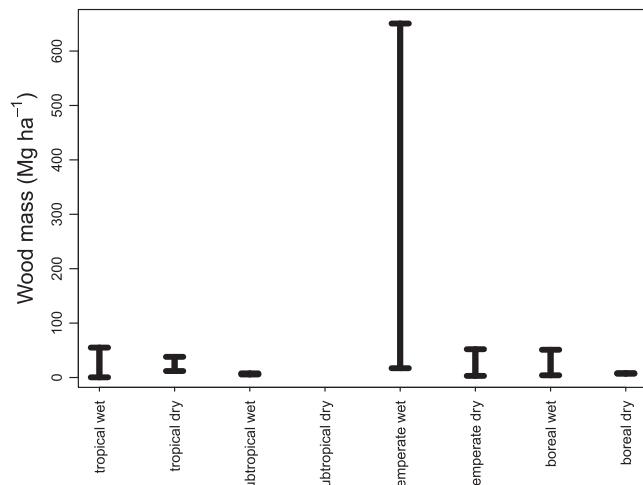


Figure 9. Ranges of downed LW mass per area from uplands in different climates, representing sites that have not been recently disturbed and have not been altered by human disturbances (e.g. logging). Values were not found for sites in subtropical dry environments unaltered by human activities. References for values are: tropical wet (Chao et al., 2008; Silva et al., 2016), tropical dry (Harmon et al., 1995; Jaramillo et al., 2003), subtropical wet (McMinn and Crossley, 1996), temperate wet (Grier and Logan, 1977; Spies et al., 1988; Muller and Liu, 1991; Davis et al., 2015), temperate dry (Arthur and Fahey, 1990; Robertson and Bowser, 1999; Herrero et al., 2014), boreal wet (Krankina and Harmon, 1995; Hély et al., 2000; Jönsson and Jonsson, 2007; Gould et al., 2008), boreal dry (Gould et al., 2008).

Table II. Comparison of upland, floodplain, and channel LW mass (in Mg ha^{-1}) in human unaltered environments. Values are means plus or minus one standard error if available, or ranges (denoted by a “-”), with Mg ha^{-1} (mass) on the first line of the cell and $\text{m}^3 \text{ ha}^{-1}$ (volume) italicized in the second line of the cell if available. Values are from this study unless otherwise indicated

Region	Upland LW (Mg ha^{-1} ; $\text{m}^3 \text{ ha}^{-1}$)	Floodplain LW (Mg ha^{-1} ; $\text{m}^3 \text{ ha}^{-1}$) ^a	Channel LW (Mg ha^{-1} ; $\text{m}^3 \text{ ha}^{-1}$) ^a
Boreal lowlands, Alaska	7.6 ^b	16.9 ± 1.8 42.3 ± 4.6	Not available
Semiarid mountains, Colorado	2.6–52 ^c <i>12.4–188.8</i>	46.5 ± 6.44 116.3 ± 16.1	95.4 ± 12.2 238.4 ± 30.5
Subtropical lowlands, South Carolina	5.6–7.7 ^d <i>11.7–15.8</i>	26.5 ± 2.6 50.4 ± 5.0	50.0 ± 11.3 94.4 ± 19.8
Old-growth boreal conifer forest, northern Sweden	7.4 ^e <i>18.5</i>	27.1^f <i>67.8</i>	36.5^g <i>91.2</i>
Tropical dry forest, central coast of Mexico	11.9 ^g <i>17.7</i>	14.8^g <i>28.4</i>	Not available
Tropical wet forest, western Amazon, Peru	30.9–45.8 ^h <i>74.7–108.8</i>	10.3 ± 6.1^h <i>42.8 \pm 20.1</i>	Not available

^aConversions of wood volumes per unit area to wood mass per unit area for the three biomes in this study assumed density of 400 kg m^{-3} for boreal lowlands, 400 kg m^{-3} for semiarid mountains, and 530 kg m^{-3} for subtropical lowlands based on approximate wood densities of tree species at each site.

^b(Gould et al., 2008), boreal forests in central Alaska, volume per area measurements were not reported in the paper.

^cOld-growth subalpine in Rocky Mountain National Park (Arthur and Fahey, 1990), (Robertson and Bowser, 1999), mature ponderosa pine stands in the Colorado Front Range (montane).

^d(McMinn and Crossley, 1996), upland hardwood in South Carolina and Georgia on land not owned by the forest industry.

^e(Jönsson and Jonsson, 2007), old-growth boreal forests in central Sweden, assumes density of 400 kg m^{-3} in order to transform wood volume per unit area to wood mass per unit area.

^f(Dahlström and Nilsson, 2006), assumes a density of 400 kg m^{-3} in order to transform wood volume per unit area to wood mass per area.

^g(Jaramillo et al., 2003)

^h(Chao et al., 2008)

Patterns of LW loads in upland forests

Due to the small number of studies on floodplain downed LW loads, it is useful to infer patterns in LW loads from upland environments unaltered by human disturbances to inform potential patterns across climates in floodplain LW loads. Figure 9 provides examples of the ranges of values for downed LW mass per area in upland forests from 17 different articles for sites in which there has not been recent natural or human disturbance. Although Figure 9 is not an exhaustive review of published values for LW loads, we expect floodplain downed LW mass to vary similarly across a range of climatic conditions. However, floodplain LW loads may be larger in most climates (Table II). The potential similarities in trends between floodplain and upland environments are exemplified by the similar trends in LW mass across climates seen in Figure 8 and Figure 9.

Conclusion

Our findings indicate that LW volumes are greatest in the semiarid temperate mountain sites, which we attribute to the combination of relatively high forest productivity and slow wood turnover time. Differences in floodplain LW loads exist between vegetation types in the semiarid boreal lowlands and the semiarid temperate mountains, and natural disturbances increase floodplain LW loads in environments where relatively slow wood decay preserves the wood recruited by these disturbances. In addition, comparisons with other studies suggest that floodplains have greater LW loads than adjacent upland forests, but smaller LW loads than adjacent channels. However, more data are needed to support these trends, as there is limited information on floodplain downed LW loads.

The lack of published data on floodplain LW loads is striking. At least 35 papers present basic data on instream LW loads in old-growth or naturally disturbed forests, but we could find only a few studies that present analogous data for naturally disturbed floodplains. This probably reflects, at least in part, the focus of LW quantification studies on relatively small, steep streams that commonly have minimal floodplain area. Nonetheless, the dearth of floodplain LW quantifications is particularly important in the context of increasing efforts to restore LW to river corridors (Abbe and Brooks, 2011; Wohl *et al.*, 2016). Although many of these efforts focus on introducing LW to channels (Lawrence *et al.*, 2013; Jones *et al.*, 2014), particularly in the form of engineered logjams (Gallisdorfer *et al.*, 2014), floodplain LW in many respects provides an easier target for restoration, although this type of restoration does not directly impact fish habitat unless flooding conditions occur. Dispersed or concentrated LW is less likely to be remobilized in floodplain environments, and to create hazards for infrastructure in the river corridor, because of the trapping potential created by living vegetation. As reviewed in the introduction, floodplain LW can provide numerous ecological benefits and create hydraulic resistance and enhanced deposition of sediment and organic matter in floodplains, thus helping to stabilize floodplains. Greater emphasis on quantifying floodplain LW in future studies will help to fill in gaps of our knowledge of LW loads in unmanaged forests in diverse environments, provide a better understanding of how floodplain LW loads have been reduced in managed riparian areas, and will facilitate more rigorous testing of some of the patterns inferred in this study.

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