



RESEARCH ARTICLE

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Key Points:

- Total carbon stored in a logjam relates to forest age and disturbance history
- Old-growth forests result in greater instream carbon storage
- This is the first study to correlate forest age with riverine carbon storage

Supporting Information:

- Readme
- Three tables

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Carbon storage in mountainous headwater streams: The role of old-growth forest and logjams

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Abstract We measured wood piece characteristics and particulate organic matter (POM) in stored sediments in 30 channel-spanning logjams along headwater streams in the Colorado Front Range, USA. Logjams are on streams flowing through old-growth (>200 years), disturbed (<200 years, natural disturbance), or altered (<200 years, logged) subalpine conifer forest. We examined how channel-spanning logjams influence riverine carbon storage (measured as the total volatile carbon fraction of stored sediment and instream wood). Details of carbon storage associated with logjams reflect age and disturbance history of the adjacent riparian forest. A majority of the carbon within jams is stored as wood. Wood volume is significantly larger in old-growth and disturbed reaches than in altered reaches. Carbon storage also differs in relation to forest characteristics. Sediment from old-growth streams has significantly higher carbon content than altered streams. Volume of carbon stored in jam sediment correlates with jam wood volume in old-growth and disturbed forests, but not in altered forests. Forest stand age and wood volume within a jam explain 43% of the variation of carbon stored in jam sediment. First-order estimates of the amount of carbon stored within a stream reach show an order of magnitude difference between disturbed and altered reaches. Our first-order estimates of reach-scale riverine carbon storage suggest that the carbon per hectare stored in streams is on the same order of magnitude as the carbon stored as dead biomass in terrestrial subalpine forests of the region. Of particular importance, old-growth forest correlates with more carbon storage in rivers.

1. Introduction

Recent work on the carbon cycle emphasizes the influence of fluvial dynamics on the export and processing of terrestrial carbon [Galy *et al.*, 2008a, 2008b; Hilton *et al.*, 2008a, 2008b; Battin *et al.*, 2009; Aufdenkampe *et al.*, 2011]. Carbon entering the freshwater network can be outgassed to the atmosphere, sequestered in sedimentary deposits, or transferred to the ocean [Aufdenkampe *et al.*, 2011]. Partitioning among these three pathways depends in part on the physical complexity of river channels. Physical complexity in the form of boundary irregularities promotes hydrological storage and retention zones that can extend the residence time of dissolved organic carbon (DOC) and fine and coarse particulate organic matter (POM) during downstream transport. Fluvial examples of storage and retention zones include marginal eddies, lee deposits downstream from obstacles [Thompson, 2008], river segments ponded by beaver dams, logjams or downstream constrictions [Lautz *et al.*, 2006; Fanelli and Lautz, 2008; Hester and Doyle, 2008], and hyporheic zones [Harvey and Fuller, 1998]. These sites provide opportunities for microorganisms to develop as attached biofilms or suspended aggregates and to metabolize carbon and other nutrients for energy and growth [Battin *et al.*, 2008]. Sites of increased nutrient retention and processing create biogeochemical hot spots with disproportionately high reaction rates relatively to the surrounding matrix [McClain *et al.*, 2003]. Any physical feature that promotes flow separation, lower velocity, and at least temporary storage of POM can facilitate the formation of hot spots. Consequently, the efficiency with which streams retain and oxidize carbon rests partly on the abundance and quality of retention zones [Peterson *et al.*, 2001; Hall *et al.*, 2002].

Headwater streams are particularly important in fluvial carbon dynamics. Because of their relatively close coupling to adjacent uplands, headwater streams receive most of the terrestrial DOC and POM [Battin *et al.*, 2008]. These streams can have substantial retention zones because of longitudinally and laterally variable channel geometry, relatively poorly sorted grain-size distributions that include large, protruding clasts, instream wood [Wohl, 2000; Gomi *et al.*, 2002], and channel-spanning obstructions such as beaver dams and logjams [Wohl, 2011b]. Headwater catchments are among the primary controls on DOC and POM variation

through time [Boyer *et al.*, 1995], making it important to document the processes that maintain POM retention zones in headwater streams.

Headwaters—defined here as first-order and second-order streams [Meyer and Wallace, 2001]—compose ~70% of total estimated river length in the United States [Leopold *et al.*, 1964], and thus can cumulatively significantly influence carbon sequestration [Gomi *et al.*, 2002]. Recent studies document headwater channels that efficiently convey large amounts of carbon as DOC and POM downstream, particularly during periods of intense precipitation and flooding [Lyons *et al.*, 2002; Hilton *et al.*, 2008b, 2011; West *et al.*, 2011; Ramos Scharron *et al.*, 2012; Wohl and Ogden, 2013], as well as headwater channels that store significant quantities of carbon in longitudinally discontinuous floodplains [Wohl *et al.*, 2012]. Among the key differences in headwater channels that do or do not sequester carbon in floodplains is the presence of channel-spanning logjams that persist for at least a few years and that contribute to the physical complexity of the channels.

Instream wood can alter a stream to create more carbon retention and biogeochemical hotspots, and can itself provide a form of carbon storage [Guyette *et al.*, 2002] or food source for aquatic organisms [Maser and Sedell, 1994; Featherston *et al.*, 1995; Eggert and Wallace, 2007; Tank *et al.*, 2010]. Leaves break down faster, but wood can be a long-term substrate for biofilms and can support microbial biomass, algal biomass, exoenzyme activity, and invertebrate density at higher levels than leaves [Eggert and Wallace, 2007], as well as breaking down into fine particulate organic matter [Ward and Aumen, 1986]. Because both the quantity and quality of a food subsidy are important for the ecosystem [Marcarelli *et al.*, 2011], the abundance of instream wood can influence stream ecosystems at many levels.

Here we examine how instream wood in mountainous headwater channels of the Colorado Front Range, USA influences riverine carbon storage (measured as total volatile carbon). We focus our analysis on channel-spanning jams, which cross the entire channel width, because they exert a more important influence on instream carbon dynamics than individual pieces of wood. Jams are particularly effective at trapping POM and finer sediment [Cordova *et al.*, 2008], which provides an abiotic substrate for nutrient uptake [Assani and Petit, 1995; Warren *et al.*, 2007]. Channel-spanning jams can also form residual pools of water which allow nutrient processing during periods of low flow [Hall *et al.*, 2002]. Jams increase hydraulic head, which can promote flux through the bioactive hyporheic zone [Fanelli and Lautz, 2008] and increase lateral connectivity during floods, facilitating increased biogeochemical activity [McClain *et al.*, 2003] and increased floodplain storage of finer sediment and carbon [Wohl *et al.*, 2012]. Previous studies indicate that jams with a greater volume of wood have a larger upstream pool and larger surface area (but not necessarily volume) of stored sediment [Bilby and Ward, 1989], and that streams flowing through old-growth forest tend to have more instream wood and channel-spanning jams [Bilby and Ward, 1991; Beckman and Wohl, 2014].

We also examine how differences in forest age and disturbance history influence instream carbon storage. Old-growth riparian forests have larger diameter trees and greater basal area, which corresponds to greater instream wood loads [Silsbee and Larson, 1983; Richmond and Fausch, 1995; Warren *et al.*, 2007] and more closely spaced channel-spanning logjams [Beckman and Wohl, 2014]. Alteration of rivers or riparian forests that results in fewer jams on headwater streams can affect the entire river system because larger streams have lesser ability to process coarse POM [Bilby and Likens, 1980; Cordova *et al.*, 2008].

Forest age has an effect on above ground biomass and carbon storage in terrestrial systems [Turner, 2010]. Old-growth forest stores more carbon than younger forest [Harmon *et al.*, 1990; Ryan and Waring, 1992; Turner, 2010], and the majority of this carbon is stored in the largest trees [Binkley *et al.*, 2003; Frolking *et al.*, 2009; McKinley *et al.*, 2011]. Carbon can be stored as living and dead biomass, although as living trees die and decompose, the forest becomes a carbon source [Harmon *et al.*, 1990; Janisch and Harmon, 2002; Turner, 2010]. In the subalpine forests of our study area, ~30% of terrestrial carbon is stored as organic matter in the soil, 33% as dead biomass, and 36% as living biomass [Arthur and Fahey, 1992]. The amount of dead biomass in a forest in the form of dead wood has been shown to change depending on the disturbance type. Clearcuts result in a net loss of carbon stored as dead wood, whereas wildfires result in a net gain [Tinker and Knight, 2000]. Such changes can be persistent, especially in cold, dry environments such as the Colorado Front Range, where tree decay and growth rates are low [Kueppers *et al.*, 2004].

Although an increasing number of studies quantify the effect of forest age and disturbance history on the amount and form of carbon in the terrestrial environment, there are no studies which explicitly link forest characteristics and carbon storage within streams. We address this gap by quantifying the volume of sediment stored upstream from channel-spanning logjams, as well as the proportion of carbon by mass in jam sediment and in sediment within other areas of the channel along headwater streams in the Colorado Front Range. We use measurements of instream wood and sediment carbon content to develop a first-order approximation of the amount of carbon stored in different forms within headwater streams, and relate these numbers to forest age and disturbance history.

We differentiate old-growth forests (stand age > 200 years), disturbed forests (stand age < 200 years as a result of natural disturbances such as wildfire, beetle infestation, or blowdown), and altered forests (stand age < 200 years as a result of logging). These three categories are referred to hereafter as forest type. We categorize forest age and disturbance history in this manner because (i) old-growth forests differ significantly from younger forests in relation to basal area, tree diameter at breast height, and species composition [Oliver and Larson, 1990] and (ii) forests with natural disturbances do not experience removal of dead trees or biomass from the site (although severe wildfires can result in combustion of biomass), whereas altered forests do experience such removal.

We examine riverine carbon storage by considering the partitioning of carbon between wood pieces > 1 m in length and 10 cm in diameter, and POM stored in the sediment deposited in the backwater area of a logjam. We expected logjams to store greater amounts of carbon than smaller zones of flow separation not associated with a channel-spanning logjam. Consequently, we examine whether the percent by mass of carbon within sediment stored in zones of flow separation differs between jam and nonjam sites. We also expected logjams in old-growth forest to store greater amounts of carbon than other forest types, so we examine correlations between forest type and total carbon stored in sediment upstream from jams, and correlations between forest type and proportion of carbon stored in the form of wood. Finally, we scale up from individual jams to estimate differences in carbon storage between stream reaches with differing forest type.

2. Field Area

Study sites are in the Cache la Poudre, Big Thompson, and North St. Vrain drainages in northern Colorado, USA (Figure 1). 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]. Although bedrock lithology does not vary substantially in the study area, the width and gradient of stream channels and valley bottoms are quite variable downstream at lengths of 10^2 – 10^3 m. Step-pool channels are most common, although cascade, plane-bed, and pool-riffle morphologies [Montgomery and Buffington, 1997] are also present. Substrate is primarily cobble-size to boulder-size clasts, although finer sand and gravel are present in zones of flow separation such as upstream from logjams.

Mean annual precipitation is 70–90 cm in the upper basins. Flow is dominated by snowmelt, which produces an annual hydrograph with a sustained May–June peak. We collected data during the summers of 2009, 2010, and 2011. The summers of 2010 and 2011 were unusual, with larger than average magnitude and duration of the snowmelt peak. In 2010, the Allenspark stream gauge along North Saint Vrain Creek recorded above-average flows during 4–15 June, with a peak of ~ 17 m³/s on 8 June. The gauge has a 20 year historic average June flow of ~ 6 m³/s. In 2011, the snowmelt peak was both larger in magnitude and longer in duration than it has been historically. The same gauge recorded above-average flows starting 6 June, and continuing until mid-July with a peak of ~ 16 m³/s on 8 July.

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 above the Pleistocene terminal glacial moraine and 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]. More mesic subalpine sites are dominated by Engelmann spruce and subalpine fir, whereas lodgepoles dominate more xeric sites and are successional to the spruce-fir community. Riparian communities include large numbers of mesic-site conifers such as Engelmann spruce and Douglas-fir (*Pseudotsuga menziesii*), as well as aspen. Age and size of individual trees vary greatly with site-specific conditions, as reflected in

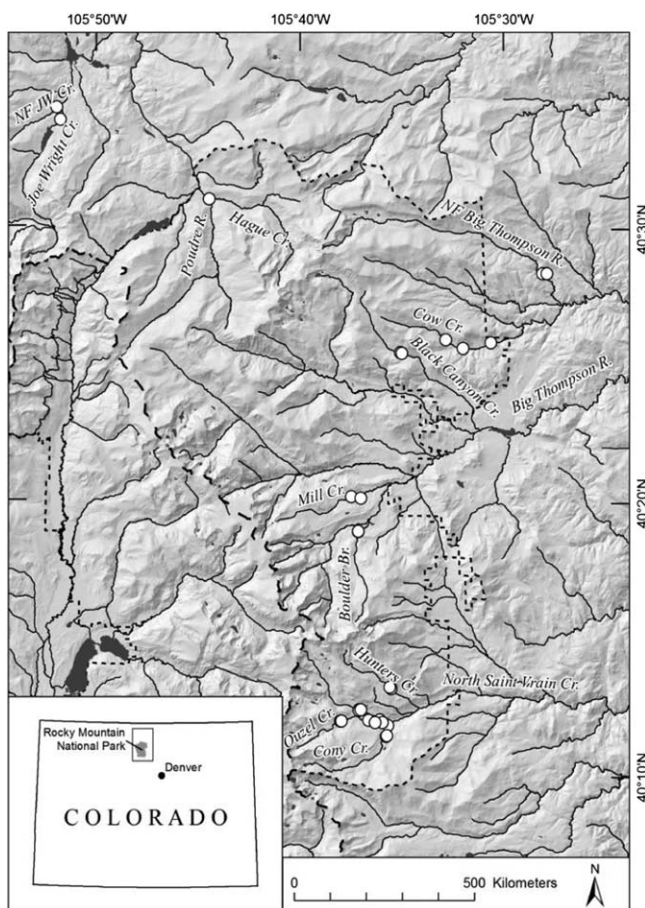


Figure 1. Location map of the surveyed logjams, shown as white circles. Continental divide is the long-dashed line at left of figure; national park boundary is the short-dashed line. Figure courtesy of Joseph Mangano.

diverse values for riparian basal area (Table 1). Old-growth riparian stands have more old and very large trees, at least in part because they are less affected by wildfire than adjacent upland stands.

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. The study area does not have frequent landslides or debris flows that can introduce large volumes of wood to the streams. Fire and insect outbreaks are the most significant in terms of extent, severity, and frequency in the laterally confined 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]. Infrequent, high-severity fires that kill all canopy trees over areas of hundreds to thousands of hectares recur at intervals >100 years in the subalpine zone [Veblen and Donnegan, 2005]. Initial colonization can be dominantly Engelmann spruce and

lodgepole pine, but spruce and fir typically become increasingly abundant after circa 100 years of stand development [Veblen *et al.*, 1991]. Patches of stand-killing disturbance in the North St. Vrain basin date to 1654, 1695, 1880, and 1978 A.D., and for the portions of the Big Thompson drainage within Rocky Mountain National Park, disturbance patches date to 1730, 1893, and 1915 [Sibold *et al.*, 2006]. For areas outside the park, no large-scale disturbance maps are available, but tree coring done as part of this study indicates that riparian stands germinated after 1770, 1810, 1850, and 1880 in the Big Thompson basin and 1710, 1790, 1860, 1870, 1910, 1930, and 1940 in the Poudre River Basin [Beckman, 2013]. Although the causes of stand-killing disturbances are not known for certain, they are assumed to be natural if they occurred >200 years ago, or if they occurred in areas with no known logging. In areas with a known history of logging (including lands managed by the USDA Forest Service), stands younger than 200 years old were assumed to be regrowth after logging. No history of forest management was available for the study area prior to its designation as national forest or national park. Because logging in the study area was performed prior to these land designations, we assume that no riparian setbacks were used, and the streamside forest was clear cut in accordance with standard practice at the time.

Regrowth of trees following disturbance varies with site conditions, seed sources, and climate, but is typically 30–60 years for the subalpine zone [Veblen and Donnegan, 2005]. Old-growth characteristics typically do not emerge for at least 200 years in subalpine forests [Veblen, 1986]. Wood recruitment to streams flowing through the disturbed area can thus increase substantially for a period of decades following a disturbance as dead and dying trees slowly topple, but is then likely to decrease during the period when all dead trees have fallen and new trees are not yet large enough for recruitment [Wohl, 2011a]: the whole process likely requires two centuries to reach predisturbance wood dynamics [Bragg, 2000].

Table 1. Summary of Jam Characteristic Data

Jam	Forest ^a (m ² /ha)	BA ^b (m ²)	Sed A ^c	Sed V ^d (m ³)	% C ^e ≤2 (mm)	All	Sed C ^f (kg)	Wood V ^g (m ³)	Wood C ^h (kg)	Total C ⁱ (kg)	C propor as wood ^j (kg/kg)	NJ C D/S ^k (%)	NJ C U/S ^l (%)
Bennett 1	A	29.8	22.3	8.3	8.2	9.5	524	0.7	151	676	0.22	n/a	n/a
Boulder 1	A	32.1	n/a	3.6	2.0	2.8	67	0.4	79	146	0.54	0.56	0.87
Boulder 2	A	34.4	2.4	0.8	0.5	0.5	3	0.2	42	45	0.94	0.67	0.56
Cow 1	A	13.8	5.5	1.9	0.9	1.0	12	0.8	181	193	0.94	n/a	1.36
Cow 2	A	20.7	7.7	3.0	1.6	1.4	28	0.5	104	132	0.79	0.72	1.94
Cow 3	A	20.7	8.1	2.7	n/a	n/a	n/a	2.0	445	n/a	n/a	n/a	n/a
Hague 1	A	32.1	3.2	1.9	1.7	1.6	21	0.4	99	120	0.83	n/a	2.31
Hague 2	A	32.1	0.8	1.6	1.5	1.4	15	1.1	240	255	0.94	1.69	n/a
Mill 1	A	18.4	4.2	2.6	1.1	1.1	19	2.2	494	513	0.96	0.95	1.71
Mill 2	A	25.3	3.2	1.2	1.1	1.1	9	1.7	375	384	0.98	1.11	n/a
Average		25.9	6.4	2.8	2.1		78	1.0	221	274	0.79	0.95	1.46
Cony 3	D	39.0	4.8	1.6	4.7	3.4	35	2.9	649	684	0.95	n/a	2.60
NSV 3	D	45.9	n/a	2.3	2.0	3.2	49	4.8	1082	1131	0.96	n/a	n/a
NSV 4	D	20.7	3.4	0.9	3.1	4.2	26	2.8	629	655	0.96	n/a	n/a
Ouzel 3	D	2.3	21.6	5.7	3.7	1.8	69	8.2	1836	1904	0.96	n/a	4.37
Ouzel 4	D	13.8	3.5	0.8	12.8	12.7	65	6.8	1534	1599	0.96	n/a	4.88
Average		24.3	8.3	2.3	5.3		49	5.1	1146	1195	0.96	n/a	3.95
BC 1	O	18.4	5.9	1.9	1.2	1.1	14	1.4	319	333	0.96	2.79	0.73
BC 2	O	16.1	6.4	3.6	8.6	18.6	443	0.9	208	650	0.32	n/a	1.05
Cony 1	O	39.0	24.1	10.2	13.2	15.6	1058	4.6	1032	2089	0.49	1.72	5.06
Cony 2	O	41.3	13.7	6.2	7.9	9.5	392	2.0	460	852	0.54	1.31	2.46
Hunter 1	O	48.2	45.9	11.3	2.9	5.0	372	2.9	654	1026	0.64	0.63	0.58
Hunter 2	O	71.2	6.3	1.8	5.5	11.1	132	2.3	523	655	0.80	4.25	0.78
NFBT 1	O	18.4	8.9	3.1	2.5	3.3	68	3.1	690	758	0.91	0.76	11.16
NFBT 2	O	2.3	21.9	8.8	6.1	3.0	176	3.6	810	986	0.82	0.92	1.62
NFBT 3	O	11.5	20.2	5.0	3.1	5.0	166	3.8	845	1011	0.84	1.86	1.03
NSV 1	O	39.0	26.8	10.8	21.4	24.5	1767	9.7	2178	3945	0.55	1.28	1.34
NSV 2	O	23.0	3.9	0.9	3.2	5.5	34	1.0	216	249	0.87	n/a	n/a
Ouzel 1	O	27.5	7.0	2.1	21.0	21.6	297	5.8	1303	1600	0.81	n/a	7.43
Ouzel 2	O	23.0	3.9	0.8	20.0	17.2	91	4.9	1098	1189	0.92	n/a	4.32
JW 1	O	32.1	15.0	4.2	3.5	2.7	77	2.0	443	520	0.85	2.06	10.14
NFJW 1	O	36.7	17.0	9.3	5.8	6.6	408	1.8	398	806	0.49	7.13	6.54
Average		29.8	15.1	5.3	8.4		366	3.3	745	1111	0.72	2.25	3.87

^aForest type: A is altered, D is disturbed, O is old-growth.

^bBasal area of adjacent riparian forest.

^cSediment surface area.

^dSediment volume.

^ePercent volatile carbon in sediment (measured through loss on ignition); first column only material <2 mm in diameter; second column all material collected.

^fMass of carbon in sediment (assuming bulk sediment density of 1330 kg/m³).

^gVolume of wood in the jam.

^hMass of total carbon in wood (assuming 450 kg/m³).

ⁱTotal carbon within a jam in the form of wood and organic matter in sediment.

^jProportion of total carbon as wood.

^kPercent volatile carbon in sediment downstream from jam.

^lPercent volatile carbon in sediment upstream from jam.

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*). Such outbreaks recur every few decades throughout the Colorado Rocky Mountains [Romme *et al.*, 2006]. The instream wood surveyed for this study was not affected by the most recent infestation because riparian trees are less susceptible than upland trees and beetle-infested trees were still standing during the summers of 2010 and 2011 and retaining their needles and so did not contribute to the instream loads of wood or POM.

3. Methods

3.1. Field Methods

We collected data on 30 distinct channel-spanning logjams distributed across 13 different drainage basins: 15 jams in old-growth forest, 10 jams in altered forest, and 5 jams in disturbed forest (Table 1). All study sites were on the eastern side of the continental divide to minimize intersite differences in regional factors such as precipitation and lithology. Jams were chosen to: be accessible by foot while carrying a laser

theodolite; span the channel and include fine sediment storage upstream; and represent the range of riparian forest ages and disturbance histories present in the region.

Once a jam was selected, we recorded latitude, longitude, and elevation using an eTrex H handheld GPS with $\sim \pm 3$ m horizontal accuracy and varying vertical accuracy. These points were used to find drainage area and stream order for each jam using the U.S. Geological Survey online program StreamStats [Ries *et al.*, 2008], which calculates basin parameters using 10 m DEMs. We characterized lateral valley confinement, based on the ratio of active channel width W_c to valley-bottom width W_v , as being unconfined ($W_v > 8X W_c$, or W_v greater than eight times W_c), partly confined ($W_v 2-8X W_c$; commonly a scenario where the channel is close to the valley wall on one side, but a floodplain and riparian forest are present on the other side of the channel), or confined ($W_v \leq 2X W_c$) [Wohl *et al.*, 2012]. This resulted in three valley-type categories for the statistical analyses.

We recorded length, diameter, piece type (bridge, left ramp, right ramp, pinned by other wood, buried in the streambed, or unattached), and decay category using a seven part system modified from Hyatt and Naiman [2001] for all logs in each jam larger than 10 cm diameter and 1 m length. These data provide a minimum volume of wood in the jam, because wood particles under 10 cm/1 m were only counted if they were included in a sediment sample, and large jams might include pieces not visible from the surface because they were hidden under other logs or partially buried in streambed sediment.

We characterized the forest cover around each jam by measuring basal area using a handheld Panama Angle Gauge sampler [Avery and Burkhardt, 2002], noting total trees and standing dead trees. The forest in a given drainage basin is commonly a spatial mosaic of differently aged stands due to local stand-replacing events such as fire or blow down. We determined stand age for each reach based on the years since germination for the majority of trees. As noted earlier, forests in the study area can have a variety of different types of disturbance. We focused on time since the last stand-killing disturbance, as this correlates with average diameter and spatial density of trees in the stand [Aplet *et al.*, 1989].

Stand age at some study reaches was based on research by Sibold *et al.* [2006] south of the Big Thompson River in Rocky Mountain National Park. For areas not mapped in the Sibold study, we collected tree core samples to estimate stand age. In order to get a measure of current stand age, cores were taken from live trees. We also took cores from dead trees at two sites where the standing dead trees were obviously much older than the live trees, and appeared to be the major source of instream wood. Cores were taken from spruce trees when they were present, because spruce/fir is the late successional species composition for this area and previous studies have found that spruce trees are commonly the oldest in a stand [Veblen, 1986; Roovers and Rebertus, 1993]. When spruce was not present, we cored pine and aspen trees. When possible, core samples were taken by angling the increment borer down in order to intercept the tree pith at ground level. If this was not feasible, samples were taken as low on the tree as possible. No correction has been made to account for the height at which the sample was taken because potential errors in tree age introduced in this manner fall within the acceptable range of variation in measurements.

The study sites are on relatively small channels (channel width averages 6.8 m and drainage area averages 21.6 km²). Consequently, we assumed limited long-distance transport capacity for wood [Marcus *et al.*, 2002] and quantified potential control variables such as riparian forest basal area and stand age in the immediate vicinity of the study reach.

We measured water elevation upstream of the jam, through pool and jam, and downstream using the laser theodolite. Upstream and downstream water elevations were taken to a distance of three channel widths. Survey points were also taken to outline the area of fine sediment behind the jam, and the depth of sediment was recorded using a 1.5 cm diameter metal rod pounded into the sediment using a hand sledge until refusal [Lisle and Hilton, 1992]. Locations at which we measured fine sediment depth formed a grid over the area of fine sediment upstream from a jam, at an approximate spacing of 0.3–0.5 m.

We collected at least three samples of fine sediment (sand size or smaller) trapped by each jam, as well as comparison samples from areas of fine sediment not associated with a jam (if any were available). Comparison sites storing fine sediments included deposits in areas of flow separation behind boulders, in channel margins, and along bars. Comparison samples were not taken in areas of flow separation created by

instream wood. If no fine sediment was found stored in the channel not associated with instream wood, then no samples were taken and a note was made.

We collected samples from the top layer of fine sediment using a sieve with a jelly bag over it. Samples included any POM that had settled on the surface. This method consistently retained all particles sand sized and finer. We air dried samples in an enclosed, ventilated space, processed them using loss on ignition techniques [Heiri *et al.*, 2001], and recorded total air-dry sample weight. We passed dried samples through an ASTM 2 mm sieve and divided particles larger than 2 mm into organic and nonorganic portions. We assumed the organic fraction >2 mm (small wood, pine needles, and pine cones) was 50% carbon by mass [Lamlom and Savidge, 2003]. We mixed the fraction <2 mm and placed three 10–15 g subsamples in pre-weighed ceramic tins in a muffle furnace set for 550°C for 24 h, then reweighed the subsamples to calculate the fraction of total volatile carbon in the sample by mass (% C).

3.2. Data Analysis

We examined riverine carbon storage by quantitatively comparing (i) percent of total volatile carbon by mass (% C) in fine sediment between jam and nonjam storage sites, (ii) volume of sediment stored at individual jams, (iii) total carbon stored in sediment (combining % C and volume) at individual jams, and (iv) carbon stored in sediment versus in carbon stored in wood within a jam. For each comparison, we statistically examined relations between the potential control variables of basin (the 30 jams were distributed across three different drainage basins, so we evaluated whether individual basins differed consistently from one another), forest type, valley type, jam size (number of pieces in the jam, and total volume of wood in the jam), and water surface elevation drop and slope through the jam, and the potential response variables of % C in fine sediment, volume of fine sediment, and carbon in sediment versus wood.

Data were statistically analyzed using analysis of variance (ANOVA) and backward step selection of variables through linear modeling. ANOVA assumes that the input variables are normally or near-normally distributed, which we tested using a Shapiro-Wilk test for normality [Royston, 1995]. In order to meet this assumption, we transformed right skewed variables using the natural log function. Natural log transformations were used with the % C and total carbon in jams. We tested equality of variance for ANOVA using a Bartlett test.

For the linear modeling backward step selections, we transformed right skewed variables using the natural log function. A natural log transform was applied to the percent C in a sample, stored sediment volume, wood volume, and number of pieces in a jam. Percent C in sediment, volume of stored sediment, sediment surface area, total volume of C in sediment, volume of wood, and total carbon (wood and sediment) were used as response variables. We evaluated models based on their ability to explain the variation (R^2) in the response variable.

4. Results

We used two data sets for these analyses: the “all sample” data set consists of individual sediment samples taken either behind jams or as nonjam comparisons. Each sediment sample taken is treated as an independent observation of the proportion of carbon in sediment. A second data set of jam characteristics groups samples by individual jams, because only one measurement of variables such as riparian forest basal area, sediment volume, and water surface elevation drop is available for each jam surveyed. We averaged all of the samples from the sediment wedge behind a particular jam to provide a single estimate of the carbon content for the jam. If comparison samples were taken upstream or downstream of the jam, they were included as a separate variable for that particular jam. Table 1 shows a summary of the variables for the jam characteristics data set. Percent C was natural log transformed in both data sets before analysis to reduce right skew.

4.1. Percent C in Sediment

ANOVA analysis on all of the jam and nonjam sediment samples indicates no significant difference in the fraction of volatile carbon, indicating that jam sediments do not have a significantly higher proportion of carbon per unit volume than other areas of fine sediment storage within the channel. When samples are compared based on their longitudinal position (Table 1), a significant difference appears between nonjam sediment sampled downstream of a jam and jam sediment, but there is no significant difference between

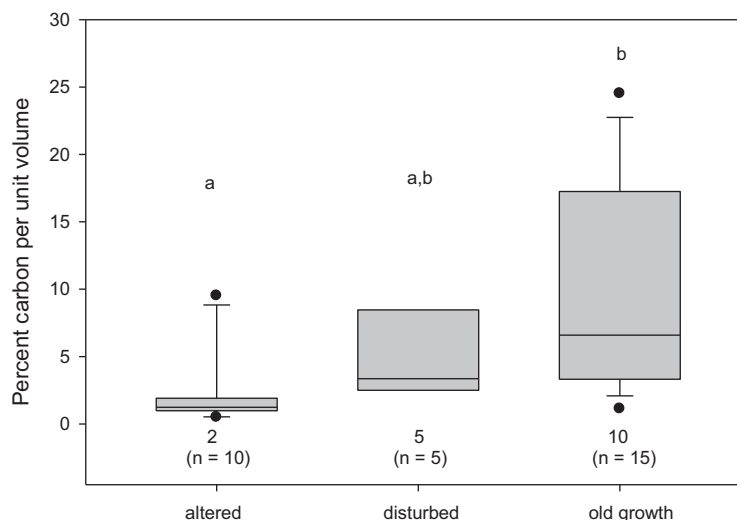


Figure 2. Box plot illustrating results of ANOVA comparing the log-transformed percent carbon (C) in sediment per unit volume within streams and comparing all samples based on forest history. Tukey's HSD indicates that there are significant differences between samples on old-growth and altered reaches, but not between old-growth and disturbed reaches or between disturbed and altered 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. Letters above the boxes indicate statistically significant groupings. Average value and sample size are listed below each box.

upstream samples and either downstream or jam samples. ANOVA analyses of differences between jam and nonjam samples in each basin indicate no significant differences in the proportion of C in sediment within basins and few significant differences between basins.

In addition to ANOVAs, we constructed a backward step linear model with transformed C content per unit volume of the sediment as the response variable. Variables included for selection were basin, stand age, valley type, water surface elevation (WSEL) drop through the jam, WSEL slope through the jam at low flow, and natural log transformed variables proportion of C per unit volume in samples taken upstream and downstream of the jams, number of pieces in the jam, volume of sediment stored behind the jam, and volume of wood in the jam. After backward step selection, stand age and log transformed volume of wood in the jam were the most significant variables, explaining ~53% of the variation in C content with a p value of 0.01 and 0.001, respectively (supporting information Table 1).

These results indicate that jams do not store proportionally more C per unit volume of sediment than other areas of fine sediment in the channel. The C content in jam sediment is not significantly different than either the sediment in nonjam sites or the sediment upstream. The only significant difference is between the proportion of C in jam sediment and the sediment stored immediately downstream of jams.

Variation in C content per unit volume between jams is explained by forest type and wood volume in jam. Forest type likely influences the background C content of sediment in the reach, based on results which show old-growth samples have a significantly different C content per unit volume than altered reaches, and that across all samples old growth has the most C content per unit volume, followed by disturbed and then altered reaches (Figure 2).

4.2. Sediment Volume

Regardless of the C content per unit volume of the sediment, the total amount of sediment C stored by jams could be significant because of the large volume of sediment that jams retain. We considered jam size and the effect of the jam on the water surface to be the factors most likely to influence the volume of stored sediment, but bivariate plots of the volume of wood in jam, local WSEL slope through the jam, WSEL drop at the jam, and the number of pieces in the jam showed no correlation.

To test the effect of multiple variables on stored sediment volume, we performed a backward step selection for a linear model with log-transformed volume of sediment as the response variable. Variables included for selection were basin, stand age, valley type, WSEL drop through jam, local WSEL slope at jam, and log-

Table 2. First-Order Estimate of Instream Carbon Loads^a

Reach Name	Estimated Total Carbon Load (kg/km Stream Length)	Estimated Total Carbon Load (Mg/ha Stream Surface Area)
Middle Ouzel	152,000	151
NSV3	43,000	34
Boulder Brook	1000	5
Mill Creek	10,000	26
Hague Creek	1000	1
Bennet Creek	13,000	9
Cow Creek	1000	7
<i>Upper Hunters</i>	<i>36,000</i>	<i>62</i>
<i>Middle Cony</i>	<i>84,000</i>	<i>97</i>
<i>Joe Wright Creek</i>	<i>6000</i>	<i>9</i>
<i>Black Canyon Creek</i>	<i>10,000</i>	<i>75</i>
<i>NFWJ</i>	<i>7000</i>	<i>16</i>
<i>NFBT1</i>	<i>33,000</i>	<i>65</i>

^aItalicized rows indicate old-growth reaches (stand age >200 years). The two bold rows (Middle Ouzel and NSV3) indicate disturbed reaches, where the stand age is <200 years due to natural events and no logging occurred. These numbers are assumed to be overestimates because jams counted at the reach level did not have to be channel spanning or retain fine sediment. The Middle Ouzel reach is probably experiencing peak wood loads following a fire in 1978.

transformed variables wood volume, and number of pieces within the jam. Of these, only WSEL slope was significant (and explained 13% of the variation), although a forward step selection model containing WSEL drop and WSEL slope explained 20% of the variation.

Bilby and Ward [1989] found that sediment wedge surface area correlates well with local slope, so we ran a second model using log-transformed sediment wedge surface area as the response variable, and the same explanatory variables. WSEL slope and WSEL drop through the jam were significant, and explained approximately 35% of the variation. Because we calculated sediment wedge volume as

the product of surface area and average depth of sediment, it is likely that the previous linear models identified the effects of WSEL slope and drop on surface area, and did not explain the variation in sediment depth.

In summary, the sediment volume stored behind jams is not well correlated with forest type or jam characteristics. No variable or combination of variables tested here explained a substantial amount of the variation in sediment storage between jams, although a combination of local WSEL slope and WSEL drop through the jam explains roughly a third of the variation in the area of fine sediment deposition.

4.3. Total Carbon Stored in Sediment (% C and Volume)

Although it is difficult to predict the volume of sediment stored behind a jam, it may still be possible to find explanatory factors for the total amount of C stored within the sediment behind a jam. We estimated the total volume of C stored in the sediment behind a jam by multiplying the percent C by the volume of sediment. Bivariate plots indicate that there is no relationship between the amount of stored sediment and the carbon content. We ran a backward step linear model starting with the variables basin, stand age, valley type, WSEL slope, WSEL drop through the jam, and the log transformed variables nonjam C, sediment surface area, wood volume in the jam, and number of pieces in the jam. Of these, forest type and log-transformed wood volume in the jam were both significant, and accounted for 43% of the variation (supporting information Table 2). Figure 3 shows the log-linear relationship between the volume of C stored by a jam and jam size (as measured by the volume of wood in a jam), and how that relationship changes in old-growth and disturbed reaches. There is no significant relationship for altered reaches, meaning that volume of C storage does not change with jam size. However, Figure 3 indicates that volume of C storage increases with jam size in old-growth and disturbed reaches, and that old growth generally has greater total C stored as sediment than disturbed or altered reaches.

In summary, forest type and wood volume within a jam together explain 43% of the variation of total organic carbon stored in sediment, with clear differences between the altered, disturbed, and old-growth forest types. The volume of C stored behind a jam correlates with the volume of wood in a jam in old-growth and disturbed areas, but there is no clear relationship in altered forests.

4.4. Carbon Stored as Wood Versus Carbon Stored in Sediment

Particulate organic matter stored in sediment is commonly mobile material such as pine needles, pine cones, and other fine organic debris. Instream wood can also be considered a reservoir of carbon within the stream channel, and is typically less mobile. For old-growth streams, increasing stand age correlates with increased volume of wood in jams, although this relationship does not appear to hold true for altered or

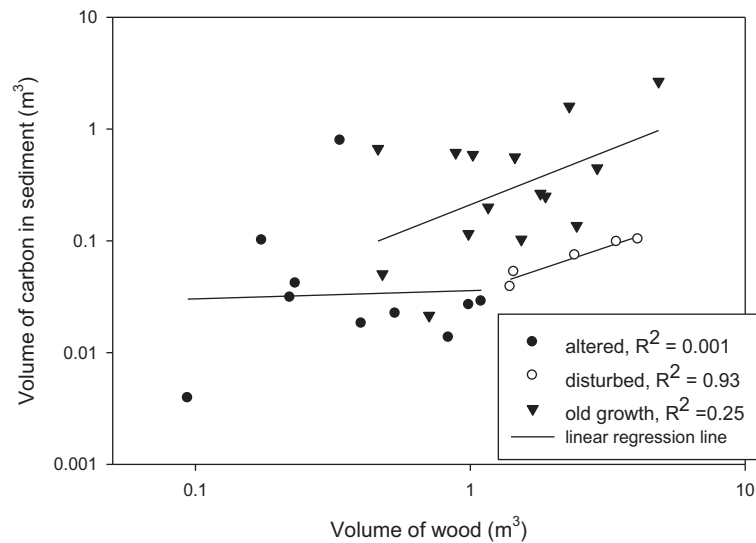


Figure 3. Volume of C in the sediment versus volume of wood in the jam, showing a significant relationship for jams in old-growth and disturbed forests, but no relationship for jams in altered (logged) forests.

disturbed reaches (Figure 4). An ANOVA comparing the volume of wood in a jam based on forest type indicates that altered stands are significantly different than disturbed or old-growth stands (Figure 5). If the amount of carbon stored as wood is larger than the amount stored as sediment, forest type may have a large impact on total carbon storage, especially in naturally fire-disturbed areas with limited C in the sediment, but large amounts of instream wood stored within the channel.

We made a first-order estimate of the total mass of carbon stored as wood by assuming a density of 450 kg/m³ for all pieces [Forest Products Laboratory, 2010] and assuming that approximately 50% of the wood is carbon [Lamlom and Savidge, 2003]. For comparison, we estimated a total mass of carbon stored in the sediment by multiplying the calculated fraction of C per unit volume by the volume of sediment and assuming a bulk density of 1330 kg/m³ for the unconsolidated sediment [Julien, 1998]. Figure 6 shows the resulting estimate of kilograms of total carbon stored within an individual jam, partitioned by source (sediment or wood). In 28 of the 30 jams, and across all forest types, more carbon is stored as wood than as C in sediment. Jams in disturbed reaches have a much larger proportion of carbon stored as wood than either

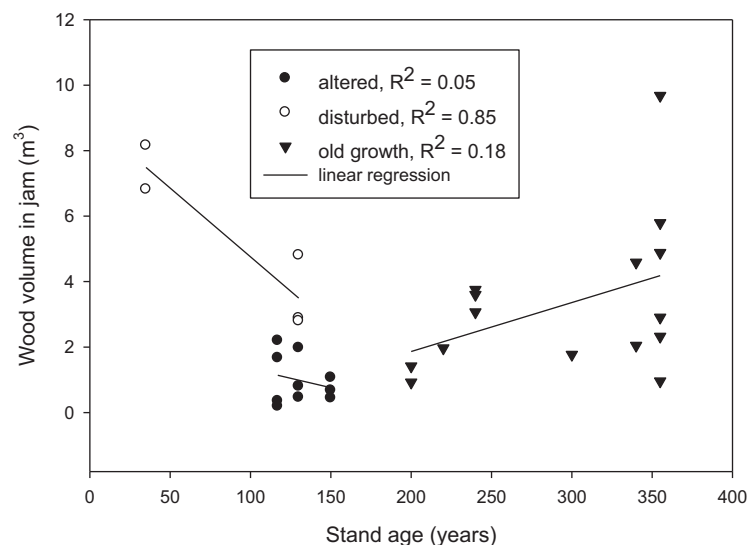


Figure 4. Wood volume in jams versus stand age of adjacent riparian forest.

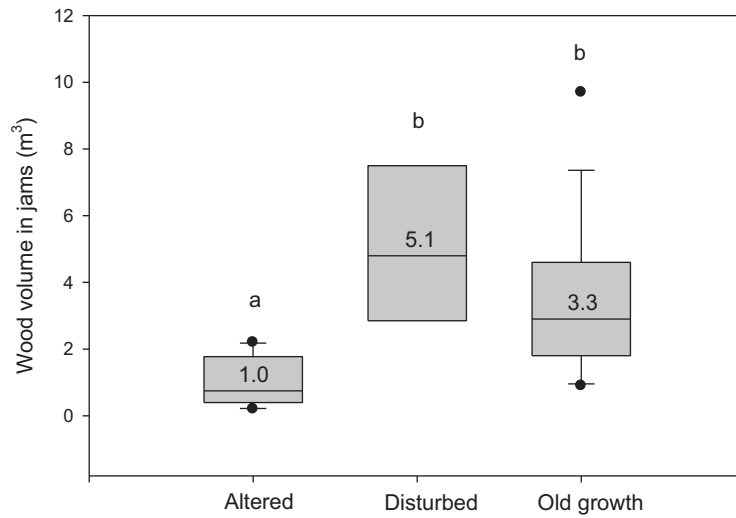


Figure 5. Results of an ANOVA for wood volume in jams by forest type. Tukey's HSD indicates that jams in disturbed and old-growth are not significantly different, but jams in altered reaches are. Average values are listed within each box. The horizontal line within each box indicates the median value, 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. Letters above the boxes indicate statistically significant groupings.

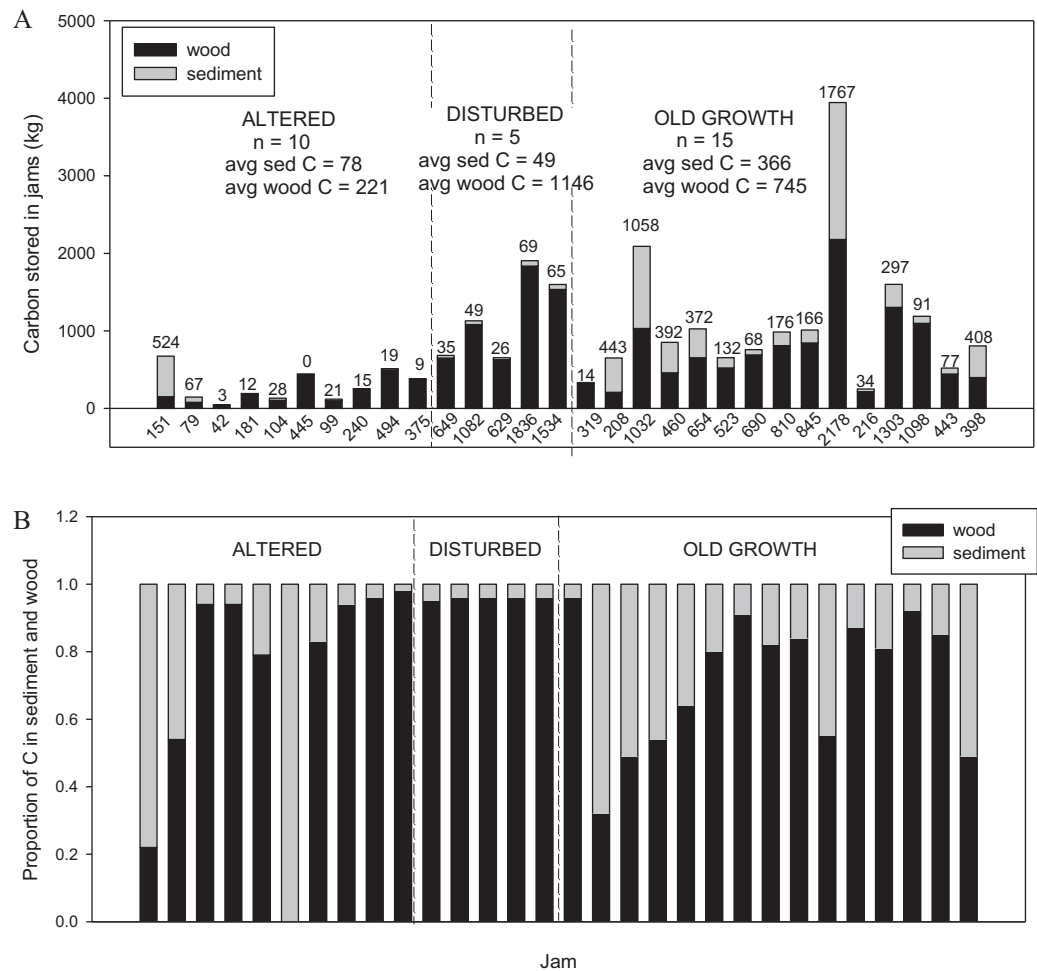


Figure 6. Bar graphs showing kilograms of carbon stored as sediment and wood for the 30 jams surveyed. Each bar represents an individual jam. (a) Total amounts of carbon. Upper number above each bar indicates carbon in sediment and lower number indicates carbon in wood. Inset text indicates sample size (n) and average value for each of the three forest types. (b) Proportion of carbon as sediment or wood for each jam.

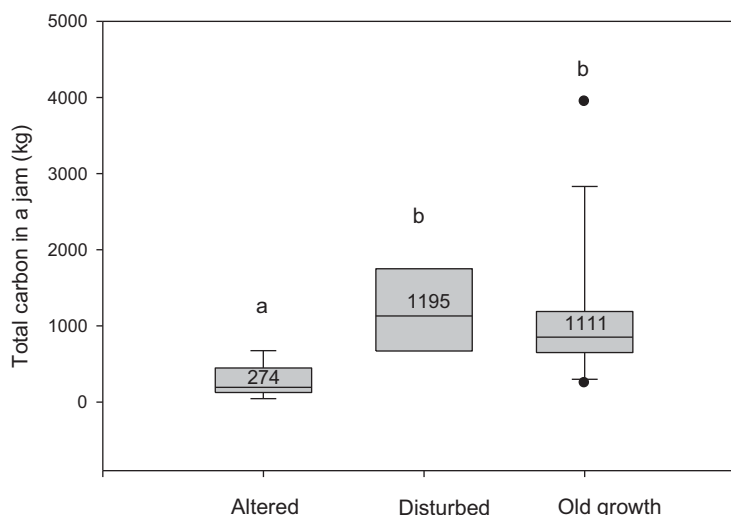


Figure 7. ANOVA of estimated total carbon from sediment and wood with Tukey's HSD. Old-growth and disturbed reaches group together, whereas altered reaches are significantly different. Letters above the boxes indicate statistically significant groupings.

altered or old-growth jams, with an average of 96% carbon as wood (Table 1). Jams in altered reaches average 79% of carbon stored as wood. Old-growth jams store the largest amount of carbon as sediment of the three forest-type categories, but because they also have the largest volume of wood, wood still contributes an average of 72% of the total stored carbon.

As these results show, a majority of the carbon within jams is stored as wood, not as C in sediment, even when the volume of sediment behind a jam is quite large. Wood volume is significantly larger in old-growth and disturbed reaches than in altered reaches. Because the C content and sediment volume are related to the volume of wood in a jam, and wood volume is related to forest type, it follows that the total carbon stored in a jam is related to forest type.

4.5. Predicting Carbon Storage in a Reach

Consideration of the total carbon in a jam, including both sediment and wood, indicates an effect based on the surrounding forest type, with old-growth and disturbed streams significantly different from altered reaches (Figure 7). This result suggests that it may be possible to estimate the relative amount of carbon stored in individual jams based on stand age and disturbance history. We performed a backward step selection to evaluate the ability of basin, forest age, forest type, valley type, and local WSEL slope variables to predict natural log transformed total carbon. We selected these variables because they are the easiest to collect or estimate remotely. The linear model with forest age, valley type and forest type explains 73% of the variation in total carbon stored at an individual jam (supporting information Table 3).

Using the results described here and in a reach-scale survey of instream wood loads and size and downstream spacing of logjams in the same study areas [Beckman and Wohl, 2014], we develop a first-order approximation of the amount of carbon stored by jams within a particular reach. Because wood in jams is a major component of carbon storage, and logjams provide the largest areas of flow separation and fine sediment storage within these steep streams, the carbon stored by jams can be used as an order of magnitude estimate of the total carbon stored within the stream. Figure 8 and Table 2 show the estimated carbon loads (in kg C/km of channel length and Mg C/ha of channel surface area) for 13 sites for which we have both reach-scale (1 km long stream surveys) [Beckman and Wohl, 2014] and individual jam surveys. Altered reaches average 5200 kg C/km, whereas old-growth reaches average more than 5 times that: 29,300 kg C/km. The two disturbed reaches average 97,500 kg C/km of channel, 15 times the average storage of altered reaches. This number is based on only two reaches, however, and is likely skewed by the fact that one of the disturbed reaches burned ~30 years ago and may currently be experiencing peak wood volume in the stream as a result of that fire [Bragg, 2000; Bragg et al., 2000]. Although these numbers represent a rough approximation, and do not include instream carbon storage not associated with logjams, it is clear that natural

Table 3. Published Estimates of Carbon Stored as Dead Biomass in Terrestrial Forest Ecosystems of the Southern Rocky Mountains Compared to Instream Carbon Loads Estimated in This Study^a

Reference	Estimate of Stored Carbon (Mg/ha)		
	Low	Mid	High
Arthur and Fahey [1990] ^b		70	
Ryan and Waring [1992] ^c	61	78	98
Tinker and Knight [2000] ^d	123		180
Binkley et al. [2003] ^e		126.5	
Kueppers et al. [2004] ^f	4.7		54
This study	1	40	151

^aAlthough slightly different methodologies were used for each of the published studies of terrestrial forest ecosystem carbon storage, the resulting values indicate the range of carbon storage in forested mountain ecosystems. Low, mid, and high refer to the ranges provide in the literature. If only one value was given, we considered this a midestimate.

^bColorado old-growth subalpine spruce-fir forest.

^cColorado subalpine lodgepole pine forest of varying age.

^dWyoming lodgepole pine forest of varying age.

^eColorado old-growth spruce-fir forest.

^fColorado old-growth subalpine forest of lodgepole pine, spruce, and fir.

disturbances and human alterations can create order-of-magnitude differences in the amount of instream carbon storage.

In related work, we demonstrate that jam density within a reach is best predicted based on the stand age, channel width, and the downstream spacing of ramp and bridge wood pieces [Beckman and Wohl, 2014]. In this paper, we demonstrate that total carbon in an individual jam in mountainous headwater streams in the Colorado study area is related to forest and valley type. Combined, these results indicate that forest type influences the total amount of carbon stored within a headwater stream reach. First-order estimates show an order of magnitude difference between reaches that have been logged and reaches that have been disturbed by natural events.

5. Discussion

The percentage of C per unit volume in the sediment impounded by a logjam can be explained by forest age (basal area) and volume of wood in the jam. We infer that forest age is important because it influences the background levels of particulate organic matter (and thus C) in the stream: old-growth forests tend to have more biomass [Ryan and Waring, 1992; Luysaert et al., 2008], more large trees close to the stream (larger riparian basal area in Table 1), and therefore, more opportunity for POM to fall into the stream. Engelmann spruce forests in Colorado produce ~170 g/m²/yr of litterfall. This is low for a coniferous forest, but it can be stored for 30 years on the forest floor because of the cold, dry environment [Arthur and Fahey, 1992]. Because large jams can raise water levels and force water onto the floodplain, fallen litter washed into the

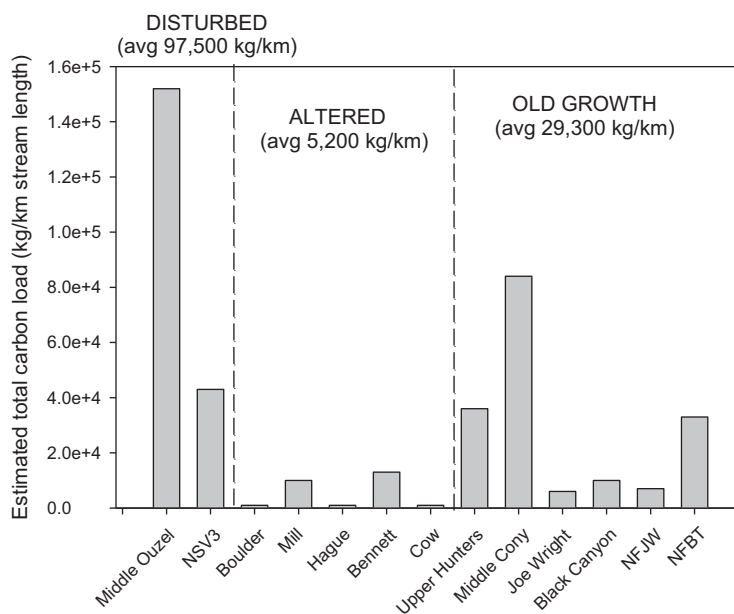


Figure 8. Estimated carbon load (in kg/km of stream) for the stream reaches in which we surveyed both jam density and individual jams. Note that the y axis is not scaled proportionally.

river with returning overbank flow during high flows may be a larger source of POM to the stream than direct litterfall. Both direct litterfall and overland transport of forest litter and duff materials into streams are likely to be greater in old-growth forests, contributing to the higher amount of carbon stored as sediment in logjams within old-growth forest streams.

Wood volume may be an indication not only of the size of the jam, but also the age or permeability of the jam. Larger jams can be more stable and have a longer time in which to trap small pieces that reduce the overall permeability of a jam [Manners *et al.*, 2007], therefore increasing the likelihood that POM will remain within the sediment pool, increasing sediment carbon storage. Because wood volume of jams tends to be greater in old-growth and disturbed reaches than in altered reaches, these stream reaches can store more carbon.

We could not identify variables which can predict the volume of sediment behind a jam, although sediment surface area can be weakly related to WSEL slope and WSEL drop. This indicates that the variables measured can explain the area over which sediment is deposited, but not the depths to which sediment is deposited. Sediment wedge volume could reflect a wide variety of variables that we did not evaluate, including: age of jam, assuming that jams that remain stable for progressively longer periods accumulate greater sediment volumes; porosity and permeability or retentiveness, assuming that jams with lower porosity and permeability more effectively retain sediment upstream; local sources of fine sediment and POM, or cumulative upstream sources of fine sediment and POM; proximity to an upstream jam, assuming that an upstream jam storing large volumes of sediment and POM limits sources of this material for the next jam downstream; site-specific and complex hydraulics within a pool upstream from a jam; and interannual variability in flow, which influences transport of fine sediment and POM, as well as jam retentiveness of these materials. The latter variable is likely to be particularly important: Given that two of our primary sampling seasons (2010 and 2011) coincided with years of above-average peak snowmelt runoff, our measurements of carbon storage may underestimate average values over a period of several years.

Although we could not correlate measured variables with sediment volume, we were able to relate the total carbon stored as sediment to stand age and the volume of wood in the jam, most likely because stand age and wood volume influence the percent of carbon stored in sediments behind a jam. C in sediment increases with stand age and wood volume. Because this carbon is generally in the form of POM, it is a particularly important source of nutrients for aquatic food webs in shaded forest streams [Tank *et al.*, 2010]. The existence of significant differences in total carbon within sediment in relation to stand age and wood volume implies that streams with older and unaltered forests and larger jams can be more biologically productive.

Comparison of the different reservoirs of carbon in a jam indicates that more carbon is stored as wood than as sediment. The overall effect on carbon dynamics in a reach due to large wood is unclear. Carbon stored as large wood is generally less available to stream biota than carbon stored in sediments, but it can be a substrate for biologically active surfaces [Eggert and Wallace, 2007], break down into biologically available FPOM [Ward and Aumen, 1986], increase flow through the bio-active hyporheic zone [Fanelli and Lautz, 2008; Sawyer *et al.*, 2012], and create channel habitat diversity [Keller and Swanson, 1979; Montgomery and Piegay, 2003], all of which encourage carbon processing. Larger jams may also encourage higher rates of instream carbon storage, because large wood is more likely to be stored for years to centuries [Guyette *et al.*, 2002], rather than the hours to years over which fine sediment and POM are stored [Fisher *et al.*, 2010]. Complicating the response is the finding that increasing wood volume also increases C storage in jam sediments. Although our estimated total carbon storage in a reach is only a rough approximation and does not include nonjam carbon storage, it is clear that natural disturbances and human alterations can have order-of-magnitude differences on the amount of instream carbon storage.

Most studies of the interactions of instream wood, biota, and carbon come from small streams in the eastern United States. Numerous studies have come out of the Hubbard Brook Experimental Forest in New Hampshire and the Coweeta Hydrologic Laboratory in North Carolina [Hall *et al.*, 2002; Meyer *et al.*, 2007; Warren *et al.*, 2007]. Both systems are dominated by seasonal inputs from deciduous trees, so leaf litter is a major source of carbon to the stream. Work at these and other sites has shown a link between instream wood and carbon retention [Angradi, 1996; Warren *et al.*, 2007], and increased transient storage when small accumulations of instream wood are present [Bilby, 1981; Hall *et al.*, 2002]. Some work has also been done

in the Pacific Northwest relating the contributions of fish to the biogeochemistry of riparian areas [Fausch and Northcote, 1992; Hyatt and Naiman, 2001]. No studies have addressed carbon storage in slightly larger streams in the conifer-dominated Rocky Mountains, or attempted to relate riparian characteristics to instream carbon storage or relate the physical characteristics of logjams to the amount of carbon stored by the jam. Our results support the earlier work and expand it to include larger streams and larger sources of boundary complexity and retentiveness.

Previous studies have also linked forest age and logging history to terrestrial carbon storage [Harmon *et al.*, 1990], identified old-growth forest as an important carbon sink at the global level [Dixon *et al.*, 1994; Turner *et al.*, 1995; Pregitzer and Euskirchen, 2004], and shown that freshwater systems are a key component of carbon processing and transport [Battin *et al.*, 2008, 2009; Aufdenkampe *et al.*, 2011]. The results of this study indicate that old-growth forest influences not only terrestrial carbon pools and overall storage, but also riverine storage, and by implication riverine processing of carbon. Our first-order estimations of reach-scale riverine carbon storage also suggest that the carbon per hectare stored in streams is on the same order of magnitude, although not as large, as the carbon stored as dead biomass in terrestrial subalpine forests of the Southern Rocky Mountains (Table 3).

Among the management implications of these findings are that efforts to protect existing old-growth riparian stands can affect not only terrestrial carbon storage, but also the storage and biogeochemical processing of carbon in riverine environments. Protection of old-growth, or mimicking the effects of old-growth within streams by manipulating the downstream spacing of ramp and bridge key pieces that help to initiate and stabilize jams, can result in enhanced riverine carbon storage in the form of large wood and the particulate organic matter that can be stored in the stream because of the backwater created by a logjam.

6. Conclusions

Because streams play a significant role in the sequestration, transport, and mineralization of organic carbon, knowledge of fluvial processes must be integrated into the traditional conceptualization of the carbon cycle [Battin *et al.*, 2009; Aufdenkampe *et al.*, 2011]. Enhancing our understanding of fluvial influences on carbon dynamics is also vital because the hydrologic cycle is exceptionally sensitive to climate change and water-borne carbon fluxes will respond to climate change [Battin *et al.*, 2009]. More intense storms, for example, may result in greater transport of terrestrial carbon to streams. To date, studies quantifying fluvial sequestration and export of organic carbon have been limited to a few environments and it is not clear how adequately the results from these studies describe catchments with different characteristics of climate, geology, land cover, or fluvial form and process. We also need to identify the hot spots within freshwater networks where carbon processing is concentrated [McClain *et al.*, 2003; Warren *et al.*, 2007; Mulholland, 2012]. These hot spots can be regional (temperate-zone storage versus tropical fluxes), reach-scale (wide segments versus steep, narrow segments), and unit-scale (behind jams versus nonjam sections). Our results suggest that the large, closely spaced, channel-spanning logjams of streams flowing through old-growth, subalpine conifer forest represent concentrated storage of riverine organic carbon in the form of wood and carbon stored in sediments. This unit-scale carbon storage likely also creates hot spots for carbon processing.

Headwaters are increasingly seen as biogeochemical hotspots where the physical conditions allow for enhanced biological processing of nutrients through longer residence time and more contact with biologically active surfaces [Peterson *et al.*, 2001; Hall *et al.*, 2002; McClain *et al.*, 2003; Battin *et al.*, 2008, 2009; Mulholland, 2012]. Hotspots may be collectively more important in carbon processing than reach averages, and may also be more affected by the hydrologic changes expected with climate change [Battin *et al.*, 2009]. Channel-spanning logjams in headwater streams can be particularly effective hotspots that increase the residence time of fine sediment and POM relative to other portions of the stream. We demonstrate that the details of carbon storage associated with these logjams reflect the age and disturbance history of the adjacent riparian forest, and that streams flowing through old-growth forest store greater volumes of carbon as instream particulate organic matter than otherwise similar streams flowing through younger forest.

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