EARTH SURFACE PROCESSES AND LANDFORMS
Earth Surf. Process. Landforms **39**, 1421–1431 (2014)

Published online 26 February 2014 in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/esp.3531

Effects of forest stand age on the characteristics of logjams in mountainous forest streams

Natalie D. Beckman and Ellen Wohl*
Department of Geosciences, Colorado State University, Fort Collins, CO, USA

Received 11 September 2013; Revised 6 January 2014; Accepted 9 January 2014

*Correspondence to: Ellen Wohl, Department of Geosciences, Colorado State University, Fort Collins, CO 80523-1482, USA. E-mail: ellen.wohl@colostate.edu

ESPL
Earth Surface Processes and Landforms

ABSTRACT: We measured longitudinal spacing and wood volume of channel-spanning logjams along 30 1-km reaches of forest streams in the Colorado Front Range, USA. Study streams flow through old-growth (> 200 year stand age) or younger subalpine conifer forest. Evaluating correlations between the volume and longitudinal spacing of logjams in relation to channel and forest characteristics, we find that old-growth forest streams have greater in-stream wood loads and more jams per kilometer than streams in younger forest. Old-growth forests have a larger basal area close to the stream and correlate with larger piece diameters of in-stream wood. Jam volume correlates inversely with the downstream spacing for ramp and bridge pieces that can act as key pieces in jams. Most importantly, old-growth streams have shorter downstream spacing for ramp and bridge pieces (< 20 m). Our results suggest that management of in-stream wood and associated stream characteristics can be focused most effectively at the reach scale, with an emphasis on preserving old-growth riparian stands along lower gradient stream reaches or mimicking the effects of old growth by manipulating the spacing of ramp and bridge pieces. Our finding that average downstream spacing between jams declines as wood load increases suggests that the most effective way to create and retain jams is to ensure abundant sources of wood recruitment, with a particular emphasis on larger pieces that are less mobile because they have at least one anchor point outside the active channel. Copyright © 2014 John Wiley & Sons, Ltd.

KEYWORDS: in-stream wood; logjams; mountain stream; forest stand age; LWD

Introduction

In-stream wood performs diverse geomorphic and ecological functions. Wood increases boundary roughness and hydraulic resistance (Keller and Tally, 1979; Manga and Kirchner, 2000; Curran and Wohl, 2003), and can result in finer streambed substrate than would otherwise be present (Buffington and Montgomery, 1999; Faustini and Jones, 2003). Wood modifies the dimensions and types of alluvial bedforms present (Montgomery *et al.*, 1996; Gurnell *et al.*, 2000; MacFarlane and Wohl, 2003). Wood enhances habitat diversity and abundance (Fausch and Northcote, 1992; Maser and Sedell, 1994) and regulates stream respiration, creating enhanced nutrient processing and insect productivity that also support riparian communities (Baxter *et al.*, 2005; Wipfli and Baxter, 2010). Wood modifies channel planform (Collins and Montgomery, 2002; Wohl, 2011) and enhances lateral connectivity between channels and floodplains (Jeffries *et al.*, 2003; Sear *et al.*, 2010; Collins *et al.*, 2012).

Concentrations of wood in the form of logjams can have a greater effect on the channel than individual pieces. Channel-spanning logjams can be particularly effective in creating boundary roughness and flow separation (Brummer *et al.*, 2006; Manners *et al.*, 2007), as well as backwater effects that promote storage of finer sediment and organic matter (Keller and Swanson, 1979; Bilby, 1981; Assani and Petit, 1995; Manga and Kirchner, 2000), hyporheic exchange (Lautz *et al.*, 2006; Fanelli and Lautz, 2008; Wondzell *et al.*, 2009), and nutrient retention and processing (Naiman and Sedell, 1979; Bilby and Likens, 1980). Logjams can also alter floodplain dynamics by influencing channel conveyance, patterns of overbank deposition and erosion, and lateral channel migration (Oswald and Wohl, 2008; Collins *et al.*, 2012; Wohl, 2013).

Wood retention and jam formation are likely to be non-linear processes in which increasing volumes of in-stream wood enhance physical channel complexity and the trapping of wood pieces in transport (Wohl and Goode, 2008; Wohl, 2011; Wohl and Beckman, 2014). Relatively stable individual pieces that trap otherwise mobile wood can serve as key pieces that nucleate *in situ* jams (Abbe and Montgomery, 1996). Proximity of wood recruitment can be especially important in nucleating jams because locally recruited wood pieces are larger and more likely to have one or both ends anchored outside the channel, and thus be more stable, than fluvially transported wood (May and Gresswell, 2003).

Old-growth forest typically results in large diameter trees. Several studies correlate old-growth forest with greater volumes of in-stream wood when geomorphic factors such as channel width and gradient are held relatively constant (e.g. Silsbee and Larson, 1983; Evans *et al.*, 1993; Ralph *et al.*, 1994; Richmond and Fausch, 1995; Hedman *et al.*, 1996; Gurnell, 2003). Relatively few studies, however, include detailed information on the distribution of in-stream wood and specifically on how the longitudinal spacing and volume of logjams vary between old growth and younger forest, or on the mechanistic influences of old-growth wood on jam characteristics. The only studies we are aware of that examine differences in jam characteristics between old-growth and younger forest are from the north-western United States (Montgomery *et al.*, 2003) and the north-central United States (Morris *et al.*, 2007). These studies indicate that old-growth forest can result in more closely spaced jams and, in the north-central United States study sites, larger jams.

The work reviewed earlier suggests a conceptual model of the interactions between riparian forest characteristics, wood recruitment, and the volume and spatial distribution of in-stream wood (Figure 1). This conceptual model underlies the design of the research summarized here, in which we examine the relative importance of forest characteristics on channel-spanning logjams in mountainous forest streams of the Colorado Front Range, and propose a mechanism to explain observed correlations between forest age and logjam characteristics. Channel-spanning logjams completely span the active channel and create longitudinal discontinuities of the water surface and stream bed across more than two-thirds of the active channel width (Wohl and Beckman, 2014). These jams are particularly effective at facilitating overbank flows and formation of multi-thread channels (Wohl, 2011). We evaluate correlations between the volume and longitudinal spacing of logjams in relation to channel characteristics (drainage area, bed gradient, channel width) and forest characteristics (stand age, disturbance history).

Streams studied here drain ~6–90 km^2 and have average bankfull channel width ~1–15 m. These channels are transport limited with respect to in-stream wood (Marcus *et al.*, 2002) and have predominantly *in situ* jams formed around an anchored key piece (Abbe and Montgomery, 2003), in part because of the lack of mass wood introductions from landslides, debris flows, or snow avalanches. Previous work in this region indicates that local geomorphic controls (e.g. valley geometry, channel gradient) more strongly influence inter-reach differences in in-stream wood distribution than do forest stand age or progressive downstream trends related to increasing drainage area or channel width (Wohl and Cadol, 2011, Wohl and Beckman, 2014). These earlier studies included sites with a broad range of drainage area, diverse valley geometry and forest stand age, and focused more on basin-scale trends. Lower gradient, wider valley segments contained substantially more in-stream wood and larger jams (greater total volume of wood per jam) than steeper, narrower valley segments (Wohl and Cadol, 2011). In the current study, we focus on the reach-scale influence of forest characteristics by examiningb predominantly lower gradient, wider valley segments with riparian forest of differing stand ages and disturbance history. Examining how forest characteristics influence wood recruitment and retention at the reach-scale (10^1–10^2 m) at which much resource management occurs (Abbe *et al.*, 2003; Collins *et al.*, 2012) is important because, despite recent advances in understanding the mechanics of fluvial wood transport (Braudrick and Grant, 2000; Manners *et al.*, 2007; Bocchiola *et al.*, 2008; Merten *et al.*, 2010), the complex interactions among wood recruitment, channel form, and channel hydraulics make it challenging to quantitatively predict wood retention and distribution (Hassan *et al.*, 2005) in diverse biogeographic settings.

Field Area

Study sites are in the Cache la Poudre, Big Thompson, and North St Vrain drainages in northern Colorado, USA (Figure 2). Each of these streams heads near the continental divide at > 4000 m elevation and flows down to ~1900 m at the base of the mountains, where the stream is tributary to the South Platte River. The basins are underlain by Precambrian-age Silver Plume granite (Braddock and Cole, 1990). Bedrock lithology does not vary substantially in the study area, but longitudinal variations in valley geometry reflect differing joint geometry and Pleistocene glaciation (Ehlen and Wohl, 2002; Wohl *et al.*, 2004). Step-pool channels (Montgomery and Buffington, 1997) are most common and substrate is primarily cobble- to boulder-size clasts, although finer sand and gravel are present in zones of flow separation such as upstream from logjams.

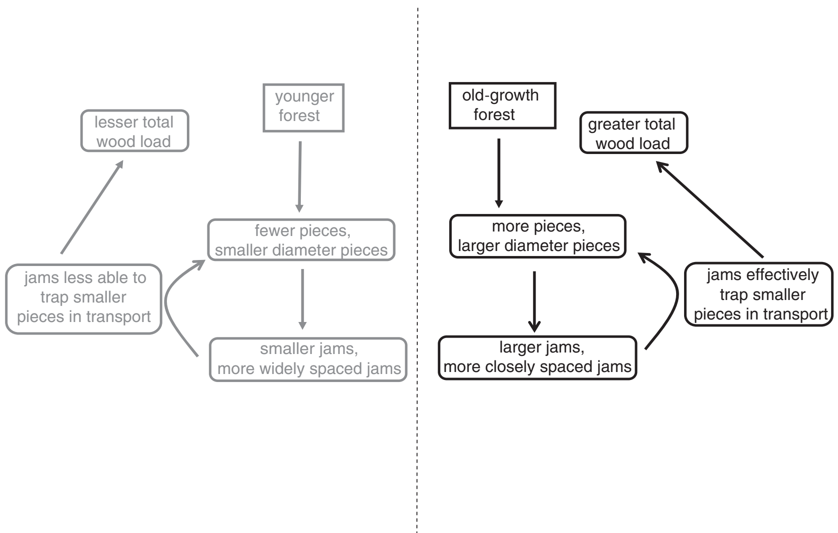

Figure 1. Conceptual model guiding this research. Starting point based on riparian forest stand age indicated by square-edged outline. Resulting in-stream processes indicated by rounded outlines. Previous studies indicate that old-growth forest can result in a greater number of wood pieces and larger diameter wood pieces recruited to moderately sized streams. If other factors influencing in-stream wood retention and formation of channel-spanning logjams (e.g. channel width and gradient) are similar between sites, we expect that forest stand age will indirectly influence the size of jams (total volume of wood within the jam) and the downstream spacing of jams. Larger and/or more closely spaced jams are more likely to effectively trap and store smaller pieces of wood in transport than are channels with small or widely spaced jams, further enhancing the total in-stream wood load. An alternative scenario for younger forest is shown on the left side of the diagram. In the research summarized here, we are testing the positive relationship indicated by each of the four arrows on the right side in this diagram.

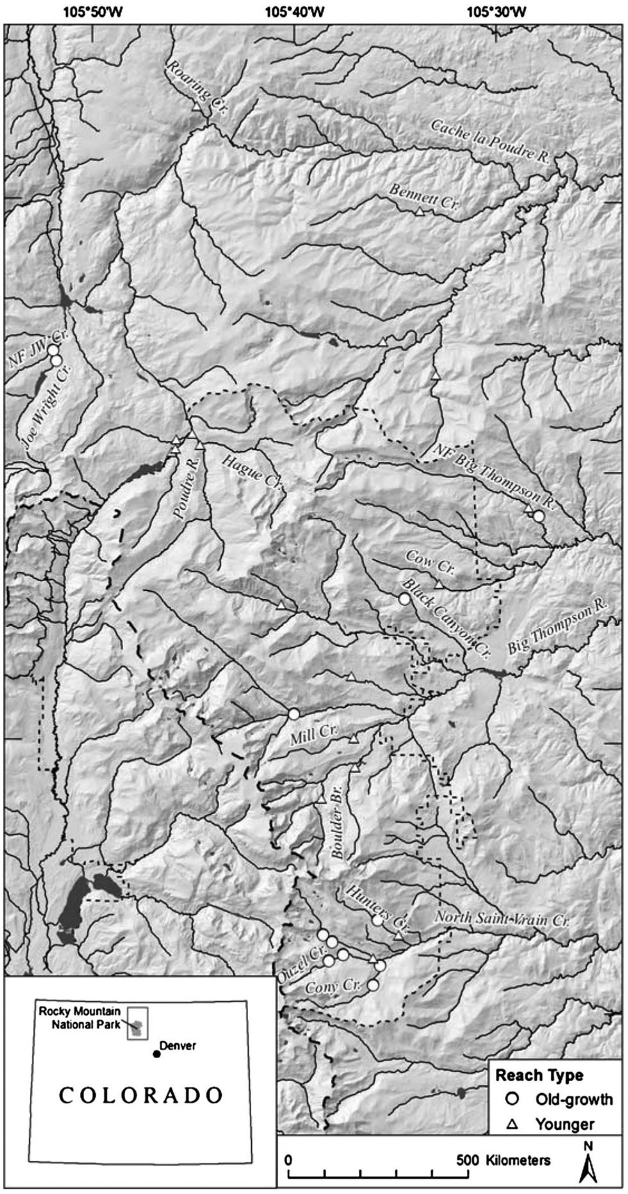

Figure 2. Location map of the study sites. Channel reaches on which in-stream wood was surveyed are indicated by white dots for old-growth sites ($n = 12$) and white triangles for younger riparian forest ($n = 18$). Rocky Mountain National Park indicated by short dashed line; continental divide indicated by long dashed line. Figure courtesy of Joseph Mangano.

Mean annual precipitation is 70 to 90 cm in the upper basins. Flow is dominated by snowmelt, which produces an annual hydrograph with a sustained May–June peak. The Allenspark stream gauge along North Saint Vrain Creek has a 20-year historic average peak flow of ~12.4 m^3/s. Field data were collected during the summers of 2009, 2010, and 2011. The summer of 2011 had snowmelt peak flows of larger than average magnitude and duration, which limited the length of the field season. In 2011, the Allenspark gauge recorded above-average flows from June 6 until mid-July, with a peak of ~16.3 m^3/s on July 8. Based on the limited record, the 2011 peak flow has a recurrence interval of about five years.

Study reaches were selected from the area a short distance below timberline (~3200 m elevation) down to ~2400 m. These portions of the catchments are predominantly covered by subalpine forests of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), and limber pine (*Pinus flexilis*) (Veblen and Donnegan, 2005). Riparian communities include large numbers of conifers such as Douglas-fir (*Pseudotsuga menziesii*) and spruce, as well as aspen. Age and size of individual trees vary greatly with site-specific conditions.

Natural disturbance in Front Range forests takes the form of wildfire, persistent drought, insect outbreak, wind blowdowns, hillslope mass movements such as debris flows, and floods. Fire and insect outbreaks (Romme *et al.*, 2006) are the most significant in terms of extent, severity, and frequency in the mountain valleys of this study, and time-since-fire appears to be the single most important control on volume of dead wood in a stand (Rebertus *et al.*, 1992; Hall *et al.*, 2006).

Regrowth of woody plants following a disturbance is slow in the semi-arid Front Range relative to other temperate forests. Regrowth following disturbance varies with site conditions, but typically requires 30–60 years in the subalpine zone for trees to reach a size at which they are likely to be retained if recruited into a stream channel (Veblen and Donnegan, 2005). Old-growth characteristics typically do not emerge for at least 200 years in subalpine forests (Veblen, 1986).

Starting in 2009 and ongoing, subalpine and montane forests in the study area have been experiencing increased tree mortality due to a severe infestation by mountain pine beetle (*Dendroctonus ponderosa*). The in-stream wood surveyed for this study was not affected by the most recent infestation because riparian trees are less susceptible than upland trees, and dead trees were still standing during collection of field data and so did not contribute to the in-stream loads.

Methods

Field methods

We surveyed 30 1-km stream reaches (12 old-growth and 18 younger forest: Table I) chosen to minimize inter-site variation in valley and channel geometry and drainage area, and maximize inter-site variation in forest stand age. One of these reaches did not contain any jams. All study sites were on the eastern side of the continental divide to minimize inter-site differences in regional factors such as precipitation and lithology. Stream reaches were chosen where (i) no major tributaries entered the stream within the reach, and (ii) there was no evidence of landslides, debris flows, or snow avalanches within the past 200 years.

The study sites are on relatively small channels (bankfull channel width averages 6.9 m, drainage area averages 21.6 km^2). Consequently, we assumed limited long-distance transport capacity for wood (Marcus *et al.*, 2002) and quantified potential control variables such as riparian forest stand age and basal area in the immediate vicinity of the study reach. Average stand age of adjacent riparian forest was obtained from published maps (Sibold *et al.*, 2006) when possible, and from coring of riparian trees at other sites (Beckman, 2013). Streams were classified as either old growth (stand age greater than 200 years) or younger (stand age less than 200 years). We measured basal area of the standing wood in the riparian forest at the start, middle and end of each reach using a handheld Panama Angle Gauge sampler (Avery and Burkhart, 2002), and used an average of these three measurements. Measurements were taken no more than 10 m from the stream banks within the surrounding stand.

Basins containing known old-growth forest were scarce, as were basins with flow gauges. In order to minimize differences due to streamflow, non-old-growth basins were chosen to match the approximate drainage area and elevation of the known old-growth reaches. If secondary channels were

Table I. Summary characteristics of study reaches

Reach	A[a] (km^2)	S[b] (%)	W[c] (m)	BA[d] (m^2/ha)	Age[e] (year)	Load[f] (m^3/ha)	Propor[g] (%)	Spacing[h] (m)	Jam ρ[i] (no./km)	Avg log D[j] (cm)		Avg log L[k] (cm)		D_{max}[l] (cm)
										jam	reach	jam	reach	
Ouzel 2	12.7	5	10.1	6.9	33	247.7	69	2.8	77	20	20	329	354	66
NSV 3	20.5	7	12.5	87.2	129	91.4	83	5.6	49	21	21	281	273	85
Boulder	10.0	12	2.3	43.6	117	51.4	4	11.4	12	14	14	311	419	48
Mill	11.4	8	4.0	16.1	117	71.7	16	11.1	23	15	15	369	398	41
LPP	22.7	2	13.2	4.6	70	5.0	52	125.0	5	20	21	282	266	42
Hague	35.2	4	9.0	13.8	150	12.8	34	52.6	4	20	19	452	163	34
Poudre	87.8	2	14.4	6.9	100	2.7	36	125.0	2	15	16	322	97	30
Corral	16.5	3	4.2	9.2	80	5.3	0	111.1	0	n/a	16	n/a	78	25
Willow	15.3	6	7.1	13.8	110	17.2	27	37.0	6	18	18	408	182	43
Bennett	20.5	2	14.7	29.8	150	27.4	47	5.8	22	16	16	299	391	35
Cow	15.3	12	2.1	11.5	130	1.2	3	11.0	9	19	19	523	—	48
Glacier	19.7	5	6.2	11.5	117	—	—	16.4	10	19	—	351	—	(39)
Pennock	32.1	5	6.0	20.7	140	—	—	19.6	4	19	—	488	—	(65)
Beaver Br	6.1	5	1.3	13.8	100	—	—	3.5	34	15	—	257	—	(27)
Beaver Cr	54.1	1	7.7	12.2	100	—	—	40.0	4	14	—	303	—	(19)
Fall	17.9	4	4.7	16.8	120	—	—	6.0	23	17	—	360	—	(52)
Roaring	22.9	1	4.3	17.4	90	—	—	12.5	11	15	—	251	—	(39)
NFBT 2	43.3	3	5.2	18.4	160	—	—	12.0	15	16	—	301	—	(58)
Average	25.8	4.8	7.2	19.7	112	48.5	36.8	35.4	17.2	17	18	346	262	45
Hunters 1	12.5	8	6.7	57.4	355	99.6	30	6.7	47	16	16	291	330	53
Hunters 2	11.7	8	5.7	84.9	355	151.4	37	5.6	49	18	18	302	331	66
Cony 1	14.1	4	8.3	103.3	500	158.7	56	5.8	63	20	20	299	311	55
Cony 2	19.0	7	8.7	107.9	500	116.7	56	5.4	62	17	17	297	307	54
Ouzel 1	7.2	9	10.0	80.3	500	132.5	43	9.8	37	25	26	280	322	78
NSV 1	10.2	14	6.1	91.8	355	146.2	25	10.6	44	20	22	253	277	70
NSV 2	16.0	4	8.6	107.9	355	121.3	60	6.0	45	22	22	289	289	70
JW	19.1	2	6.6	34.4	220	78.5	28	11.8	11	20	21	441	445	70
BC	11.8	3	1.3	18.4	200	—	—	2.8	26	18	—	337	—	(64)
NFJW	9.0	4	4.3	27.5	300	—	—	9.6	9	19	—	310	—	(38)
Fern	7.3	18	4.0	13.8	280	—	—	4.6	52	17	—	303	—	(54)
NFBT 1	45.3	4	5.1	10.6	240	—	—	5.8	35	19	—	325	—	(43)
Average	15.3	7.1	6.3	61.5	347	125.6	41.9	7.0	40.0	19	20	311	326	64

[a]Drainage area at downstream end of reach.
[b]Average channel gradient.
[c]Average bankfull channel width.
[d]Average basal area of adjacent riparian forest.
[e]Age of trees in adjacent riparian forest.
[f]Total wood load in m^3 wood/ha of channel surface area.
[g]Proportion of total wood load in jams.
[h]Average downstream spacing of ramp and bridge pieces.
[i]Average number of jams per kilometer of channel.
[j]Average log diameter (in jams and in the reach as a whole).
[k]Average log length (in jams and in the reach as a whole).
[l]Maximum log diameter for all wood within reach; numbers in parentheses are maximum log diameter within jams.
Note: Gaps in table represent reaches in which total wood load was not measured.

present, wood in the secondary channels was included in the analysis and the channel width of both channels was recorded.

We recorded latitude, longitude and elevation for the start and end points of the reach in the field using an eTrex handheld global positioning system (GPS) with a horizontal accuracy of approximately ± 3 m and varying vertical accuracy. These points were used to find drainage area and stream order for each reach using the US Geological Survey online program StreamStats (Ries *et al.*, 2008), which calculates basin parameters using 10 m digital elevation models (DEMs). Drainage areas were measured from the most downstream point of the reach.

We measured channel parameters using a TruPulse 360B laser rangefinder with ± 10 cm accuracy. We measured channel width at 10 m intervals, using indicators of bankfull (average peak annual) flow such as changes in vegetation, stains on stream boulders, and breaks in bank slope. These values were used to compute an average width for each 1-km study reach. We measured channel gradient at major breaks in slope or at 100 m intervals.

We measured only wood pieces with diameter > 10 cm and length > 1 m. We measured volume and cumulative longitudinal spacing of channel-spanning jams, and characteristics of all ramp (wood piece with one end resting above bankfull) and bridge (both ends resting above bankfull) pieces because of the importance of ramps and bridges in nucleating jams. Jam volume was based on the sum of all individual pieces within the jam, and a piece was considered to be part of a jam if it touched at least two other pieces. For each piece, we measured total piece length (including length outside the channel) and piece diameter. We noted piece type (bridge, left ramp, right ramp, pinned by other wood, buried in the streambed, or unattached), and decay class using a seven part system modified from Hyatt and Naiman (2001). For the subset of 19 streams surveyed in 2009 and 2010, we also measured the dimensions of every piece of wood located within the bankfull width of the stream, measured the piece's cumulative longitudinal spacing (i.e. distance downstream from the start of the study reach), and noted piece type and decay class. Sustained peak flows during summer 2011 limited field time, so we surveyed only in-stream wood forming a ramp, a bridge or within a jam for the remaining 11 streams. Because our analyses focused on jam characteristics, the reduction in variety of data collected does not affect the results discussed later.

Statistical analyses

For statistical analyses, we calculated the variables drainage area, channel bed slope, stream order, elevation, riparian forest basal area and stand age, bankfull channel width, jam density (number of jams per kilometer of channel), jam volume (average volume of wood in a jam, calculated by summing the volume of all pieces measured and using total piece length), average log length and diameter, and ramp and bridge spacing (average downstream spacing between ramp or bridge pieces). For the subset of streams in which all wood pieces were measured, we also derived the variables total wood load (m^3 wood/ha of channel surface) and proportion of wood in jams. Total wood load was based on the sum of total piece length. Because jam density and total wood load are highly correlated (bivariate linear regression $R^2 = 0.84$), jam density is treated as an indicator of total wood load within a stream.

The surveyed reaches cover a range of slopes, drainage areas and channel widths, but are all located within three basins. Before testing for differences based on local controls, we evaluated whether there is an underlying pattern to the channel characteristics for each basin that might influence statistical models. We used a k-means cluster analysis to evaluate whether reaches naturally group themselves by basin when compared based on slope, channel width, drainage area and elevation. For cluster analysis, drainage area and slope were natural log transformed. All variables (stream order, transformed slope, transformed drainage area, channel width and elevation) were normalized by subtracting the mean and dividing by standard deviation. Normality for each variable was checked using the Shapiro–Wilk Normality test and standard Q-Q plots. Results indicate no definitive basin structure to the clustering: instead, clustering reflects mostly drainage area (Beckman, 2013). Consequently, basin level processes do not have a strong influence on reach characteristics.

We also evaluated whether basin and reach-scale parameters varied significantly between the populations of old-growth and younger streams. The non-parametric Wilcoxon Mann-Whitney test indicated that the two groups do not vary significantly with respect to channel gradient ($p = 0.1267$) or channel width ($p = 0.8655$), although drainage area is significantly lower for the sites with old-growth forest streams ($p = 0.0292$). This reflects the tendency of old-growth to be present in small patches in the most remote and inaccessible portions of drainages in the study area.

Basin and reach-scale characteristics (slope, channel width, drainage area) could strongly correlate with the number or size of log jams. Because the basins included in this study are largely ungauged, drainage area is used as a surrogate for discharge. We used bivariate linear regressions to evaluate potential correlations between basin and reach-scale characteristics and jam density. Bivariate linear regressions indicate no significant correlations between reach-scale slope and jam density ($R^2 = 0.16$), channel width and jam density ($R^2 = 0.01$), or drainage area and jam density ($R^2 = 0.16$) (Beckman, 2013). Given the lack of evidence that basin- or reach-scale characteristics strongly influence the number of logjams in a channel reach, we evaluated whether forest age correlates with jam characteristics.

We used bivariate linear regressions, analysis of variance (ANOVA) and generalized linear modeling (GLM) to evaluate influences on jam density and jam volume. ANOVA assumes that input variables are normally or near-normally distributed. In order to meet this assumption, right skewed variables were transformed using the natural log function. Natural log transformations were used with jam density, slope, drainage area, ramp and bridge spacing. For the GLM selection, right skewed variables were transformed using the natural log function. A natural log transform was applied to jam density, slope, drainage area, ramp and bridge spacing and jam volume. Jam density and jam volume were used as response variables. Jam density was modeled as both Poisson and negative binomial distributed, and the model with the best Akaike Information Criterion (AIC) was chosen.

Results

Longitudinal spacing of jams

We first present the results from bivariate linear regressions, then the results from GLM. ANOVA and Tukey HSD analysis indicates that old-growth forests have significantly ($p = 0.002$) more jams per kilometer than younger forests (Figure 3). We evaluated basal area, ramp and bridge spacing, and piece dimensions as potential influences on the observed difference in jam density.

Old-growth streams have a significantly larger basal area within 10 m of the stream than younger stands (Table I; Figure 4A). A larger crop of standing wood is important to jam formation because of the potential for local recruitment of large wood pieces. Results indicate a weak direct relationship between basal area and jam formation for some reaches, but other reaches show increased jam density with no corresponding increase in basal area (Figure 4B). Consequently, local basal area alone cannot be used to directly predict jam density.

Stand age may also affect in-stream wood loads by increasing the number of anchored pieces in the channel, because these anchored pieces can nucleate jam formation. Old-growth reaches have significantly shorter downstream spacing for ramps and bridges than reaches with younger forest (Figure 5). Younger forest also has much more variable ramp and bridge spacing. Ramp and bridge spacing correlates significantly with

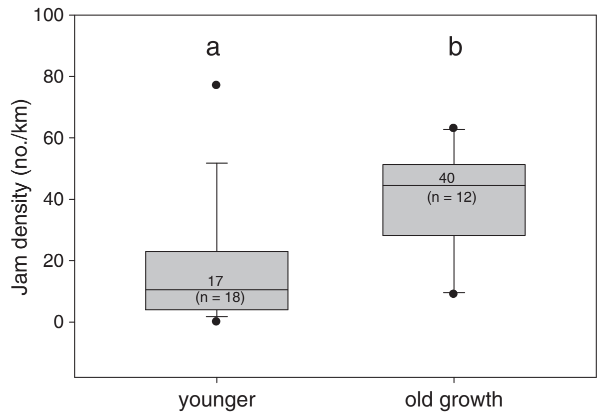

Figure 3. Jam density in old growth and younger reaches. The horizontal line within each box indicates the median value, which is also listed within the box. Box ends are the 25th and 75th percentiles, whiskers are the 10th and 90th percentiles, and solid dots are outliers. The average value and sample size are noted within each box. The letters above the boxes indicate statistically significant groupings.

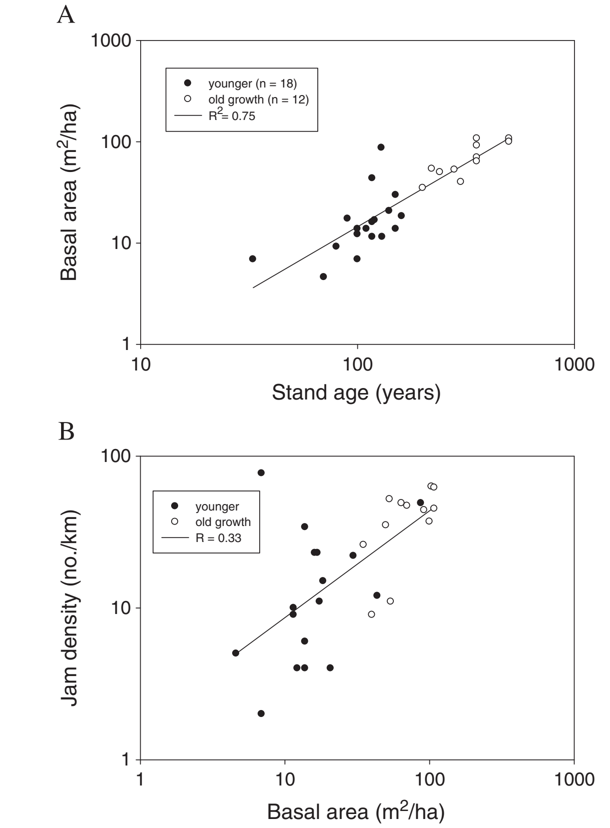

Figure 4. (A) Basal area of riparian forest adjacent to the channel versus stand age. Relationship is significant at $\alpha = 0.01$. There is more standing wood in old-growth forests and therefore a greater potential supply of local wood to the streams. (B) Jam density versus basal area. Relationship is significant at $\alpha = 0.01$, but the substantial scatter in jam density for a given basal area suggests that local basal area is not a useful predictor of jam formation.

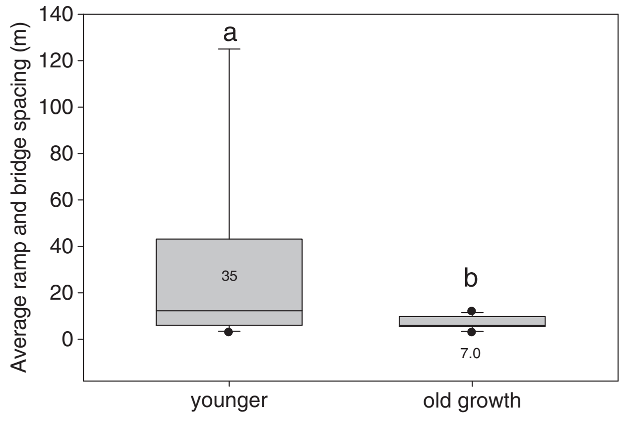

Figure 5. Ramp and bridge spacing versus stand age. A higher value for ramp and bridge spacing corresponds to a larger distance between key pieces. Although younger forests can have closely spaced ramps and bridges, spacing is not as consistent as in old growth forest.

jam density (Figure 6), with an apparent threshold at 20 m between key pieces. All of the old-growth reaches have ramp and bridge spacing of less than 20 m.

Wood from old-growth forests may also have different characteristics than wood supplied by younger forests. Because total wood loads were not measured for every stream, results that compare total (reach) in-stream wood to in-stream wood trapped in jams are only comparing the 19 reaches for which total wood loads are available. Logs in jams have slightly smaller diameters than the general population of logs in the stream (Table I). Although the relationship is not statistically significant, the results suggest that smaller, more mobile logs are more likely to be trapped in a logjam, and that without logjams or key pieces, those smaller pieces are not stable within a reach. Smaller pieces are more likely to move, and therefore more likely to get trapped by a jam or key piece or, in the absence of key pieces and jams, to be transported out of a reach. The correlation between stand age and diameter of in-stream wood is statistically significant (at $\alpha = 0.01$) only in the 84th percentile (D_{84}) (Figure 7) and maximum (D_{max}) (Table I) diameter wood measurements. As might be expected, old-growth forests include some trees with particularly large diameters. Based on observed sizes of standing riparian trees, these large diameter pieces are most likely to be Engelmann spruce or subalpine or Douglas-fir. Average tree diameter is not necessarily larger in old-growth forests (Bradford *et al.*, 2008), however, because even old-growth stands include some younger trees of smaller diameter. The ratio of log length to stream width can also be an important factor in jam formation (Gurnell *et al.*, 2002), but old-growth reaches do not have a higher ratio of log length to channel width than younger stands (Figure 8). This likely reflects the lack of substantial differences in tree height with age in the study area once the trees exceed ~100 years in age (Bradford *et al.*, 2008).

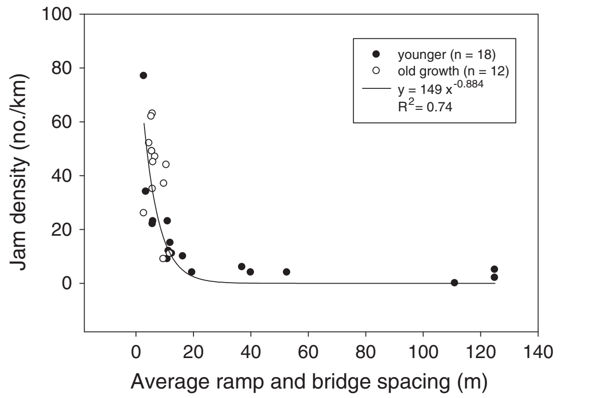

Figure 6. Ramp and bridge spacing versus jam density plotted on normal axes, demonstrating the strong threshold at approximately 20 m ramp and bridge spacing. Relationship is significant at $\alpha = 0.01$.

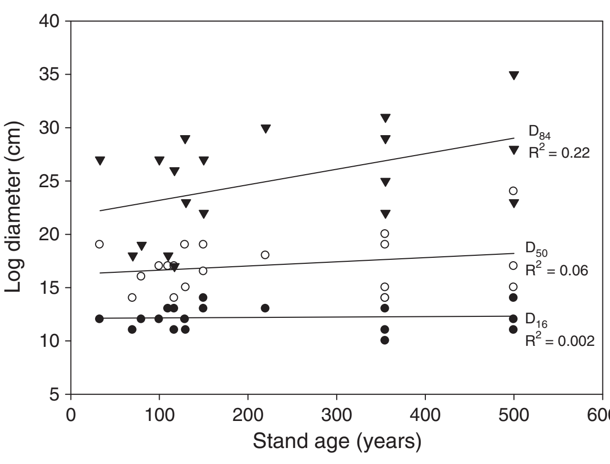

Figure 7. Diameter versus stand age for all logs within the reach, showing that stand age has little to no effect on the diameter distribution for the smaller diameter logs, but may influence larger log diameters. D_x in this figure refers to log diameters in the xth percentile of the total distribution of log diameters. Triangles indicate D_{84}, open circles indicate D_{50}, and solid circles indicate D_{16}. The correlation is significant at $\alpha = 0.10$ for D_{84}.

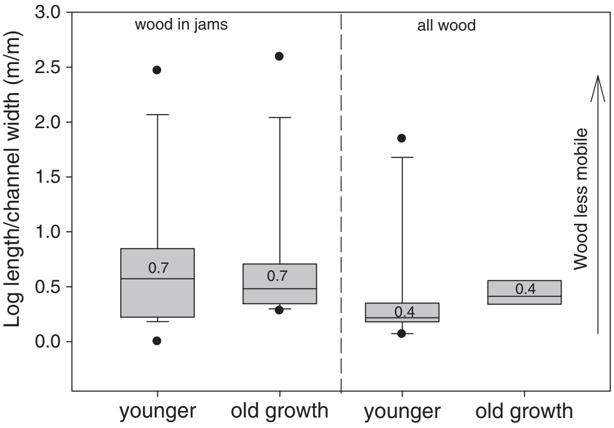

Figure 8. Average log length (in meters) divided by average channel width (in meters) versus stand age for the total population of logs in the stream and only logs found in jams. As the ratio of log length to channel width increases, wood pieces should become less mobile.

In summary, bivariate linear regression analyses of correlations between forest age and in-stream wood characteristics indicate that old-growth forests have greater basal area, slightly larger logs in the D_{84} and $D_{\max}$ categories, closer downstream spacing between ramp and bridge pieces that can serve as key pieces in logjams, and more jams per kilometer of stream. The closer downstream spacing between ramps and bridges appears to be the most significant influence on downstream jam spacing and therefore on differences in total wood load between old-growth and younger forest streams.

Based on simple bivariate regression models, the best predictor of jam density is total wood load. However, total wood load is so well correlated with jam density that wood load tends to dominate any predictive model of jam density. In order to test the relative importance of other factors, we performed a backward step selection for a generalized linear model without including total wood load as an independent variable. Instead, slope, drainage area, channel width, stand age, and ramp and bridge spacing were used to predict jam density. Basal area was highly correlated with forest age ($R^2 = 0.85$), and so was not included in the model. The distribution of jam density was assumed to be either Poisson with a log transformation or negative binomial.

The AIC model fit criteria for the Poisson and negative binomial distribution were not significantly different. The best fit model for both distributions included forest age (correlated with basal area), channel width, and ramp and bridge spacing. In both cases, the most significant variable was ramp and bridge spacing (see Supplementary Material, Table S1). A second set of backward step generalized linear models was run with the same variables, but with the addition of average diameter and average length to the backwards step selection. This model was run using only the 19 reaches for which all pieces in the stream had been surveyed, to avoid biasing the model with only logs in jams. Again, the Poisson and negative binomial distributions produced equally good models, with forest age (correlated with basal area), ramp and bridge spacing, and piece length significant in both models, with ramp and bridge spacing being the most significant (see Supplementary Material, Table S2).

The results of the GLM thus strongly support the results of the simple bivariate regression models. Forest stand age and the downstream spacing of ramps and bridges best predict the downstream spacing of jams, with the latter variable being the single best predictor of jam spacing: more closely spaced ramps and bridges equate to more closely spaced jams.

Average jam size

Average jam size at the reach scale is calculated as the total volume of wood in jams divided by the number of jams in a reach to give an average volume of wood per jam on a particular reach. A simple bivariate plot of average jam volume within a reach versus ramp and bridge spacing indicates no consistent relationship for old-growth stands and a slight decrease in jam volume for younger forest (Figure 9A). The total wood stored in jams within a reach declines substantially as ramp and bridge spacing increases up to a spacing of approximately 20 m, and total wood volume then remains consistently lower with more widely spaced ramps and bridges (Figure 9B).

Because average jam size is a continuous variable and is not right skewed, it can be modeled using a linear model (LM) instead of a generalized linear model. The independent variables used in the backward step selection include jam density, drainage area, channel width, slope, stand age, ramp and bridge spacing, and the median diameter and length of logs in jams. Of these, drainage area, slope and ramp and bridge spacing were natural log transformed to remove right skewness.

Backward step selection indicated that the important factors in jam volume are channel width, log transformed slope, log transformed ramp and bridge spacing, and median diameter of logs in jam. Of these, the most significant is ramp and bridge spacing, which has a negative effect on jam size (Table II).

Using the same independent variables as those for the average jam size analysis, we used a backward step selection to identify the variables that are related to the total amount of wood stored in jams within a reach. The response variable was natural log transformed to remove right skewness, and three reaches were removed from the dataset due to negative

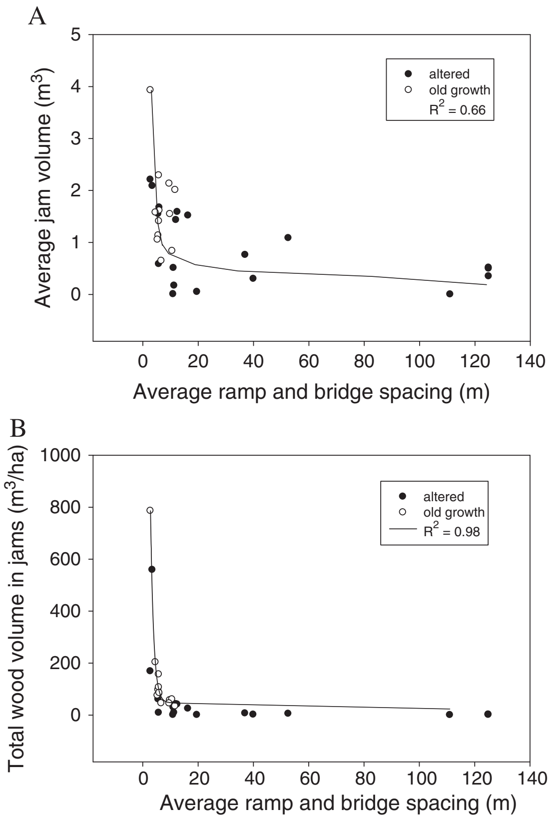

Figure 9. Using either (A) the average volume of wood within each jam or (B) the total volume of wood in jams within a reach indicates that jam size declines as average spacing of ramp and bridge pieces increases in both younger and old-growth forest stands.

Table II. Summary of linear model results for the 29 reaches with jams, and including jam piece characteristics as a variable[a]

Response variable	Assumed distribution	R_2 for model	Tested independent variables	Significant independent variables		
				Coefficient	Standard error	p Value
Jam volume	Gaussian	0.6344	Intercept	–1.111	0.907	2.32E-01
			Jam density	—	—	—
			ln(Drainage area)	—	—	—
			ln(Slope)	–0.528	0.143	1.19E-03
			Stand age	—	—	—
			Channel width	–0.073	0.035	4.58E-02
			ln(Ramp/bridge spacing)	–0.479	0.124	7.57E-04
			Jam average diameter	0.150	0.048	4.36E-03
			Jam average piece length	—	—	—
			Width × Jam average piece length	—	—	—
			Drainage area × Slope	—	—	—
			Drainage area × Channel width	—	—	—
			Slope × Channel width	—	—	—

[a]Bold variables were identified as significant during the backward step selection process. Coefficients, standard errors and p-values have been included for all significant variables.

or missing values of transformed total volume of wood in jams within a 1-km reach. The resulting significant variables were channel width, log transformed ramp and bridge spacing, and the median diameter of logs in jam (Table III). The results support the bivariate linear regressions, and are similar in magnitude and direction to the factors which influence individual jam size.

Discussion

Our results indicate that effects of old-growth stands on instream wood characteristics include an increased amount of wood entering the channel, an increase in the number of large diameter logs entering the channel, and close spacing of key anchoring pieces that can trap other pieces and form jams. Of these effects, the presence of closely spaced key pieces appears to be the most important influence on overall jam density and average jam size within a reach. These results agree with other studies of headwater streams in old-growth forests, which indicate that: *in situ* jams are the most abundant type of jam (Abbe and Montgomery, 2003), and that old-growth forest results in more closely spaced jams (Montgomery *et al*., 2003; Morris *et al*., 2007) and larger jams (Morris *et al*., 2007). Our results suggest the mechanistic importance of closely spaced, large diameter ramp and bridge pieces in facilitating larger jams and greater jam density in streams flowing through old-growth forest. A revision of the conceptual model presented in Figure 1 based on our results would thus explicitly include more closely spaced and larger diameter ramp and bridge pieces, rather than just 'more pieces, larger diameter pieces' in the second box in the flow sequence on the right side of the figure (Figure 10).

Regional differences in downstream jam spacing appear in a comparison of diverse old-growth forests (Table IV): the spacing of jams in our Colorado study site falls in the mid-high range of values for diverse sites. Of the studies cited in Table IV, only Morris *et al*. (2007) report jam volumes. For their sites, jam volume averages 50 m^3 (range 6–175 m^3) in old-growth sites. Our average value of 3.3 m^3 (range 0.9–9.7 m^3) in old-growth sites is very small by comparison, which may reflect the greater transport capacity associated with larger drainage areas and greater discharge at the Michigan sites of Morris *et al*. (2007). Further support for this comes from the much greater spacing between jams at the Michigan sites (Table IV). These disparities in jam characteristics among diverse old-growth forests highlight the need to collect basic field data from several biomes before attempting to generalize about channel-spanning logjams.

Table III. Summary of linear model results for the 29 reaches with non-zero total jam wood volume, including jam piece characteristics as a variable[a]

Response variable	Assumed distribution	R_2 for model	Tested independent variables	Significant independent variables		
				Coefficient	Standard error	p Value
ln(Total volume of wood in jams)	Gaussian	0.8987	**Intercept**	4.945	0.822	3.91E-06
			Jam density	—	—	—
			ln(Drainage area)			
			ln(Slope)	—	—	—
			Stand age	—	—	—
			Channel width	–0.139	0.036	7.15E-04
			ln(Ramp/bridge spacing)	–1.197	0.123	1.36E-09
			Jam average diameter	0.152	0.048	4.16E-03
			Jam average piece length	—	—	—
			Width × Jam average piece length	—	—	—
			Drainage area × Slope	—	—	—
			Drainage area × Channel width	—	—	—
			Slope × Channel width	—	—	—

[a]Bold variables were identified as significant during the backward step selection process. Coefficients, standard errors and p-values have been included for all variables used in the model.

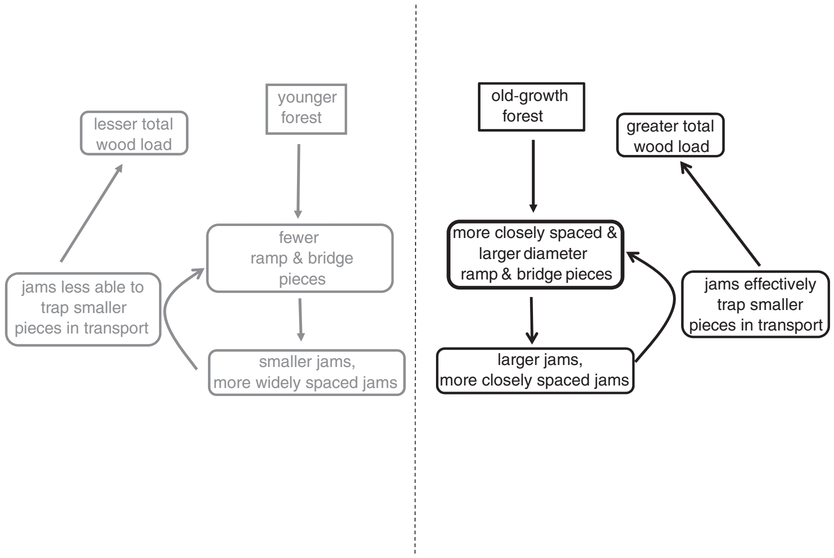

Figure 10. Initial conceptual model revised to reflect the results reported in this paper. The role of ramp and bridge pieces is highlighted by the heavier outline around that text box.

Table IV. Reported values of jam frequency for diverse old-growth forests

Location	A^a (km^2)	L^b (km)	Characteristics	Jams (km)^c	Reference
Washington, USA	0.5–20	(8–20× bankfull width)	Temperate rainforest	10–175	Abbe and Montgomery, 2003
Oregon, USA	6–22	(10–20× bankfull width)	Temperate rainforest	21–37	Montgomery *et al.*, 2003
Argentina	5–12.9	0.03–0.1	Nothofagus forest	16.2	Mao *et al.*, 2008
This study	6.1–87.8	1	Subalpine conifer forest	9–62	
Michigan, USA	40	0.3	Hardwood-hemlock forest	0.1–0.5	Morris *et al.*, 2007

[a]Drainage area at study reaches.
[b]Length of channel surveyed.
[c]Number of jams per kilometer of channel.

Jam density is not directly related to basal area in all of our study reaches, but a subset of reaches show a strong relationship. Basal area measures only the standing wood volume, not how much of that wood actually enters the channel or the characteristics of that wood. For reaches without a strong relationship, either the wood is not entering the channel, or some other control counteracts the amount of available wood. Examples of possible factors include a lack of key pieces, smaller diameter logs, or insect-damaged, standing dead logs that tend to snap into smaller, more mobile pieces when they fall.

Jam volume for individual jams is related to channel width, slope, ramp and bridge spacing, and median log diameter. The total volume of jams in a reach is related to channel slope, ramp and bridge spacing and median log diameter. In both cases, the most significant variable is ramp and bridge spacing, which correlates inversely with jam size. The implication is that more closely spaced ramps and bridges lead to smaller jams, presumably because wood is not able to travel far before it is trapped. Each jam has a smaller 'tributary area' within which it can recruit wood than it would if the key pieces were more widely spaced. Tributary area is a structural engineering term which refers to the area of a structure supported by a given element. We use this term to describe the area of stream channel upstream from a key piece to the next upstream jam or key piece. Wood that enters a channel within a piece's tributary area is available to be trapped by that key piece or jam. Where key species are closely spaced, wood may not be able to travel far enough to accumulate into channel-spanning jams, which suggests an upper threshold to the number of very large jams along a stream reach.

Because this is an observational study, there are several confounding factors. Reach data were collected during three different years, but all of the data in the North St Vrain basin (including seven of the 12 old-growth reaches) were collected in 2009 before the unusually large snowmelt runoff seasons of 2010 and 2011. The sample size and design of this study did not allow us to test for effects based on the year in which a reach was surveyed. Another possible confounding effect occurs if logs are recruited from upstream, so that our assumption that adjacent forest age reflects the primary recruitment source for most logs in a reach is not correct, despite the observed correlations. There is known old-growth forest upstream of at least two sites (Ouzel 2, NSV 3), but in other basins it was not feasible to determine the age of upstream forest stands, so it was not possible to control for upstream old growth. One site (Ouzel 2) likely has elevated wood loads because the adjacent forest burned in 1978. Working on forests in Wyoming, Bragg (2000) found that peak loads from natural disturbances occur ~30 years after the disturbance.

Stand age influences jam density within a reach, and outliers (Ouzel 2, NSV 3) to this trend suggest that natural stand-replacing disturbances can actually increase the number of jams in a reach, while human disturbances that remove wood from a watershed decrease jam density. Stand age is sometimes used as a proxy for disturbance history, but the type of disturbance and stand age prior to disturbance may be as important as the time since disturbance. Our results suggest that naturally disturbed forest acts like old-growth in many respects, despite a temporarily lower input of wood to the stream. This likely reflects the overall importance of key pieces, which tend to increase after a disturbance such as fire, insect outbreak or blow down.

Conclusions

The results summarized here indicate that local forest age exerts an important influence on the quantity and characteristics of in-stream wood. Higher wood loads, as measured by jam density, and piece characteristics differ significantly between stream reaches in old-growth and younger forests. The differences appear to be driven by both increased wood supply (as measured by basal area) and the increased number of key pieces for jam formation.

In-stream wood in jams tends to have a slightly smaller diameter distribution than wood not trapped in jams, which suggests that jams trap pieces that would otherwise be transported through the reach. Factors such as slope, stand age, channel width, and the spacing of key pieces may create favorable conditions for jams.

Total wood load is the main variable correlated with jam density. There is likely a positive feedback mechanism through which streams with increased wood loads tend to form more jams, and jams tend to trap more wood within a reach. In other words, both increased wood load and increased jam frequency create debris roughness (Braudrick and Grant, 2000) that enhances wood retention.

Jam size is negatively correlated with channel width, slope, ramp and bridge spacing, and positively correlated with median log diameter. Closely spaced ramps and bridges have a smaller 'tributary area' to provide mobile pieces relative to more widely spaced key pieces.

Several aspects of the results summarized here have implications for managing in-stream wood loads and the associated sediment storage and ecosystem productivity. Downstream spacing of jams shows little correlation with basin size, but does correlate with reach-scale characteristics including stand age, spacing of ramps and bridges and to a lesser extent average channel gradient. This suggests that management of in-stream wood can be focused most effectively at the reach scale. Given the current desire to increase in-stream wood loads in order to enhance fish habitat, management can emphasize either preserving old-growth stands along lower gradient stream reaches, or mimicking the effects of old growth by enhancing debris roughness through manipulating the spacing of ramps and bridges. Among the more important findings of the analyses summarized here are that average downstream spacing between jams declines as wood load increases, which suggests that the most effective way to create and retain jams is to ensure abundant sources of wood recruitment, with a particular emphasis on larger pieces that are less mobile because they have at least one anchor point outside the active channel.

Acknowledgements—The authors thank Cole Green-Smith, Allison Jackson, Richard Beckman, Michael Magyar, Mario Jimenez, David Dust and Bryan Scholl for field assistance. Earlier drafts of the manuscript were improved by comments from Jeff Niemann, Stephanie Kampf, Sara Rathburn, Andrés Iroumé and two anonymous reviewers. Jason Sibold, Julian Scott, Jonathan Friedman, Greg Auble and Jesse Bright helped with tree core collecting and analyses. The Geological Society of America, the Colorado Mountain Club and the American Water Resources Association provided funding for this research to NDB. The authors also thank Rocky Mountain National Park for access to research sites.

References

Abbe TB, Brooks AP, Montgomery DR. 2003. Wood in river rehabilitation and management. In The Ecology and Management of Wood in World Rivers, Gregory SV, Boyer KL, Gurnell AM (eds). American Fisheries Society Symposium 37. American Fisheries Society: Bethesda, MD; 367–389.

Abbe TB, Montgomery DR. 1996. Large woody debris jams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers: Research and Management* **12**: 201–221.

Abbe TB, Montgomery DR. 2003. Patterns and processes of wood debris accumulation in the Queets river basin, Washington. *Geomorphology* **51**(1–3): 81–107.

Assani AA, Petit F. 1995. Log-jam effects on bed-load mobility from experiments conducted in a small gravel-bed forest ditch. *Catena* **25**(1–4): 117–126.

Avery TE, Burkhart HE. 2002. Forest Measurements. McGraw-Hill: New York.

Baxter CV, Fausch KD, Saunders WC. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* **50**(2): 201–220.

Beckman ND. 2013. Crossing a Threshold: The Legacy of 19th Century Logging on Log Jams and Carbon Storage in Front Range Headwater Streams. PhD Dissertation, Colorado State University, Fort Collins, CO.

Bilby RE. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology* **62**(5): 1234–1243.

Bilby RE, Likens GE. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* **61**: 1107–1113.

Bocchiola D, Rulli MC, Rosso R. 2008. A flume experiment on the formation of wood jams in rivers. *Water Resources Research* **44**(2): 1–17. DOI. 10.1029/2006WR005846

Braddock WA, Cole J. 1990. Geologic Map of Rocky Mountain National Park and Vicinity, Colorado. Rocky Mountain National Park: Fort Collins, CO.

Bradford JB, Birdsey RA, Joyce LA, Ryan MG. 2008. Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests. *Global Change Biology* **14**: 2882–2897.

Bragg DC. 2000. Simulating catastrophic and individualistic large woody debris recruitment for a small riparian system. *Ecology* **81**(5): 1383–1394.

Braudrick CA, Grant GE. 2000. When do logs move in rivers? *Water Resources Research* **36**(2): 571–583.

Brummer CJ, Abbe TB, Sampson JR, Montgomery DR. 2006. Influence of vertical channel change associated with wood accumulations on delineating channel migration zones, Washington, USA. *Geomorphology* **80**: 295–309.

Buffington JM, Montgomery DR. 1999. Effects of hydraulic roughness on surface textures of gravel-bed rivers. *Water Resources Research* **35**: 3507–3521.

Collins BD, Montgomery DR. 2002. Forest development, wood jams, and restoration of floodplain rivers in the Puget Lowland, Washington. *Restoration Ecology* **10**(2): 237–247.

Collins BD, Montgomery DR, Fetherston KL, Abbe TB. 2012. The floodplain large-wood cycle hypothesis: a mechanism for the physical and biotic structuring of temperate forested alluvial valleys in the North Pacific coastal ecoregion. *Geomorphology* **139–140**: 460–470.

Curran JH, Wohl EE. 2003. Large woody debris and flow resistance in step-pool channels, Cascade Range, Washington. *Geomorphology* **51**: 141–157.

Ehlen J, Wohl E. 2002. Joints and landform evolution in bedrock canyons. *Transactions, Japanese Geomorphological Union* **23**(2): 237–255.

Evans BF, Townsend CR, Crowl TA. 1993. Distribution and abundance of coarse woody debris in some southern New Zealand streams from contrasting forest catchments. *New Zealand Journal of Marine and Freshwater Research* **27**: 227–239.

Fanelli RM, Lautz LK. 2008. Patterns of water, heat, and solute flux through streambeds around small dams. *Groundwater* **46**(5): 671–687.

Fausch KD, Northcote TG. 1992. Large woody debris and salmonid habitat in a small British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 682–693.

Faustini JM, Jones JA. 2003. Influence of large woody debris on channel morphology and dynamics in steep, boulder-rich mountain streams, western Cascades, Oregon. *Geomorphology* **51**: 187–205.

Gurnell AM. 2003. Wood storage and mobility. In The Ecology and Management of Wood in World Rivers, Gregory SV, Boyer KL, Gurnell AM (eds). American Fisheries Society Symposium 37. American Fisheries Society: Bethesda, MD; 75–91.

Gurnell AM, Petts GE, Hannah DM, Smith BPG, Edwards PJ, Kollmann J, Ward JV, Tockner K. 2000. Wood storage within the active zone of a large European gravel-bed river. *Geomorphology* **34**: 55–72.

Gurnell AM, Piegay H, Swanson FJ, Gregory SV. 2002. Large wood and fluvial processes. *Freshwater Biology* **47**: 601–619.

Hall SA, Burke IC, Hobbs NT. 2006. Litter and dead wood dynamics in ponderosa pine forests along a 160-year chronosequence. *Ecological Applications* **16**(6): 2344–2355.

Hassan MA, Hogan DL, Bird SA, May CL, Gomi T, Campbell D. 2005. Spatial and temporal dynamics of wood in headwater streams of the Pacific Northwest. *Journal of the American Water Resources Association* **41**(4): 899–919.

Hedman CW, Van Lear DH, Swank WT. 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.

Hyatt TL, Naiman RJ. 2001. The residence time of large woody debris in the Queets River, Washington, USA. *Ecological Applications* **11**(1): 191–202.

Jeffries R, Darby SE, Sear DA. 2003. The influence of vegetation and organic debris on flood-plain sediment dynamics: case study of a low-order stream in the New Forest, England. *Geomorphology* **51**: 61–80.

Keller EA, Swanson FJ. 1979. Effects of large organic material on channel form and fluvial processes. *Earth Surface Processes* **4**: 361–380.

Keller EA, Tally T. 1979. Effects of large organic debris on channel form and fluvial processes in the coastal redwood environment. In Adjustments of the Fluvial System, Rhodes DD, Williams G (eds). Allen and Unwin: Dubuque, IA; 169–197.

Lautz LK, Siegel DI, Bauer RL. 2006. Impact of debris dams on hyporheic interaction along a semi-arid stream. *Hydrological Processes* **20**(1): 183–196.

MacFarlane WA, Wohl E. 2003. Influence of step composition on step geometry and flow resistance in step-pool streams of the Washington Cascades. *Water Resources Research* **39**(2): 1–13.

Manga M, Kirchner JW. 2000. Stress partitioning in streams by large woody debris. *Water Resources Research* **36**(8): 2373–2379.

Manners RB, Doyle WM, Small MJ. 2007. Structure and hydraulics of natural woody debris jams. *Water Resources Research* **43**(6): 1–17.

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

Marcus WA, Marston RA, Colvard CR, Gray RD. 2002. Mapping the spatial and temporal distributions of woody debris in streams of the Greater Yellowstone Ecosystem, USA. *Geomorphology* **44**: 323–335.

Maser C, Sedell JR. 1994. From the Forest to the Sea: The Ecology of Wood in Streams, Rivers, Estuaries, and Oceans. St Lucie Press: Delray Beach, FL.

May CL, Gresswell RE. 2003. Large wood recruitment and redistribution in headwater streams in the southern Oregon Coast Range, U.S.A. *Canadian Journal of Forest Research* **33**(8): 1352–1362.

Merten E, Finlay J, Johnson L, Newman R, Stefan H, Vondracek B. 2010. Factors influencing wood mobilization in streams. *Water Resources Research* **46**(10): 1–13.

Montgomery DR, Abbe T, Buffington JM, Peterson NP, Schmidt KM, Stock JD. 1996. Distribution of bedrock and alluvial channels in forested mountain drainage basins. *Nature* **381**: 587–589.

Montgomery DR, Buffington JM. 1997. Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* **109**(5): 596–611.

Montgomery DR, Massong TM, Hawley SCS. 2003. Influence of debris flows and log jams on the location of pools and alluvial channel reaches, Oregon Coast Range. *Geological Society of America Bulletin* **115**(1): 78–88.

Morris AEL, Goebel PC, Palik BJ. 2007. Geomorphic and riparian forest influences on characteristics of large wood and large-wood jams in old-growth and second-growth forests in northern Michigan, USA. *Earth Surface Processes and Landforms* **32**: 1131–1153.

Naiman RJ, Sedell JR. 1979. Relationships between metabolic parameters and stream order in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 834–847.

Oswald EB, Wohl E. 2008. Wood-mediated geomorphic effects of a jökulhlaup in the Wind River Mountains, Wyoming. *Geomorphology* **100**: 549–562.

Ralph SC, Poole GC, Conquest LL, Naiman RJ. 1994. Stream channel morphology and woody debris in logged and unlogged basins of western Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 37–51.

Rebertus AJ, Veblen TT, Roovers LM, Mast JN. 1992. Structure and dynamics of Engelmann Spruce-Subalpine Fir in Colorado. In *Proceedings, Old Growth Forests in the Southwest and Rocky Mountain Region Workshop, 9–13 March*, Portal, AZ; 1–15.

Richmond AD, Fausch KD. 1995. Characteristics and function of large woody debris in subalpine Rocky Mountain streams in northern Colorado. *Canadian Journal of Fisheries and Aquatic Sciences* **52**(8): 1789–1802.

Ries KGI, Buthrie JD, Rea AH, Steeves PA, Stweart DW. 2008. StreamStats: A Water Resources Web Application, USGS Fact Sheet FS 2008-3067. US Geological Survey: Reston, VA.

Romme WH, Clement J, Hicke J, Kulakowski D, Macdonald LH, Schoennagel TL, Veblen TT. 2006. Recent Forest Insect Outbreaks and Fire Risk in Colorado Forests: A Brief Synthesis of Relevant Research. Colorado State Forest Service Report: Fort Collins, CO. http://coloradoforestrestoration.org/CFRIpdfs/2006_InsectOutbreakFireRisk.pdf

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

Sibold JS, Veblen TT, Gonzalez ME. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography* **33**(4): 631–647.

Silsbee DG, Larson GL. 1983. A comparison of streams in logged and unlogged areas of Great Smoky Mountains National Park. *Hydrobiologia* **102**: 99–111.

Veblen TT. 1986. Treefalls and the coexistence of conifers in subalpine forests of the Central Rockies. *Ecology* **67**(3): 644–649.

Veblen TT, Donnegan JA. 2005. Historical Range of Variability for Forest Vegetation of the National Forests of the Colorado Front Range. http://www.fs.fed.us/r2/projects/scp/tea/HRVFrontRange.pdf

Wipfli MS, Baxter CV. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. *Fisheries* **35**(8): 373–387.

Wohl E. 2011. Threshold-induced complex behavior of wood in mountain streams. *Geology* **39**(6): 587–590. DOI. 10.1130/G32105.1

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

Wohl E, Beckman ND. 2014. Leaky rivers: implications of the loss of longitudinal fluvial disconnectivity in headwater streams. *Geomorphology* **205**: 27–35.

Wohl E, Beckman ND. 2014. Controls on the longitudinal distribution of channel-spanning logjams in the Colorado Front Range, USA. *River Research and Applications* **30**: 112–131.

Wohl E, Cadol D. 2011. Neighborhood matters: patterns and controls on wood distribution in old-growth forest streams of the Colorado Front Range, USA. *Geomorphology* **125**(1): 132–146.

Wohl E, Goode JR. 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. *Water Resources Research* **44**(9): 1–14. DOI. 10.1029/2007WR006522

Wohl E, Kuzma JN, Brown NE. 2004. Reach-scale channel geometry of a mountain river. *Earth Surface Processes and Landforms* **29**(8): 969–981.

Wondzell SM, LaNier J, Haggerty R, Woodsmith RD, Edwards RT. 2009. Changes in hyporheic exchange flow following experimental wood removal in a small, low-gradient stream. *Water Resources Research* **45**: W05406. DOI. 10.1029/2008WR007214

Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's web-site.