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Carbon pools in stream-riparian corridors: legacy of disturbance along mountain streams of south-eastern Wyoming

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ABSTRACT: Streams and their accompanying riparian environments are intrinsic components of terrestrial carbon cycling. However, they have been understudied in terms of the magnitude of their storage components and the role of disturbance in determining carbon storage capacity. This study presents partial carbon budgets for stream-riparian corridors along six study reaches in mountain headwater streams of southeast Wyoming to evaluate the impact of tie-driving, a historic disturbance legacy, on contemporary carbon storage. Detailed measurements of biomass were collected for in-stream components of carbon including fine and coarse particulate organic matter and in-stream large wood. Biomass was also estimated for riparian components including standing trees (live and dead), regenerating conifers, shrubs and herbaceous vegetation, downed wood, litter, and duff (partially decayed litter). Biomass was converted to carbon for all components and differences in storage were compared between tie-driven and non-driven reaches. Carbon content in riparian soils (to approximately 20 cm) was also measured. Twice the amount of carbon was stored in the riparian areas relative to the streams; most carbon was stored in standing trees (live and dead). While overall carbon storage within the riparian areas and streams were similar between disturbance conditions, the amount of carbon stored in large in-stream wood and downed wood on the floodplain was significantly higher in systems that were not tie-driven. The results of this study indicate that legacies of tie-driving influence carbon storage within the region, while also capturing baseline estimates of carbon storage in the wake of recent bark beetle infestations. Copyright © 2015 John Wiley & Sons, Ltd.

KEYWORDS: carbon budget; in-stream carbon; riparian carbon; disturbance; bark beetle

Introduction

Despite significant progress in revealing the mechanisms that regulate terrestrial carbon (C) cycling (Schimel *et al.*, 2001), streams have only recently been recognized as critical components of terrestrial C budgets (Cole *et al.*, 2007; Battin *et al.*, 2008; Aufdenkampe *et al.*, 2011). Fluvial networks are significant locations for C storage (Wohl *et al.*, 2012; Beckman and Wohl, 2014), processing (Battin *et al.*, 2008) and export (Pawson *et al.*, 2012). Increased efforts exploring terrestrial and aquatic transfers of C coincide with the recognition that human alteration of the environment rivals that of other geomorphic agents (Hooke, 1999). Headwater streams are closely coupled with adjacent riparian and hill slope systems and constitute the majority of total stream length within a network. However, the current understanding of C dynamics in headwater systems is particularly lacking when compared to other aquatic environments (Cole *et al.*, 2007). Given the limited information on the role of streams in terrestrial C cycling, more research is needed to address the implications of human disturbance on contemporary C storage in headwater streams.

While empirical relationships between C storage and stream environments are underdeveloped, feedbacks between the channel and riparian area that may directly influence organic matter (OM) dynamics have been studied from both geomorphic (Wohl and Goode, 2008) and ecological perspectives (Tank *et al.*, 2010). Experimental investigations in headwater stream-riparian corridors, including studies of litter inputs, leaf, and wood removals and/or additions, have shown that in-stream OM dynamics are sensitive to riparian manipulations (e.g. Hall *et al.*, 2000; Eggert *et al.*, 2012). However, OM values are rarely quantified in terms of C so it is unclear exactly how these different pools respond to such alterations.

The forms and processes of stream ecosystems are fundamentally influenced by adjacent riparian zones, particularly through allochthonous OM subsidies (Figure 1; Gregory *et al.*, 1991). The riparian area serves as a source of large wood (LW) to stream channels which influences flow patterns (Gippel, 1995; Daniels and Rhoads, 2004), OM and sediment storage (Thompson, 1995; Daniels, 2006), bedforms (Montgomery *et al.*, 1995), and ecological functions including nutrient cycling and habitat diversity (Bilby and Likens, 1980; Gurnell *et al.*, 1995; Wondzell and Bisson, 2003). Coarse

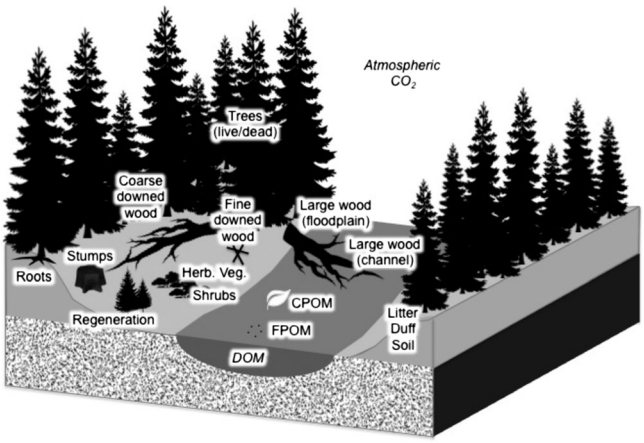

Figure 1. Conceptual diagram of riparian and in-stream carbon pools. herbaceous vegetation (Herb. veg.), coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), and dissolved organic matter (DOM). Pools in italics (DOM and Atmospheric CO2) were not directly measured as part of this study.

downed wood (CDW) is stored on floodplains in the same size class range as in-stream large wood (LW) and has been estimated to account for 10 to 20% of total biomass within forests (Brown, 2002; Wohl *et al.*, 2012), suggesting that both CDW and LW in the stream-riparian corridor represent significant components of C storage. The quantity, quality, and seasonal availability of allochthonous sources of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) to in-stream aquatic communities reflects the characteristics of riparian trees, shrubs, and herbaceous plants (Webster *et al.*, 1999) adjacent to the channel as well as any fine downed wood (FDW) on the riparian floor that could potentially be delivered to the channel. While C has rarely been quantified for standing stocks of CPOM or FPOM, available estimates suggest that this represents a minimal component of overall C storage in channels (Beckman and Wohl, 2014). Biomass of mature and regenerating trees, shrubs, and herbaceous vegetation can be further divided into above- and below-ground components and can vary considerably across space (Freudenberger *et al.*, 2012). Standing tree biomass is a significant component of C storage while vegetation in the understory is relatively minor in many forest types (Turner *et al.*, 1995). As litter accumulates and decomposes into duff on the forest floor, dissolved organic C is leached downward through the soil where it can enter the stream through lateral flow (Wagener *et al.*, 1998). The total C storage in forest floor components is wide-ranging but litter and duff are estimated to comprise an average of approximately 6% of stored C in forests while soils comprise an average of 50% of total stored C in the same ecosystems (Turner *et al.*, 1995). Estimates of dissolved organic matter (DOM) in stream reaches vary widely with respect to flow conditions in response to seasonal runoff (Kaushal and Lewis, 2005) and storm events and the riparian environment, although they are consistently a large component of in-stream C (Dalzell *et al.*, 2007).

Due to the close coupling between stream channels and riparian areas, disturbances have the potential to severely impact C dynamics in both environments. In forested areas, C stocks and fluxes have been radically altered by wildfires (Law *et al.*, 2004). Land-use practices, such as logging and agriculture, have been associated with altered C fluxes at the national scale (Houghton *et al.*, 1999). Although the effects of disturbances on C storage within stream-riparian corridors have not been directly studied, alterations in the storage and processing rates of OM have undoubtedly occurred following events such as logging, wild fires, and windthrow (Stevens and Cummins, 1999; Naiman *et al.*, 2002; Marcus *et al.*, 2011). The historic removal of LW from streams in the Pacific Northwest (Bilby and Ward, 1991) and coastal Maine (Magilligan *et al.*, 2008) to facilitate the passage of timber downstream is an example of an anthropogenic disturbance legacy. These removal activities have altered contemporary regional in-stream wood loads and impacted geomorphic heterogeneity through increased sediment transport, channel widening, and habitat simplification (Czarnomski *et al.*, 2008; Magilligan *et al.*, 2008; Mellina and Hinch, 2009). Ample empirical evidence links riparian and geomorphic mechanisms

Figure 2. Tie driving in the Medicine Bow National Forest, southeast Wyoming. (a) Railroad ties were cut and stored in the riparian area adjacent to the stream channel. (b) Ties were floated downstream following peak flow. (c) Extensive tie jams were a routine event during drives. (d) Ultimately, tie drives accumulated in larger rivers to be delivered to processing centers downstream. Photographs courtesy of the Grand Encampment Museum. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

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with OM dynamics, yet to our knowledge there is no published research that quantifies contemporary C pools in the riparian-stream corridor within the context of a disturbance legacy.

Streams in the Rocky Mountain region have also undergone extensive, historic wood removal known as tie-driving (Figure 2; Wohl 2001, 2006). As the railroads were extended west towards the Rocky Mountains during the mid-1800s, regional streams were the primary method for transporting railroad ties to processing facilities (Sedell *et al.*, 1991). The vast majority of ties were cut from lodgepole pine ranging in size from 28 to 40 cm diameter at breast height (DBH; Anonymous, 1916; Rosenberg, 1984). Harvests occurred across the forest, including riparian areas, and through all seasons. Ties were stacked along stream banks until high flows following snowmelt could transport the load downstream in 'tie-drives'. The magnitude of each tie-drive varied, depending on year and watershed but records indicate that anywhere from 80 000 to as many as 500 000 ties could be driven down one river per year (Rosenberg, 1984). For streams to be made 'drivable', debris jams and boulders were removed and surge dams and feeder flumes were built to increase flow (Anonymous, 1916). The impacts of these tie-drives on regional streams includes simplified stream channels, depauperate wood loads, and altered riparian plant communities (Young *et al.*, 1994; Ruffing *et al.*, 2015), yet it remains unclear how tie-driving has influenced contemporary C storage in stream-riparian corridors (Ruffing *et al.*, 2015). Quantifying C storage is especially pertinent given that this region faces further large-scale alterations in C dynamics due to pervasive tree mortality associated with recent bark beetle infestations (Raffa *et al.*, 2008).

The objective of this investigation was to quantify the C budget of headwater streams to evaluate the impact of historic tie-driving on the distribution and size of C pools and in the riparian-stream corridor. We define the riparian corridor as the terrestrial environment within 25 m of the top of the stream bank during bankfull conditions. This width reflects the approximate height of mature trees and thus captures the potential sources of LW and smaller allochthonous material available to the stream channel. We created a partial OM budget to quantify in-stream and riparian C pools and examine potential differences in C storage between tie-driven and non-driven disturbance regimes. We hypothesized that:

1. Tie-driven streams will have lower amounts of C stored compared to non-driven streams because of the history of wood removal and the decreased storage capacity of the channel.
2. Riparian areas along tie-driven streams will have lower amounts of C storage compared to non-driven streams because of the history of timber harvest and removal.
3. Overall C storage (stream + riparian) will be lower in tie-driven reaches than non-driven reaches because of combined factors related to the legacy of timber harvest and in-stream wood removal.

Study Area and Site Description

The study sites are located in the Sierra Madre and Snowy Ranges of the Medicine Bow National Forest in southern Wyoming (Figure 3). In the Sierra Madre Range, elevations range from approximately 2200 to 3600 m above sea level; in the Snowy Range, elevations range from 2500 to 3640 m above sea level. The underlying geology of the area is primarily Precambrian granite and gneiss with isolated areas of metasedimentary and metavolcanic rocks and glacial deposits (Love and Christiansen, 1985). Both the Snowy Range and Sierra Madre were glaciated during the Pleistocene resulting in numerous till fields, moraines, and lakes throughout the area (Dillon *et al.*, 2005).

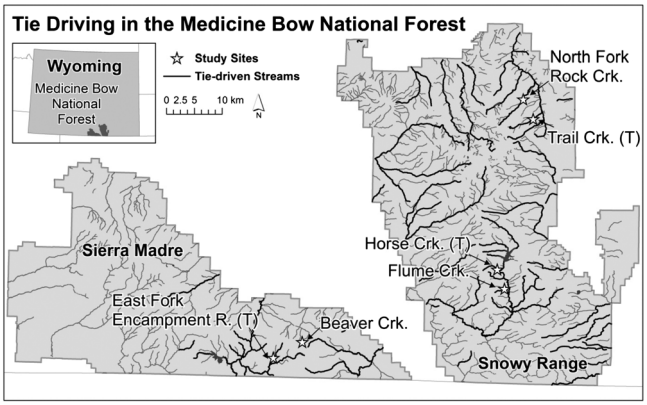

Figure 3. Location of tie-driven streams and study reaches in the Medicine Bow National Forest, southeast Wyoming. Heavy lines indicate all known tie-driven streams. Study reaches that were tie-driven are denoted by (T).

The majority of the region's annual precipitation falls as snow from October until May. Mean annual precipitation increases from approximately 28 cm at lower elevations to 670 cm at the highest elevations. Average annual temperatures decrease with increasing elevation but typically range from a low of −1.31 °C to 11.65 °C. The coldest temperatures occur during January and warmest temperatures typically occur in July (PRISM Climate Group). The flow regime is snowmelt dominated and peak flows usually occur in June. Dominant vegetation types vary by elevation but montane forest conditions prevail over a large portion of both the Sierra Madre and Snowy Ranges. Forests at higher elevations are dominated by lodegepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). The western portion of the Sierra Madre is dominated by aspen (*Populus tremuloides*). Willows (*Salix* spp.), other woody riparian shrubs, and herbaceous species, occur along many riparian reaches, but are dominant in wider valley bottoms with less conifer cover.

Stream channel morphology in the area is consistent with other mountainous regions and includes cascade, step-pool, plane-bed, and pool-riffle channel types (Montgomery and Buffington, 1997). Local controls on morphology include gradient, surficial geology, and large in-channel wood (Wohl and Goode, 2008; Wohl and Merritt, 2008). Also, many low-order streams in the area were glaciated, and streams developed between lateral moraines, resulting in fairly narrow conifer-dominated floodplains. Natural disturbances in the area include flooding, wildfire, mass wasting events, and bark beetle epidemics; anthropogenic disturbances range from historic activities such as removal of beaver, placer mining and tie-driving, to present day activities associated with resource management, development, and recreation (Wohl, 2001, 2006).

Site selection

We adopted a paired-reach sampling design, with each reach pair consisting of one tie-driven reach and one reach with no evidence of tie driving activity (referred to hereafter as "non-driven"). Two pairs (four reaches) were located in the Snowy Range and one pair (two reaches) in the Sierra Madre (Table I; Figure 3). Reach pairs were located in close proximity to control for localized differences in geology, elevation, and riparian vegetation. Reach pairs were chosen so that each shared the following physiographic criteria: stream order, reach slope, valley bottom morphology, and surficial geology.

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Table I. Study reach characteristics. Letters in parenthesis represent reach pairs

Stream (Pair)	Drive	Stream order	Reach length (m)	Basin area (km^2)	Elevation (m)	Gradient ($m\ m^{-1}$)	Average bankfull width (m)
Beaver Creek (A)	Non	1	91.4	2.66	2884	0.06	3.64
East Fork Encampment River (A)	Tie	1	92.3	4.27	2728	0.04	3.34
Flume Creek (B)	Non	1	88.5	3.47	2698	0.02	2.61
Horse Creek (B)	Tie	1	90.25	7.28	2835	0.02	3.05
North Fork Rock Creek (C)	Non	2	208.0	14.24	2948	0.03	7.1
Trail Creek (C)	Tie	2	226	8.26	2991	0.04	6.54

Note: Letters in parenthesis represent reach pairs.

Significant geomorphologic differences associated with tie-driving were identified along these reaches in a previous study (Ruffing *et al.*, 2015). When channel geometry was scaled to contributing watershed area, tie-driven channels were narrower and more shallow, had smaller cross-sectional areas, greater width-to-depth ratios, and lower roughness values compared to non-driven reaches. First-order tie-driven streams had significantly lower wood loads than first order non-driven reaches. Total wood loads in second-order study streams were similar, although most wood in Trail Creek (tie-driven) was found in debris jams while wood in North Fork Rock Creek (non-driven) was evenly distributed throughout the study reach. First-order tie-driven reaches were dominated by riffle and run morphologies while the second-order tie-driven reach had a large proportion of wood-forced pools caused by wood jams (Ruffing *et al.*, 2015).

Methods

We used a combination of stream and terrestrial sampling techniques to calculate the mass and biomass of C pools within the stream-riparian corridor. All components quantified in our budget are defined in Table II. Later, we provide information on field sampling protocols, laboratory procedures, C conversion, and statistical analysis. Specific details on mass and biomass calculations as well as C conversion are also included in Table II.

In-stream C budget components

CPOM and FPOM standing stocks

In-stream OM samples were collected at each study reach in July 2013 following recession of peak flow and therefore represent mid-season standing stocks. Sample collections occurred along seven separate sampling transects (each 1 m wide) extending the width of the channel and positioned perpendicular to flow for each reach. The entire transect was then sampled for OM by dislodging and collecting material by hand or with a D-net (500 μm nylon mesh). Invertebrates and rocks were removed from the collected material and samples were elutriated using nested sieves to separate into CPOM (>1 mm) and FPOM (<1 mm and > 500 μm) size classes. In the laboratory, sorted FPOM samples were filtered through glass fiber filters (particle retention size = 1.6 μm), and both CPOM and FPOM samples were dried at 60 °C. Dried CPOM samples were sub-sampled for elemental analysis before being reweighed, then ashed at 450 °C, and reweighed to determine ash-free dry mass (AFDM). For CPOM samples, percent AFDM was applied to the total mass of the sample. Mass of CPOM and FPOM was averaged by stream area sampled to calculate an estimated value for the reach.

In-stream large wood (LW)

All large in-stream wood occurring within the study reaches was tallied and measured. The total length of each piece of LW and the length of the portion within the channel were measured to estimate storage within the channel (LWC) or on the floodplain (LWF). Diameters were measured at both ends of each piece and volume was calculated separately for LWC and LWF using Equation 1 (Lienkaemper and Swanson, 1987):

$$\text{Volume} = \frac{\pi\left(D1^2 + D2^2\right)L}{8} \tag{1}$$

where D_1 and D_2 are end diameters (in meters) for each piece and L is the piece length (in meters).

Riparian C budget components

Forest canopy and understory

Riparian vegetation (live and dead standing trees, conifer regeneration in the understory, shrubs, herbaceous plants and roots of live plants) was sampled in 0.05-ha circular plots (25.2 m in diameter). The number of plots per reach varied (two to five) depending on reach length, with at least one plot located on each side of the channel. Plot-centers were established to position each riparian plot as close to the adjacent stream as possible, with the streamside plot perimeter along the stream bank edge. Within each plot, species and DBH were recorded on all live and dead trees (diameter classes for trees, saplings, and seedlings are reported in Table II). Evidence of mountain pine beetle (MBP) was recorded for each standing lodgepole pine tree (*Pinus contorta*, live or dead); similarly, spruce beetle (SB) incidence was recorded for each standing Engelmann spruce (*Picea engelmanii*, live or dead). Information recorded on live saplings included species, DBH and estimated height. Within the inner 0.0125-ha of each plot (radius = 6.31 m), live seedlings were tallied by species. Percent cover of shrubs, herbaceous vegetation, and litter was visually estimated for each plot.

Downed wood and riparian floor

All downed wood was tallied within each plot (see Table II for size classes). Length and two end diameters were measured on each piece — or portion of each piece — that occurred within the plot perimeter. The height, basal diameter (above the root swell), and diameter at the cut surface were measured for all stumps located in each plot. Decay status of downed LW pieces and stumps was noted as either sound or rotten. Three transects (12.63 m in length) starting from plot center and extending to the perimeter on randomly selected bearings were established in each plot to sample FDW, litter, and duff. FDW loads were estimated using the planar intercept method for characterizing fuel loads in three size classes (Table II; Brown, 1974). The smallest size class was tallied for the first 6.3 m and the two larger size classes were tallied along the entire transect length (Lutes *et al.*, 2006; Riccardi *et al.*, 2007). Depth of litter and duff was measured every meter along each transect (Lutes *et al.*, 2006). Three to four soil samples were collected to an average depth of 20 cm in each plot using a split-core sampler of known volume.

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Table II. Carbon pools and sampling methods for C pools measured for each reach in this study. Individual pools are defined where appropriate. Factors for converting biomass to carbon estimates varied with component; references are provided when a simple multiplication factor was used

	Defined components	Sampling strategy	Biomass/mass calculation	Carbon conversion
Stream carbon pools				
Fine particulate organic matter (FPOM)	particles ≥ 500 um but <1 mm	Collected along seven transects, each 1 m wide, per reach	Samples were dried, weighed, and ashed to determine ash-free dry mass (AFDM)	Assumed to be equivalent to organic fraction of the sample
Coarse particulate organic matter (CPOM)	particles ≥ 1 mm but < 1 m.	Collected along seven transects, each 1 m wide, per reach	Samples were dried, weighed, and ashed to determine AFDM	Percentage measured using Carlo Erba NA 1500 Analyzer and applied to entire sample
Large wood in channel (LWC)	Wood pieces or portions within the channel ≥ 1 m long and ≥ 10 cm in diameter	All pieces within the reach were inventoried	Volume directly calculated, assumed average density of 400 kg m^{-3}	Multiplication factor = 0.5 (Forest Products Laboratory, 2010)
Large wood on floodplain (LWF)	Wood pieces or portions on the floodplain ≥ 1 m long and ≥ 10 cm in diameter	All pieces within the reach were inventoried	Volume directly calculated, assumed average density of 400 kg m^{-3}	Multiplication factor = 0.5 (Forest Products Laboratory, 2010)
Riparian carbon pools				
Live Trees (≥5 cm diameter at breast height [DBH])	Above-ground biomass	All stems within each plot were inventoried	Biomass calculated from genera specific allometric equations	Multiplaction factor = 0.48(Lamlon and Savidge, 2003)
	Below-ground biomass	Estimated	Estimated to be 20% of AG biomass	Multiplaction factor = 0.48 (Lamlon and Savidge, 2003)
Dead trees (≥5 cm DBH)	Above-ground biomass	All stems within each plot were inventoried	Estimated to be 30% less than biomass calculated from genera specific allometric equations	Multiplaction factor = 0.48(Lamlon and Savidge, 2003)
	Below-ground biomass	Estimated	Estimated to be 20% of above-ground biomass	Multiplaction factor = 0.48(Lamlon and Savidge, 2003)
Coarse downed wood – sound	All pieces > 8.0 cm in diameter	All pieces within each plot were inventoried	Volume directly calculated, assumed average density of 400 kg m^{-3}	Multiplication factor = 0.5 (Forest Products Laboratory, 2010)
Coarse downed wood – rotten	All pieces > 8.0 cm in diameter	All pieces within each plot were inventoried	Volume directly calculated, assumed average density of 300 kg m^{-3}	Multiplication factor = 0.5 (Forest Products Laboratory, 2010)
Stumps	Remnant of harvested trees	All stumps within each plot were inventoried	Volume directly calculated, assumed average density of 400 kg m^{-3}	Multiplication factor = 0.5 (Forest Products Laboratory, 2010)
Fine downed wood	Three piece diameter classes: 0–0.6 cm; 0.6–2.5 cm; and 2.5–8.0 cm	Tallied along three radial transects within each plot		Multiplication factor = 0.5 (Forest Products Laboratory, 2010)
Regenerating conifers	Above-ground live saplings ≥ 2.5 cm to < 5 cm	All stems within each plot were inventoried	Biomass calculated from genera specific allometric equations	Multiplication factor = 0.42–0.52 (Lamlon and Savidge, 2003)
	Below-ground live saplings ≥ 2.5 cm to < 5 cm	Estimated	Estimated to be 20% of above-ground biomass	Multiplication factor = 0.42–0.52 (Lamlon and Savidge, 2003)
	Above-ground live saplings < 2.5 cm	All stems within each plot were inventoried	Regressing dry weights of harvested plants with measured heights	Multiplication factor = 0.42–0.52 (Lamlon and Savidge, 2003)
	Below-ground live saplings < 2.5 cm	Estimated	Estimated to be 20% of above-ground biomass	Multiplication factor = 0.42–0.52 (Lamlon and Savidge, 2003)
	Seedlings	All stems tallied within inner 0.0125-ha of each circular plot were inventoried	Regressing dry weights of harvested plants with measured heights	Multiplication factor = 0.42–0.52 (Lamlon and Savidge, 2003)

(*Continues*)

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Table II. (Continued)

	Defined components	Sampling strategy	Biomass/mass calculation	Carbon conversion
Herbaceous vegetation		Percent areal coverage estimated for each plot	Calculated using allometric equations for dominant species	Multiplication factor = 0.42–0.52 (Turner *et al.*, 2004)
Shrubs		Percent areal coverage estimated for each plot	Calculated using allometric equations for dominant species	Multiplication factor = 0.42–0.52 (Turner *et al.*, 2004)
Soil		Depth measured and 3–4 samples taken randomly within each plot	Samples were taken with a known volume, then dried and weighed to determine mass	Percentage measured using Carlo Erba NA 1500 Analyzer and applied to entire sample
Litter	Accumulated dead plant material	Depth measured every meter along three radial transects within each plot 12 depths per transect; 36 depths per plot	Estimated from volume and density measurements from a previous study	Multiplication factor = 0.48 (Wohl *et al.*, 2012)
Duff	Partially decomposed litter	Depth measured every meter along three radial transects within each plot 12 depths per transect; 36 depths per plot	Estimated from volume and density measurements from a previous study	Multiplication factor = 0.35 (Wohl *et al.*, 2012)

Note: Individual pools are defined where appropriate. Factors for converting biomass to carbon estimates varied with component; references are provided when a simple multiplication factor was used.

Calculation of C pools

We used direct C analysis and previously published conversion factors to convert mass and biomass calculations to C for each pool. For CPOM and soils, we analyzed C content of field-collected subsamples using a Carlo Erba NA 1500 Analyzer (Carlo Erba; Thermo Electron Corp., Milan, Italy). We then applied the resulting percentages of C to sample mass to determine the amount of C stored in CPOM and soils. Because the size of the FPOM samples was too small to subsample, the C content was estimated to be equivalent to the organic fraction of the sample.

Published values for biomass and C content of terrestrial plants are readily available (Cairns *et al.*, 1997; Jenkins *et al.*, 2003; Turner *et al.*, 2004; Wohl *et al.*, 2012). We selected the published values that were most appropriate for the vegetation components sampled and were conservative in applying them (Table II). For stumps and downed wood in the riparian area and the channel, we assumed a density of 400 kg m^{-3} for sound pieces and 300 kg m^{-3} for rotten pieces (Forest Products Laboratory, 2010). We considered all in-stream wood to be sound since decay times are slower in the stream environment compared to the floodplain. Volumes from the in-stream and riparian wood surveys were multiplied by the appropriate density to calculate biomass. Biomass calculations of above-ground vegetation were supplemented with estimates of below-ground biomass based on previously published data in similar biomes (Cairns *et al.*, 1997). Biomass of all wood was converted to C content using a multiplication factor of 0.5 (Forest Products Laboratory, 2010).

Relationships between depth and weight for a known volume of litter and duff were determined in a previous study (Wohl *et al.*, 2012) and used here to estimate litter and duff volume. Resulting volume estimates were then converted to C content using multiplication factors of 0.48 for litter and 0.35 for duff, also determined previously (Wohl *et al.*, 2012).

Data analysis

In-stream C pools included LWC, LWF, CPOM, and FPOM and riparian C pools included both live and dead trees, sound and rotten CDW, stumps, FDW, regenerating conifers, herbaceous vegetation, shrubs, soil, litter and duff. Carbon values for above-ground (AG) and below-ground (BG) biomass of trees, saplings, shrubs, and herbaceous vegetation were summed to estimate total plant biomass C. Estimates of C for both size classes of saplings were combined with estimates for seedlings to generate one component reflecting regenerating conifers.

Estimates of total C storage were standardized by area (in Mg/ha) and then averaged across sampling transects for stream pools and sampling plots for riparian pools. Independent *t*-tests were then used to evaluate differences in tie-driving on total C storage between sites. Normality was assessed using the Shapiro–Wilk test and homogeneity of variance was assessed using Levene's test. Variables that did not meet assumptions of normality were compared using the Mann–Whitney Rank Sum Test. All statistical analyses were performed in RStudio (v 0.98.987; R Development Core Team, 2012) using the Vegan package (Oksanen *et al.*, 2013).

Results

We sampled C pools in stream channels and associated riparian areas at six sites (n = 6; Table I). Four reaches were located along first-order streams and two were located along second-

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order streams. The length of each reach was approximately 30 times average stream width to represent the valley and channel morphology. Calculated values of biomass and subsequent conversion to C were scaled to units of mass per hectare then averaged to determine average total C storage for each component at each site (Table III).

In-stream C components

Relative to C stored in other in-stream components, FPOM and CPOM represented minimal amounts of overall total C storage (Table III). Averages of the organic fraction of FPOM samples ranged from 33% to 57% of dry mass (in non-driven Flume and tie-driven Trail Creeks, respectively). Averages of total C for CPOM ranged from 37% to 49% in Beaver and North Fork Rock Creek (both non-driven), respectively. The quantity of C contained in CPOM was highest in non-driven Flume Creek and lowest in both North Fork Rock Creek (non-driven) and Horse Creek (tie-driven). Although values of C for CPOM samples were greater for non-driven sites (Figure 4A), total C did not differ between disturbance conditions (Table IV). Estimated C contained in FPOM was highest in non-driven North Fork Rock Creek and lowest in non-driven Beaver Creek (Table III), and averages of total C for this compartment were similar across disturbance conditions (Figure 4B; Table IV).

LW dominated calculated C storage for in-stream pools. Horse Creek (tie-driven) had only two pieces of LW in the reach and therefore had the lowest amount of C stored as LW. Beaver Creek (non-driven) had the largest amount of C (Table III). On average, 60% of C stored in-stream is contained in the portion of LW on the floodplain (LWF) while 40% is stored within portions contained within the channel (LWC). Tie-driven reaches had slightly lower values of C attributed to LW (LWC + LWF) (Figures 4C and 4D), although total C was not statistically significant (Table IV).

Riparian C components

Live and dead trees

Species distributions and stand characteristics reflect legacies of tie-driving in the region. Lodgepole pine, used almost exclusively for railroad ties, was the dominant species in tie-driven plots whereas subalpine fir and Engelmann spruce were more dominant in the non-driven riparian plots (Figure 5). The basal area at Beaver Creek (non-driven), was dominated by subalpine fir with approximately 52% of the trees sampled (live and dead). Tie-driven reaches have a larger proportion of mature (DBH > 25 cm) lodgepole pine trees than non-driven reaches (Figure 6).

Stored C in live trees was greatest in North Fork Rock Creek while C stored in dead trees was greatest in Beaver Creek, both non-driven streams (Table III). Horse Creek (tie-driven) had the lowest values of C stored in trees (live and dead). The measured above-ground biomass of dead trees exceeded that of living trees in all reaches except North Fork Rock and Trail Creeks (Table III). Despite the similarities in C stored in standing dead trees, it is worth noting that the distributions of standing dead trees reflect dominant species at each site. Most dead trees along tie-driven streams were lodgepole pine, while subalpine fir and Engelmann spruce comprised the majority of dead trees along non-driven reaches (Figure 5). Plot totals of C stored in live and dead tree biomass (Figure 7) were not significantly different between disturbance conditions (Table IV).

Understory vegetation

Understory vegetation components, including regenerating conifers, shrubs, and herbaceous cover contributed relatively little to plot-level C storage compared to trees and large downed wood. Storage of C in shrubs and herbaceous vegetation was relatively consistent across sites (Figure 8). Flume Creek (non-driven) had the greatest stored C for regenerating conifers (stems < 5 cm DBH) while Beaver Creek (non-driven) had the lowest (Table III). No significant differences were found in C pools for shrubs, herbaceous cover, or regenerating conifers between disturbance conditions (Table IV).

Downed wood and stumps

CDW and FDW comprised the second largest component of biomass within the sampled riparian areas. Stored C in rotten CDW and FDW was highest in Flume Creek (non-driven) while North Fork Rock Creek (non-driven) had the largest amount of C in sound CDW (Table III). Stumps were a relatively large component of C in East Fork Encampment River (tie-driven), but overall were relatively minor for other study reaches (Table III). There were no stumps in the riparian plots for Beaver (non-driven) or Horse Creeks (tie-driven), although stumps were observed near the Horse Creek study reach.

The distribution of C in sampled sound and rotten CDW was similar across reaches (Figures 9A and 9B). Total average C storage of rotten CDW and FDW was significantly greater in non-driven riparian reaches compared to tie-driven reaches ($P = 0.0107$, $t = 3.671$ and $P = 0.0208$, $t = 2.958$; Table IV). Sound CDW was slightly higher in non-driven reaches although not significantly different. Stumps were the only component of C storage representing woody vegetation where quantities were highest in tie-driven reaches (Figure 9D) although differences in total C for this compartment were not significant (Table IV).

Forest floor and soil

Average litter layer depth ranged from 0.5 cm along non-driven Flume Creek (non-driven) to 2.2 cm along tie-driven East Fork Encampment River (tie-driven). While average litter depth was slightly greater in tie-driven plots (Figure 10A), differences for total C stored in litter were not significant (Table IV). The average depth of the duff layer ranged from 0.5 cm along tie-driven Horse Creek to 3.8 cm along tie-driven East Fork Encampment River. Carbon stored in duff was similar between disturbance conditions (Figure 10B). In soils, the measured percentage of C was low, despite relatively large values for mass (Table III). Although C content of soils in non-driven streams was higher (Figure 10C), there were no significant differences in total C stored in soil between disturbance conditions (Table IV).

Total C in stream-riparian corridors

Overall, C stored in the stream-riparian corridors of the study reaches is characterized by many small pools and a few large pools. FPOM, CPOM, understory vegetation, stumps, litter, duff, and soil account for approximately 5% of total stored C in both non-driven and tie-driven sites (Figure 11). Carbon stored in soils is the largest of these pools at 3.5% of C in the entire stream-riparian corridor.

Live and dead trees, large in-stream wood, and downed wood in the riparian area account for 95% of the total C stored within the stream-riparian corridor (Figure 12). The largest of these pools is C stored in dead tree biomass (above-ground + below-ground) followed by that stored in live tree biomass (above-ground + below-ground; Figure 13). Approximately 99% of in-stream C was contained in LWC and LWF for all study streams (Figure 12). Downed wood, the third largest pool

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Table III. Measured carbon pools for in-stream and riparian components of study reaches. Data are means and standard error for 3 tie-driven and 3 non-tie driven reaches. Reach values are organized by disturbance condition (non-driven or tie-driven) and reach corresponding pairs are denoted with letters (A, B, or C). Both LWC and LWF values for Horse Creek are raw data values because of the low sample size

		Non-driven			Tie-driven		
		Beaver Creek (A)	Flume Creek (B)	North Fork Rock Creek (C)	East Fork Encampment River (A)	Horse Creek (B)	Trail Creek (C)
Stream components							
Fine particulate organic matter (FPOM)	Biomass (kg ha^{-1})	0.11 ± 0.003	0.35 ± 0.013	0.33 ± 0.034	0.32 ± 0.008	0.15 ± 0.007	0.08 ± 0.002
	C Content (kg ha^{-1})	0.04 ± 0.001	0.12 ± 0.004	0.28 ± 0.035	0.15 ± 0.003	0.05 ± 0.002	0.05 ± 0.001
Coarse particulate organic matter (CPOM)	Biomass (Mg ha^{-1})	0.06 ± 0.005	0.14 ± 0.007	0.006 ± 0.000	0.02 ± 0.001	0.008 ± 0.000	0.022 ± 0.002
	C Content (Mg ha^{-1})	0.02 ± 0.002	0.07 ± 0.003	0.003 ± 0.000	0.008 ± 0.000	0.003 ± 0.000	0.011 ± 0.001
Large wood in channel (LWC)	Biomass (Mg ha^{-1})	94.64 ± 0.66	29.32 ± 0.32	15.36 ± 0.07	27.35 ± 0.96	1.11 ± 0.25	19.22 ± 0.11
	C Content (Mg ha^{-1})	47.32 ± 0.33	14.66 ± 0.16	7.68 ± 0.04	13.67 ± 0.48	0.55 ± 0.12	9.61 ± 0.06
Large wood on floodplain (LWF)	Biomass (Mg ha^{-1})	159.14 ± 2.91	31.12 ± 1.73	23.13 ± 0.18	40.59 ± 20.29	0.42	31.31 ± 0.35
	C Content (Mg ha^{-1})	79.57 ± 1.45	15.56 ± 0.87	11.56 ± 0.09	20.29 ± 1.61	0.21	15.66 ± 0.18
Riparian components							
Live tree biomass – above-ground	Biomass (Mg ha^{-1})	98.67 ± 8.88	53.92 ± 14.88	177.91 ± 29.44	81.20 ± 6.95	44.79 ± 11.04	138.02 ± 24.11
	C Content (Mg ha^{-1})	49.34 ± 4.44	26.96 ± 7.44	88.96 ± 14.72	40.60 ± 3.47	22.39 ± 5.52	69.01 ± 12.06
Live tree biomass – below-ground	Biomass (Mg ha^{-1})	19.73 ± 1.78	10.78 ± 2.98	35.58 ± 5.89	16.24 ± 1.39	8.96 ± 2.21	27.60 ± 4.82
	C Content (Mg ha^{-1})	9.87 ± 0.89	5.39 ± 1.49	17.79 ± 2.94	8.12 ± 0.69	4.48 ± 1.10	13.80 ± 2.41
Dead tree biomass – above-ground	Biomass (Mg ha^{-1})	212.78 ± 76.84	99.33 ± 22.49	84.11 ± 24.16	94.45 ± 20.92	57.25 ± 10.75	128.38 ± 38.96
	C Content (Mg ha^{-1})	106.39 ± 38.42	49.66 ± 11.25	42.05 ± 12.08	47.22 ± 10.46	28.62 ± 5.37	64.19 ± 19.48
Dead tree biomass – below-ground	Biomass (Mg ha^{-1})	42.56 ± 15.37	19.87 ± 4.50	16.82 ± 4.83	18.89 ± 4.18	11.45 ± 2.15	25.68 ± 7.79
	C Content (Mg ha^{-1})	21.28 ± 7.68	0.51 ± 0.42	0.46 ± 0.30	9.44 ± 2.09	5.72 ± 1.07	12.84 ± 3.90
Coarse downed wood – sound	Biomass (Mg ha^{-1})	3.84 ± 0.11	17.64 ± 5.75	39.42 ± 15.00	15.62 ± 9.68	1.91 ± 0.73	13.76 ± 5.10
	C Content (Mg ha^{-1})	1.84 ± 0.06	8.47 ± 2.76	18.92 ± 7.20	7.50 ± 4.65	0.92 ± 0.35	6.60 ± 2.45
Coarse downed wood – rotten	Biomass (Mg ha^{-1})	18.24 ± 3.47	23.96 ± 1.93	14.93 ± 7.01	8.05 ± 4.72	0.63	8.29 ± 1.89
	C Content (Mg ha^{-1})	8.76 ± 1.66	11.50 ± 0.93	7.16 ± 3.37	3.86 ± 2.27	0.3	3.98 ± 0.91
Stumps	Biomass (Mg ha^{-1})	N/A	1.25 ± 0.61	0.59 ± 0.31	8.08	N/A	0.61 ± 0.19
	C Content (Mg ha^{-1})	N/A	0.60 ± 0.21	0.28 ± 0.15	3.89	N/A	0.29 ± 0.09
Fine downed wood	Biomass (Mg ha^{-1})	16.13 ± 2.7	21.98	9.16 ± 4.3	9.72 ± 3.4	1.29	1.66
	C Content (Mg ha^{-1})	8.06 ± 1.3	10.99	4.58 ± 2.1	4.86 ± 1.7	0.65	0.83
Above-ground Regen ≥ 2.5 cm to < 5 cm	Biomass (Mg ha^{-1})	0.02	1.56 ± 0.24	0.09 ± 0.02	0.18	0.43 ± 0.15	0.72 ± 0.46
	C Content (Mg ha^{-1})	0.01	0.78 ± 0.12	0.05 ± 0.01	0.09	0.22 ± 0.07	0.36 ± 0.23
Below-ground Regen ≥ 2.5 cm to < 5 cm	Biomass (Mg ha^{-1})	0.002	0.16 ± 0.02	0.01 ± 0.002	0.02	0.04 ± 0.01	0.07 ± 0.05
	C Content (Mg ha^{-1})	0.001	0.08 ± 0.01	0.005 ± 0.001	0.01	0.02 ± 0.01	0.04 ± 0.02
Above-ground Regen < 2.5 cm	Biomass (Mg ha^{-1})	0.03	0.46 ± 0.09	0.04 ± 0.01	0.08 ± 0.01	0.18 ± 0.08	0.08 ± 0.03
	C Content (Mg ha^{-1})	0.01	0.23 ± 0.04	0.02 ± 0.005	0.04 ± 0.01	0.09 ± 0.04	0.04 ± 0.01
Below-ground Regen < 2.5 cm	Biomass (Mg ha^{-1})	0.009	0.14 ± 0.03	0.01 ± 0.003	0.02 ± 0.003	0.06 ± 0.02	0.02 ± 0.009
	C Content (Mg ha^{-1})	0.004	0.07 ± 0.01	0.006 ± 0.002	0.01 ± 0.001	0.03 ± 0.01	0.01 ± 0.004
Herbaceous vegetation	Biomass (Mg ha^{-1})	0.0004 ± 0.00007	0.002 ± 0.0004	0.002 ± 0.005	0.001 ± 0.0004	0.002 ± 0.0005	0.002 ± 0.0005
	C Content (Mg ha^{-1})	0.0002 ± 0.000003	0.0009 ± 0.0002	0.0008 ± 0.0002	0.0006 ± 0.0004	0.0008 ± 0.0002	0.0007 ± 0.0002

(*Continues*)

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Table III. (Continued)

		Non-driven			Tie-driven		
		Beaver Creek (A)	Flume Creek (B)	North Fork Rock Creek (C)	East Fork Encampment River (A)	Horse Creek (B)	Trail Creek (C)
Shrubs	Biomass (Mg ha^{-1})	0.001 ± 0.0006	0.0009 ± 0.0002	0.002 ± 0.001	0.002	0.0006 ± 0.0001	0.001 ± 0.0009
	C Content (Mg ha^{-1})	0.002 ± 0.0004	0.0004 ± 0.00007	0.0009 ± 0.0005	0.0007	0.0003 ± 0.00009	0.0007 ± 0.0004
Soil	Biomass (Mg ha^{-1})	8.42 ± 1.35	9.11 ± 0.64	6.68 ± 1.29	5.06 ± 0.63	8.67 ± 1.18	13.5 ± 2.47
	C Content (Mg ha^{-1})	0.29 ± 0.09	0.32 ± 0.04	0.28 ± 1.35	0.13 ± 0.02	0.20 ± 0.03	0.17 ± 0.04
Litter	Biomass (Mg ha^{-1})	1.44 ± 0.10	0.86 ± 0.11	1.33 ± 0.13	1.86 ± 0.11	0.98 ± 0.08	1.45 ± 0.34
	C Content (Mg ha^{-1})	0.69 ± 0.05	0.41 ± 0.05	0.64 ± 0.06	0.89 ± 0.05	0.47 ± 0.04	0.7 ± 0.16
Duff	Biomass (Mg ha^{-1})	3.88 ± 0.37	3.42 ± 0.70	1.24 ± 0.37	5.52 ± 0.47	0.79 ± 0.16	1.59 ± 0.62
	C Content (Mg ha^{-1})	1.40 ± 0.13	1.23 ± 0.25	0.45 ± 0.13	1.99 ± 0.17	0.29 ± 0.06	0.57 ± 0.22

Note: Data are means and standard error (SE) for three tie-driven and three non-tie driven reaches. Reach values are organized by disturbance condition (non-driven or tie-driven) and reach corresponding pairs are denoted with letters (A, B, or C). Both LWC and LWF values for Horse Creek are raw data values because of the low sample size.

of C next to trees, was also higher in non-driven reaches compared to tie-driven reaches although the only differences in rotten CDW and FDW were significant (Figure 12). Although there was more C stored in the large pools in non-driven reaches, total C was not significantly different between disturbance conditions (Figure 13, Table IV).

Discussion

Non-driven and tie-driven reaches had similar quantities of C stored in stream-riparian corridors, with the majority of C storage occurring within the riparian area. However, legacies of tie-driving are evident in differences in C storage for rotten large downed wood (LDW) and fine downed wood (FDW). Standing trees represent the largest component of C across all sites. Although differences in total C do not directly reflect tie-driving, variations in species composition suggest some correlation to the activity. The dominance of lodgepole pine in tie-driven riparian areas is probably an artifact of historic site selection, since tie-driven streams were more likely to be located where lodgepole pine was the dominant species.

Our estimates of total C stored in the stream-riparian corridor are conservative partly due to methods. We inventoried the largest components of biomass completely for each sampling unit (riparian plot or stream reach) so that we would not overestimate biomass. The density estimates used to calculate wood biomass are conservative across species and assume low moisture content (Forest Products Laboratory, 2010). For smaller pools, we likely underestimated the amount of C stored, particularly for CPOM and FPOM. FPOM was underestimated because of the lower limit of the size class we used. The snowmelt driven flow regime of the area resets standing stocks that have accumulated during the year and considerable transport of both CPOM and FPOM occurs during times of high flow (Webster *et al.*, 1999). Midsummer sampling was necessary for logistical reasons (site access and safety) yet this period likely corresponds with the lower limit of annual standing stocks. Finally, soils have been characterized as a large storage compartment for C in other ecosystems (Bradford *et al.*, 2008), however little is known about the C content of riparian soils in our study area. By directly measuring percent carbon (%C), we were able to accurately constrain our estimates of this portion of the C budget.

Another caveat to our budget was that DOM was not included as a component. Even though C stored in DOM has been identified as a large pool in stream environments (Wagener *et al.*, 1998), it is regulated by a variety of controls which likely confound differences due to legacy disturbances. Additionally, DOM is timed with snowmelt in these systems and is therefore variable throughout the year.

We are aware of few studies that quantify the biomass and C of in-stream components. Our estimates for C storage of LW in non-driven streams are slightly higher than published values for streams in British Columbia (Chen *et al.*, 2005) and comparable to estimates made for younger forest stands elsewhere in the Rocky Mountains (Beckman and Wohl, 2014). However, estimates of C storage in LW compartments for tie-driven streams were much lower than other reported values (Chen *et al.*, 2005). The lack of significant differences found for in-stream wood in this study may reflect the disparity in wood loads between first- and second-order streams which could confound differences related to wood loading between disturbance conditions. However, the depauperate wood loads that characterize streams in this region (Ruffing *et al.*, 2015) represent a conservative estimate of C in-stream storage when compared to LW loads for other forested ecosystems.

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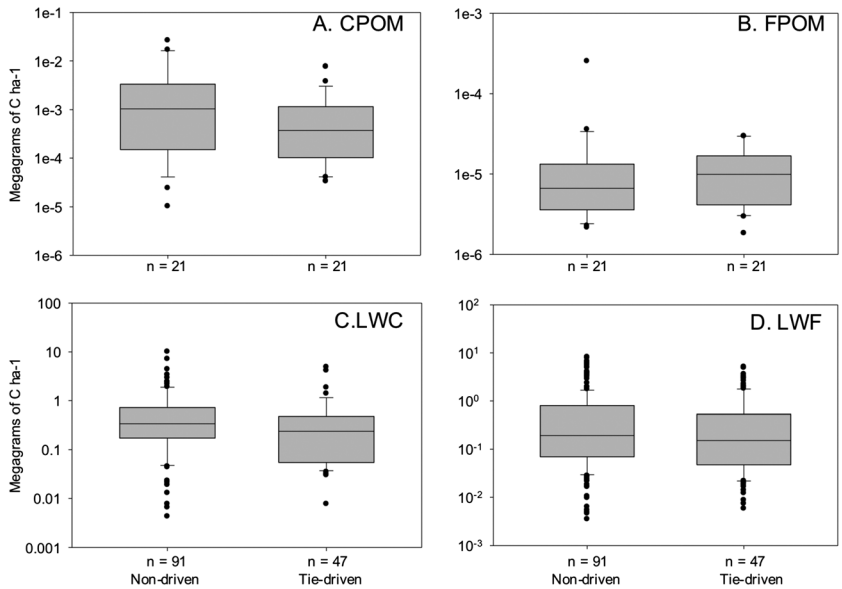

Figure 4. Distribution of C in non-driven and tie-driven reaches for samples of coarse particulate organic matter (CPOM), samples of fine particulate organic matter (FPOM), surveyed in-channel large wood (LWC) and the portion of in-channel large wood stored on the floodplain (LWF). Values are plotted on a log scale and sample sizes are reports on the x axis.

Table IV. Results of independent *t*-tests evaluating differences in average total carbon storage in stream and riparian pools between non-driven and tie-driven conditions

	F	df	*t*-Test	*P*-Value
Stream carbon pools				
Fine particulate organic matter (FPOM)	0.826	4	0.478	0.329
Coarse particulate organic matter (CPOM)	0.17	4	1.174	0.153
Large wood in channel (LWC)	0.417	4	1.192	0.15
Large wood on floodplain (LWF)	0.514	4	1.029	0.181
Stream total	0.482	4	1.09	0.169
Riparian carbon pools				
Live trees (≥5 cm diameter at breast height [DBH])	0.523	4	0.49	0.325
Dead trees (≥5 cm DBH)	0.827	4	0.554	0.304
Coarse downed wood – sound	0.229	4	0.88	0.214
Coarse downed wood – rotten	0.873	4	3.671	0.0107*
Stumps	0.426	4	–0.833	0.226
Fine downed wood	0.695	4	2.958	0.0208*
Regenerating conifers	562	4	–0.0458	0.483
Herbaceous vegetation	0.548	4	–0.11	0.459
Shrubs	0.705	4	1.058	0.175
Soil	0.066	4	–0.394	0.357
Litter	0.494	4	–0.703	0.261
Duff	0.621	4	0.127	0.452
Riparian total	0.116	4	1.044	0.178
Corridor total	0.745	4	1.175	0.153

Our plot level estimates for C storage in riparian components are among the most complete yet published (see Sutfin *et al.*, in press). Conifer dominated riparian areas in the study region are less diverse floristically and structurally than streamside forests in other ecoregions, and we evaluated most C components that are usually considered in terrestrial C assessments. The most notable difference between tie-driven and non-driven riparian conditions was in amounts of CDW and FDW. We interpret the lower abundance of rotten CDW along tie-driven reaches as the result of historic clearing activities while the lower abundance of FDW could be related to altered community structure or beetle damage.

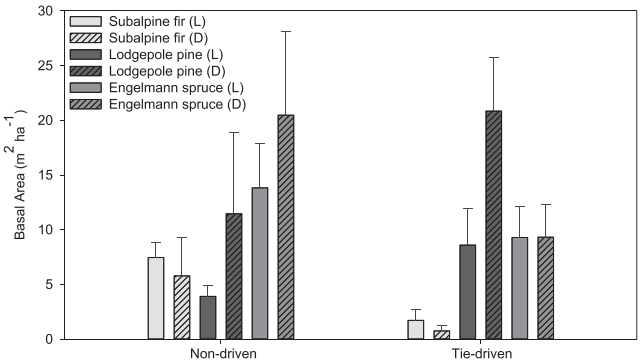

Figure 5. Live and dead basal area (means ± SE) for subalpine fir, lodgepole pine, and Engelmann spruce in non-driven and tie-driven riparian plots.

Feedbacks between riparian and in-stream C pools

An increasing number of studies have quantified the effect of forest age and disturbance history on the amount and form of C in the terrestrial environments (Houghton *et al.*, 1999; Myneni *et al.*, 2001; Fang *et al.*, 2014). The large number of lodgepole pine of different size classes reflects the growth release of small uncut trees and understory forest regeneration following the removal of lodgepole during the tie-drive era. Non-driven reaches have greater densities of subalpine fir and Engelmann spruce and high levels of mortality. However, except for preliminary work exploring C storage within mountain headwater valleys (Wohl *et al.*, 2012; Beckman and Wohl, 2014), few studies have explicitly linked forest characteristics and in-stream C storage. Carbon pools have only recently been quantified in streams of the Rocky Mountains, although this work has focused on relatively pristine streams that are not actively managed for public and commercial use (Wohl *et al.*, 2012; Beckman and Wohl, 2014).

Our general hypothesis that differences in CPOM and FPOM would be positively related to legacies associated with channel roughness and complexity was not supported, despite observed differences in channel complexity (Ruffing *et al.*, 2015). Debris dams, channel morphology,

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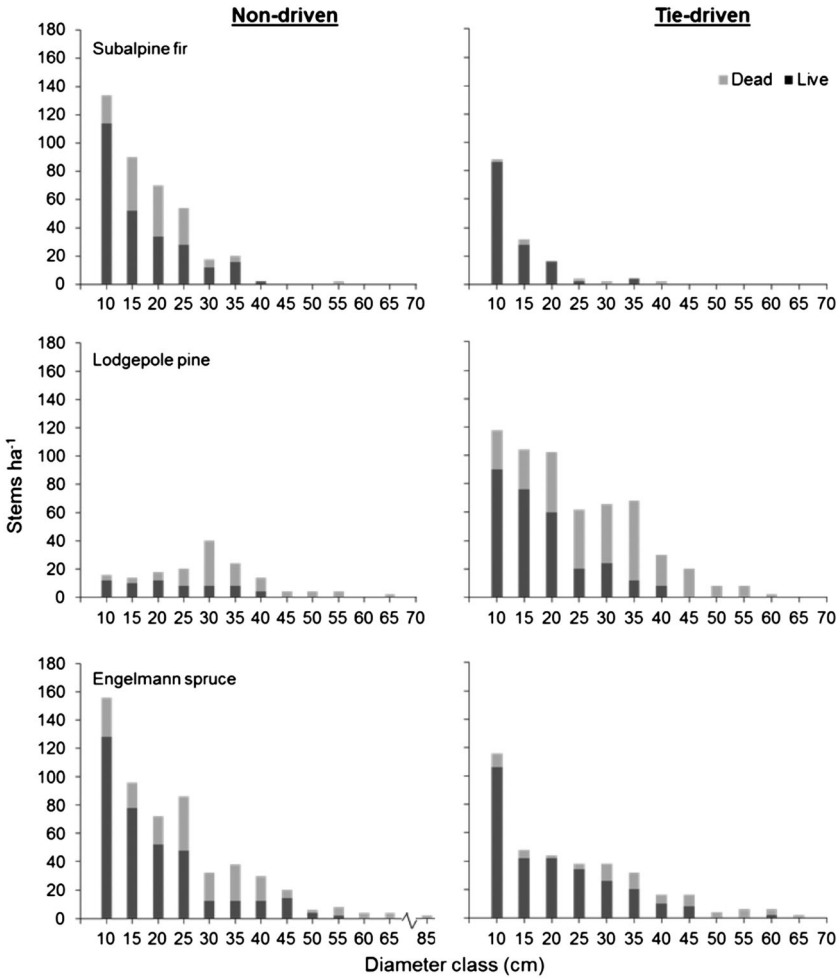

Figure 6. Density (stems ha-1, live and dead, ≥ 10 cm DBH) of subalpine fir, lodgepole pine, and Engelmann spruce stems by diameter class (5 cm increments) for non-driven and tie-driven riparian plots.

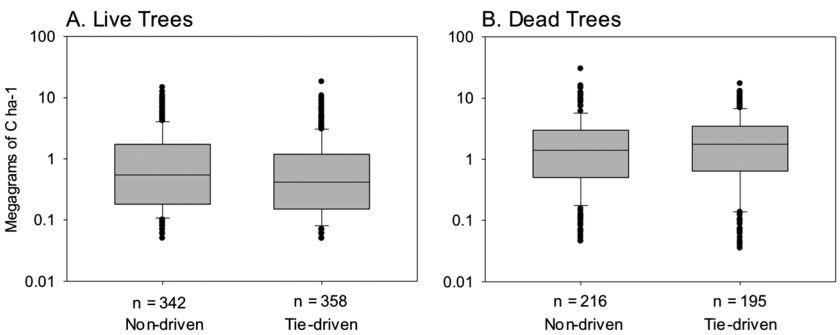

Figure 7. Distribution of C stored in sampled tree biomass of (A) live and (B) dead trees in non-driven and tie-driven reaches. Values are plotted on a log scale and sample sizes are reported on the x axis.

riparian vegetation and discharge are channel elements controlling both the transport and retention of particulate organic material (Brookshire and Dwire, 2003; Daniels, 2006) and wood jams function as storage sites for considerable quantities of in-stream C (Beckman and Wohl, 2014). The lack of wood and simplified channel morphology characteristic of tie-driven streams were not associated with decreased retention of particulate OM which further suggests that seasonal high flows flush accumulated material from both channel types. Functional connectivity between channel processes and OM dynamics is embodied in the retentive capacity of the stream; seasonal flow variability may be a primary driver of channel storage in these streams.

The magnitude of differences in C pools between tie-driven and non-driven stream-riparian corridors is relevant at different temporal scales as well. Allochthonous OM drives aquatic food webs in headwater streams and OM inputs and turnover generally occur over seasonal or annual timescales. Non-driven streams had significantly more FDW on the floodplain, which corresponds to the same size class as CPOM. The small size of FDW represents a component of C storage which will be turned over at relatively short timescales due to decomposition or transport into the stream.

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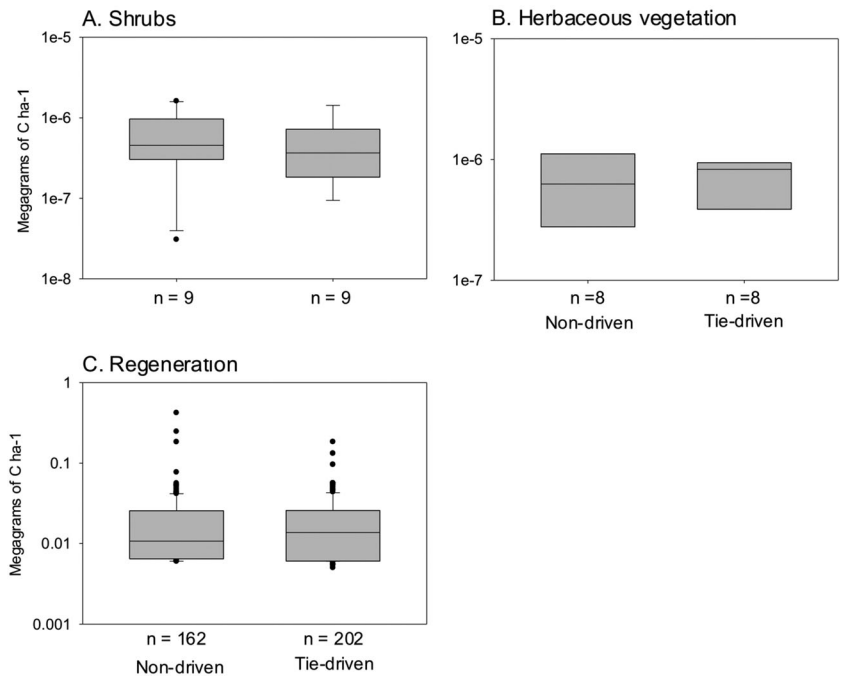

Figure 8. Distribution of measured C stored in sampled understory vegetation in non-driven and tie-driven reaches. Values are plotted on a log scale and sample sizes are reported on the x axis.

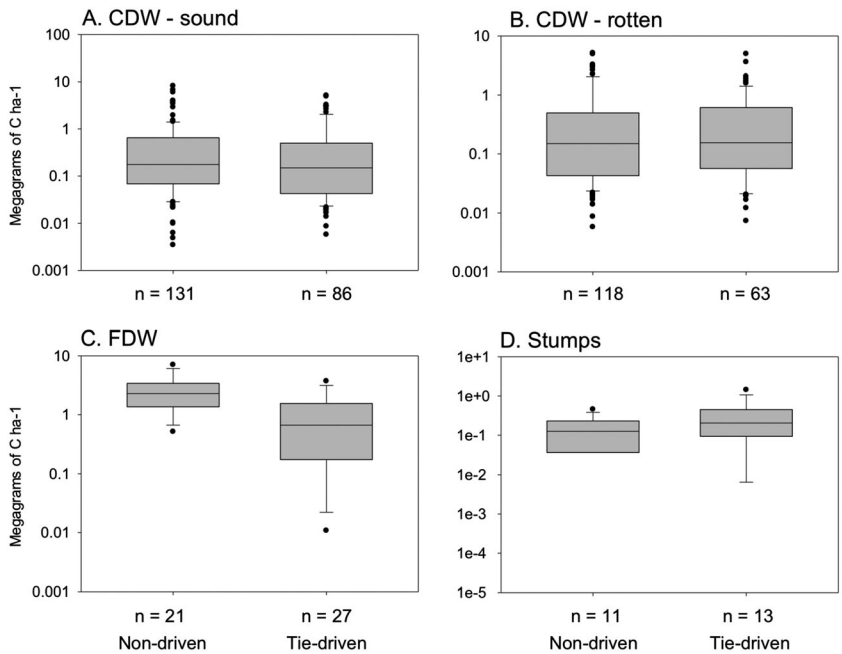

Figure 9. Distribution of measured C stored in downed wood and stumps in the riparian area for non-driven and tie-driven reaches. Values are plotted on a log scale and sample sizes are reported on the x axis.

In contrast, C stored in wood in the channel, on the floodplain adjacent to the channel, or on the riparian floor is relevant at much longer timescales. Wood of this size is broken down through a combination of leaching of soluble compounds, abrasion and fragmentation, and decomposition and submerged wood decays more slowly than wood exposed to the air (Collier and Bowman, 2003). Despite the similarity in transformation processes, a considerable portion of LW is recalcitrant and thus very slow to breakdown, especially in the relatively cool, dry setting of Wyoming mountain headwater streams. It is also possible for LW in the channel to be moved through geomorphic and hydrologic processes, although headwater streams are notoriously limited in their capacity to transport LW (Wohl and Jaeger, 2009).

Influence of beetle-caused canopy mortality on stream and riparian C pools

Over the past decade, MPB and SB outbreaks have resulted in extensive tree mortality and altered species composition throughout the forests of western North America (Jenkins *et al.*, 2008; Raffa *et al.*, 2008). Within the Medicine Bow National Forest, these outbreaks are occurring on a landscape that has already been influenced by a history of disturbance (Wohl, 2001). While the extent and impacts of bark beetle mortality is increasingly being documented (Kulakowski *et al.*, 2003; Kurz *et al.*, 2008; Liang *et al.*, 2014), limited information is available for riparian areas (Dwire *et al.*, 2015).

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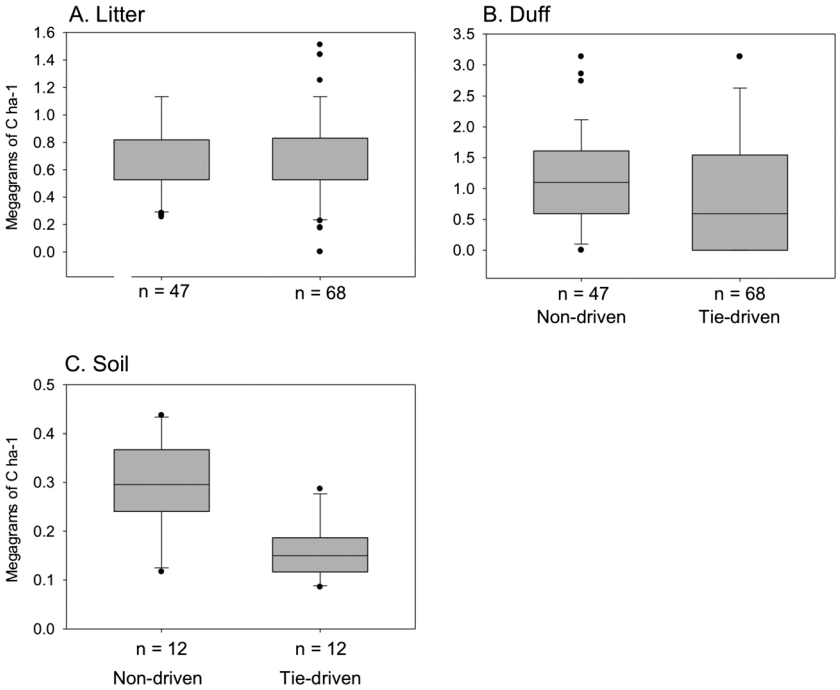

Figure 10. Distribution of measured C stored in forest floor compartments the riparian area for non-driven and tie-driven reaches. Values are plotted on a log scale and sample sizes are reported on the x axis.

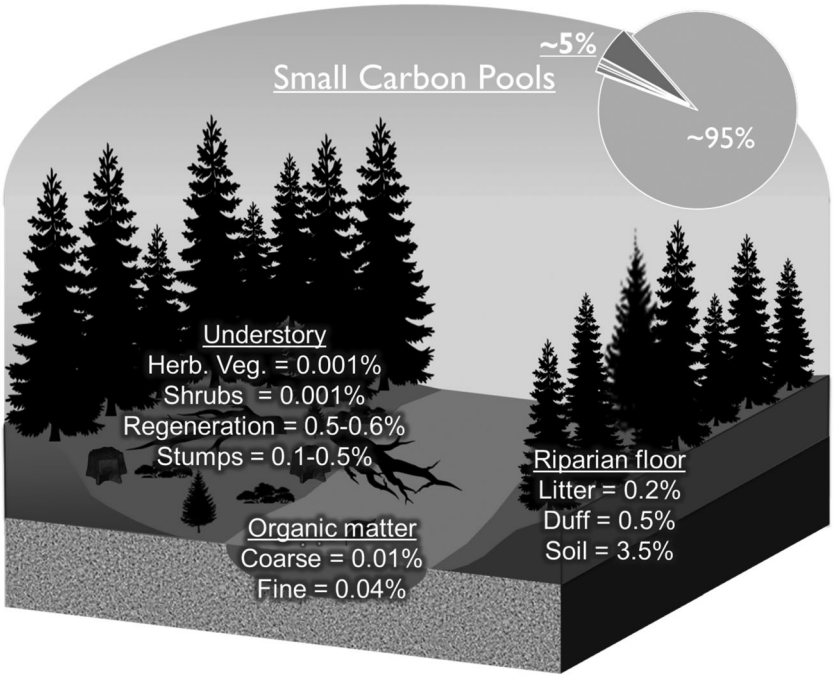

Figure 11. Small C pools averaged across non-driven and tie-driven sites. The small pools account for approximately 5% of total C stored in stream-riparian corridors of both non-driven and tie-driven streams.

For lodgepole pine and Englemann spruce, the distribution of live versus dead trees reflects the recent MPB and SB epidemics in the region (Dwire *et al.*, 2015). Tree biomass was the largest single C component and approximately 37% was comprised of dead, beetle-killed lodgepole pine or spruce trees. This represents a significant shift of stored C from live to dead biomass and increased contributions to litter compartments (Hicke *et al.*, 2012). Eventually, C stored in standing dead trees will shift to detrital or in-stream components as needles drop and trees eventually fall. Patterns of tree fall and wood recruitment to either the stream or floodplain will vary depending on local terrain, wind patterns, and riparian forest structure. Although it has been predicted that up to 90% of infested trees will fall within 10–15 years (Mitchell and Preisler 1998), fall rates will vary depending on local conditions. The high number of dead trees leaves the area susceptible to other disturbances such as wildfires and blowdowns (Jenkins *et al.*, 2008; Dwire *et al.*, 2015).

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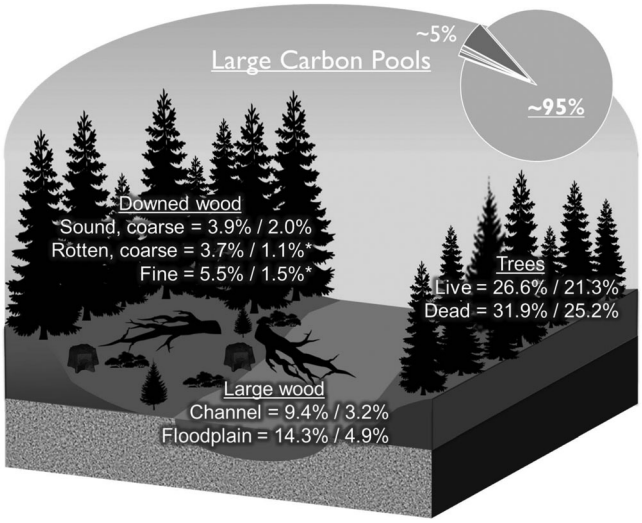

Figure 12. Large C pools measured across non-driven and tie-driven sites (values listed are in non-driven/tie-driven order). The large pools account for approximately 95% of total C stored in stream-riparian corridors of both non-driven and tie-driven streams. An '*' denotes pools which were significantly different.

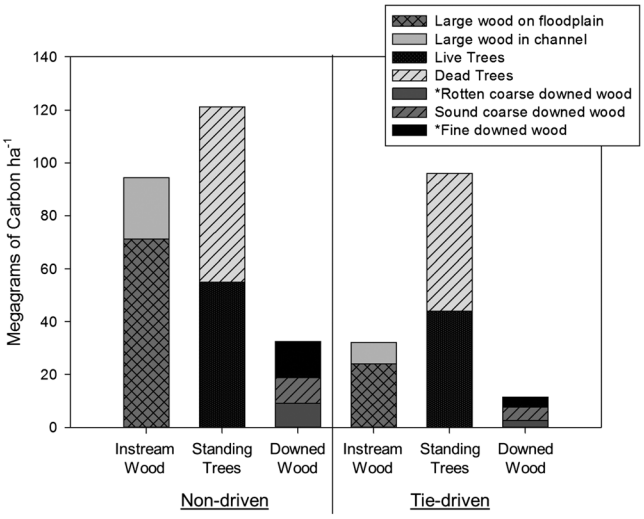

Figure 13. Average total carbon pools of the largest ecosystem components for tie-driven and non-driven streams. Significant differences with P values < 0.1 are indicated by '*'. Quantities of carbon in coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) as well as stumps, regenerating conifers, and herbaceous vegetation were too small to report on this graph.

Conclusion

Tie-driving is a notable disturbance that has partially shaped contemporary C storage in stream-riparian corridors. Non-driven streams have a larger proportion of C stored as rotten and FDW in the stream-riparian corridor. While the legacies of this disturbance are evident across the landscape, our findings suggest that contemporary ecosystems are undergoing another and perhaps greater disturbance related to the unprecedented epidemics of bark beetles in the region. Incorporating geomorphic and riparian mechanisms of C storage with ecological metrics quantifying fluxes between systems improves the current understanding of feedbacks between streams and riparian systems while further developing their role in the global C cycle. Despite the current understanding of connectivity between streams and riparian areas, this study is one of few that examines the effect of a historic disturbance on discrete C pools within this type of ecosystem.

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