

**INFLUENCE OF LEGACY DISTURBANCE ON FUNCTIONAL CONNECTIONS
BETWEEN GEOMORPHOLOGY AND ORGANIC MATTER DYNAMICS IN
MOUNTAIN STREAMS**

by

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B.S., Frostburg State University, 2006

M.A., University of Missouri, 2010

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Geography
College of Arts and Sciences

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Abstract

Geomorphic properties of streams are linked to ecosystem function through processes related to storage, transport, and other drivers regulating biogeochemical conditions. Disturbances altering the physical template of a stream are associated with cascading impacts on ecosystem function. However, few disturbances are studied at long time scales and so the legacy of such events and the implications for ecosystem structure and function are not well understood. This research investigates the role of historic tie-driving, a channel disturbance legacy, in shaping present-day stream channel conditions in the Rocky Mountain region and the associated implications for organic matter dynamics. Using a combination of geomorphic and riparian surveys, organic matter and vegetation sampling, and modeling, I show that components of mountain stream ecosystems have recovered from tie-driving at varying rates. First, I addressed how tie-driving has altered channel morphology and wood loading. Tie-driven streams are narrower, shallower, less rough, and have less wood than non-driven reference reaches. In a second study, I focused on differences in carbon storage within the stream and riparian area between tie-driven and non-driven streams. Carbon stored on the landscape represents a long-term component of the terrestrial carbon cycle and some, but not all, components have been impacted by tie-driving. Large instream wood, coarse downed wood, and fine downed wood were identified as carbon storage components that were significantly smaller in tie-driven stream-riparian corridors. Finally, I modeled whole stream ecosystem metabolism and tested whether abiotic drivers influenced variations in rates of gross primary productivity (GPP), ecosystem respiration (ER), and net ecosystem productivity (NEP). Results from this work suggest that rates of GPP were significantly different between tie-driven and non-driven streams and were partially explained by variations in light related to canopy structure. However, variations in ER and NEP were not significantly different between tie-driven and non-driven sites. Taken as a whole, this work shows that ecosystems bear the imprint of historic disturbances but individual ecosystem components recover at differing rates. Additionally, integrating stream hydro-geomorphic and ecological dynamics is an effective approach to understanding the impact of channel disturbances in shaping ecosystem function at a variety of spatial and temporal scales.

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Major Professor
Melinda Daniels

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Dedication

This dissertation is dedicated to my family. My parents have been endlessly supportive of my academic pursuits and I would have never made it this far if it were not for them. They also both (unknowingly) introduced me to the outdoors and sparked my love of water. I am grateful for my mother for showing me how rewarding it is to pursue a career you are passionate about. Her grace and intelligence are second to none and her work ethic and perseverance are just a few of the reasons why she is my most important role model. My father taught me that if I found a job I love, I would never work a day in my life. He told me to stay in school, a lesson I obviously took to heart. His curiosity about the world and passion for learning continuously inspire me. My sister has taught me how to approach life with humor and to never take myself too seriously. This past summer she and her husband blessed me with the birth of my beautiful niece. I have never been more excited to share my love of rivers and the outdoors than I am to share them with her.

Preface

This dissertation is the result of concepts and approaches that I developed in collaboration with my major professor and dissertation committee members. The work contained herein is presented in third person in keeping with traditional peer-reviewed format. At the time of this writing, Chapter 2 is in press in *Geomorphology* with Melinda Daniels and Kate Dwire as coauthors. Chapter 3 has been submitted and is currently under revision for *Earth Surface Processes and Landforms* with Kate Dwire and Melinda Daniels as coauthors. Chapter 4 is formatted for publication in *Freshwater Science* with Walter Dodds and Melinda Daniels as coauthors.

Chapter 1 - Introduction

The role of disturbances in shaping stream ecosystem patterns and processes is well recognized and is a central paradigm in freshwater science (Resh et al. 1988, Stanley et al. 2010). Disturbances in stream environments are discrete events that are characterized by frequencies of occurrence and intensity that would be considered outside of an expected or predictable range and result in the alteration of landscape structure and biological processes (Resh et al. 1988). This definition builds on work by White and Pickett (1985) which defines disturbances as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource, substrate availability, or the physical environment" to incorporate variability outside of the expected dynamism of ecosystems. Other definitions of disturbance have been proposed (e.g. Bender et al. 1984; Lake 2000), but the dynamic nature of stream environments requires that any definition of disturbance capture the unique characteristics of the event itself in terms of duration and magnitude (Lake 2000). Ecologists have established paradigms which capture the nuances of disturbance magnitude and frequency (e.g. Intermediate Disturbance Hypothesis; Connell 1978; Townsend et al. 1997), temporal patterns (e.g. Press vs. Pulse; Bender et al. 1984; Lake 2000), and the manifestation of disturbances on landscapes (e.g. Patch Dynamics Concept; Townsend 1989). While these paradigms have varied themes, they each incorporate the role of spatial and temporal scale as a way to assess disturbance characteristics and response.

Disturbance legacies are imprints left on the landscape from past anthropogenic or natural disturbance events. Examples of human-caused disturbance legacies include the effects of historic land use change on the physical and biotic template of streams (Maloney et al. 2008), the role of mill dams in changing geomorphic conditions in mid-Atlantic streams (Walter and Merritts 2008), and residual mercury contamination in stream sediment (Rhoades et al. 2009). These conditions are notable because even though they do not capture the system response or ecological consequences immediately following the original disturbance, they provide insight into system adjustments and the trajectory of recovery. Disturbance legacies have not been well studied compared to the more immediate effects of disturbance events themselves, partially because of their subtle nature. For example, many foundational principles of modern

geomorphology were made based on observations of streams in the northeastern United States (Leopold et al. 1964). However, it has only recently been recognized that these same streams systems have been fundamentally altered through the construction and subsequent infilling of mill dams during the 1700s (Walter and Merritts 2008).

Over the past decade there has been a growing interest in approaching the study of lotic environments from an interdisciplinary perspective. Several conceptual papers articulate these hybrid approaches as ecogeomorphology (the integration of ecology and geomorphology; Frothingham et al. 2002; Thoms and Parsons 2002) and hydrogeomorphology (Sidle and Onda 2004) and supporting theoretical frameworks draw largely from principles of landscape ecology to establish the link between geomorphic forms and processes and ecosystem communities and function (Poole 2002; Poole 2010). Current trends in these disciplines point towards an integrative understanding of physical stream conditions and ecosystem function such as inundation hydrology and flowpath dynamics and the resulting effects on biogeochemical cycling and stoichiometry (Poole 2010; Fischer et al. 2004). Investigations that integrate structural and functional dynamics in lotic environments from an ecogeomorphic approach promote these burgeoning fields while simultaneously contributing to contemporary water resource challenges.

Past integrative research linking fluvial geomorphology and stream ecology has resulted in great progress in understanding the relationships between organism distributions and abiotic habitat availability (Lamouroux et al. 2002). These advances regarding the relationships between habitat heterogeneity, biodiversity, and population persistence (Yarnell et al. 2006) directly inform contemporary water resource management. For example, common stream restoration techniques, such as the installation of cross-vanes, j-hooks, and natural bank revetments, are frequently employed to increase channel stability by preventing meander migration and channel incision while providing ecological benefits such as habitat complexity (Lave 2009). However, recent studies evaluating geomorphic manipulations to habitat such as those associated with stream restoration suggest factors other than geomorphic forms may drive biodiversity (Bernhardt et al. 2005; Palmer 2009). Additionally, stream restoration practices meant to increase habitat complexity have been associated with adverse effects on foundational ecosystem processes that determine basal trophic dynamics such as organic matter retention (Muotka and Laasonen 2002), organic matter processing (Entekin et al. 2008), stream

metabolism and nutrient uptake (Sudduth et al 2011). Unfortunately, progress in improving water resource management and stream restoration, in particular, is hindered by the gap in knowledge centered on the connections between geomorphic conditions and biogeochemical processes (Elosegi et al. 2010). Legacy disturbances provide an opportunity to evaluate these feedbacks in an integrative context.

Streams in the Rocky Mountain region have undergone extensive historic disturbances since Euro-American settlement such as the removal of the beaver, gold and silver placer mines, flow diversion, and timber floating (Wohl 2001). Timber floating is a practice that is common to many mountain stream systems throughout the world; however the effects of this activity have largely gone unstudied in streams of the Rocky Mountains. As was common throughout the United States (e.g. Sedell et al. 1991), streams in this region were the primary method for transporting timber for mine props, building materials, and (most notably) railroad ties. The westward expansion of the railroads created an intense demand for railroad ties and the forests of the Rocky Mountains provided a vast supply of lumber well suited for this purpose. Most of the railroad ties were cut from lodgepole pine (*Pinus contorta*) ranging in size from 28-40 cm diameter at breast height (DBH; Anonymous 1916; Rosenberg 1984). Harvests occurred across the forest, including riparian areas, throughout the year beginning in 1868 until 1940. As ties accumulated, they were stacked along stream channels or floodplains, until high flows following spring snowmelt could transport the loads downstream in what were referred to as “tie drives”. The magnitude of each tie-drive varied, depending on the 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). Alterations to the stream channel were necessary for streams to be made ‘drivable’, so any obstructions such as debris jams and boulders were removed and surge dams and feeder flumes were built to increase flow in some areas (Anonymous 1916).

The immediate effect of tie drives on stream channels is unknown. Historical records identify streams that were tie-driven and in some instances provide the years that tie-driving took place and an idea of the types of channel modifications that were employed to facilitate the passage of ties downstream. In the only study we are aware of that documents the legacy of tie drives, Young et al. (1994) found that when compared to reference streams, tie-driven streams had fewer pieces of large wood in the channel, contained more riffles and fewer pools, and lacked habitat diversity overall. They used an inventory-based approach to evaluate differences

in disturbance conditions so it is unknown what types of morphodynamic or ecological impacts are associated with the contemporary structure of these altered systems.

The overall goal of this dissertation is to advance our understanding of the functional connections between stream geomorphology and organic matter dynamics in mountain streams within the context of tie-driving. The research presented within integrates the role of the physical environment with carbon storage and ecosystem metabolism, two biogeochemical processes that are influenced by abiotic drivers at different temporal and spatial scales (Fig. 1.1). In Chapter 2, I document alterations to geomorphic structure and instream wood loading related to tie-driving. Disturbance legacies are evaluated in relation to channel geometry, reach planform, substrate characteristics, wood loading, and wood recruitment. In Chapter 3, I quantify differences in stored carbon within the channel and riparian area of study reaches. A variety of carbon components are emphasized to capture the complexity of stream-riparian corridors and include estimates of overstory, understory, forest floor, and instream components. In Chapter 4, I integrate measurements of ecosystem metabolism with the geomorphic metrics related to tie-driving. I test for interactions between geomorphic and riparian characteristics and gross primary productivity (GPP), ecosystem respiration (ER), net ecosystem production (NEP), and aeration (k) using known abiotic drivers as well as specific characteristics altered by tie-driving. Chapter 5 summarizes the findings of the previous chapters. At the time of this writing, Chapter 2 is in press at *Geomorphology*, Chapter 3 is in revision for *Earth Surface Processes and Landforms*, and Chapter 4 is formatted for submission to *Freshwater Science*.

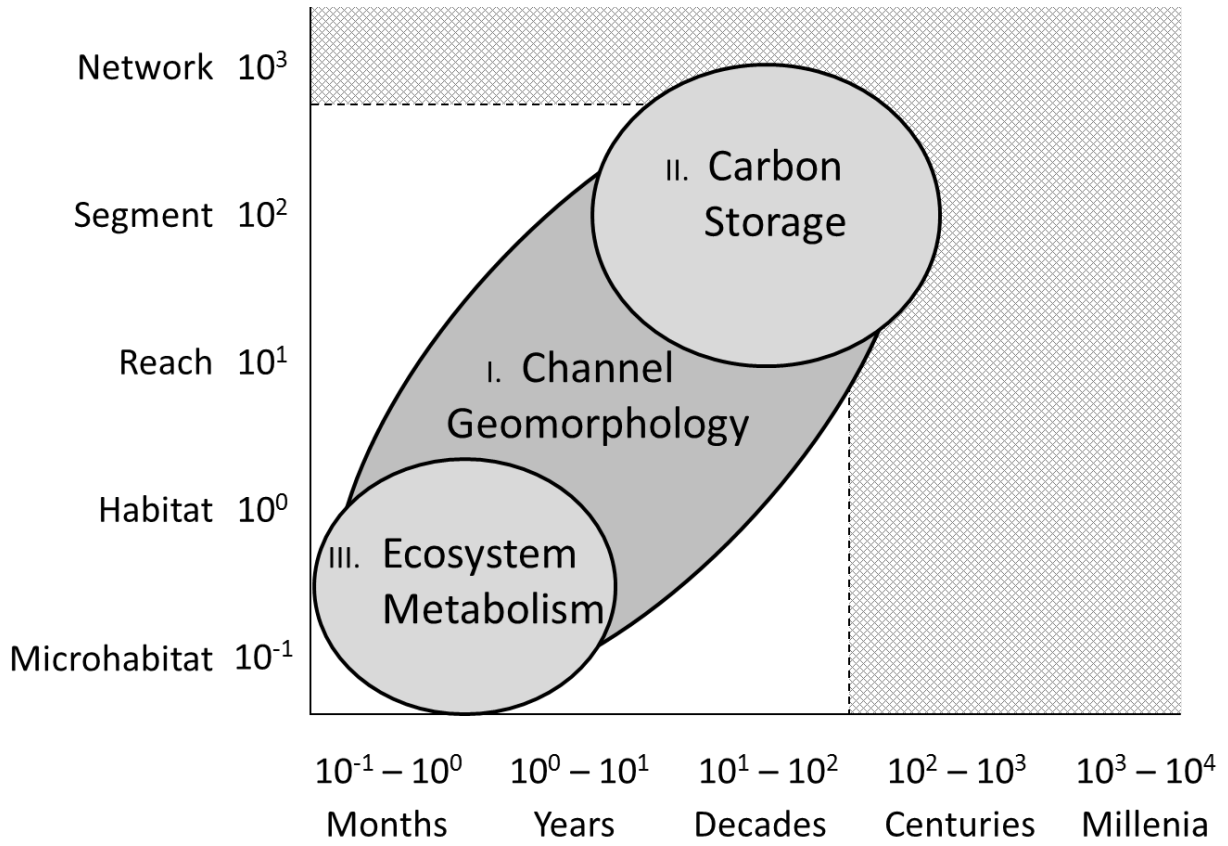
References

- Anonymous. 1916. Timber sale contract, Medicine Bow National Forest, 8/11/16. Grand Encampment Museum, Encampment Wyoming.
- Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1-13.
- Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. C Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G.M. Kondolf, P.S. Lake, R. Lave, J.L. Meyer, T.K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. *Science* 308: 636-637.
- Elosegi, A., J. Diez, and M. Mutz. 2010. Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. *Hydrobiologia* 657:199-215.
- Entrekin, S.A., J.L. Tank, E.J. Rosi-Marshall, T.J. Hoellein, and G.A. Lamberti. 2008. Responses in organic matter accumulation and processing to an experimental wood addition in three headwater streams. *Freshwater Biology* 53(8): 1642-1657.
- Fisher, S.G., R.A. Sponseller, and J.B. Heffernan. 2004. Horizons in stream biogeochemistry: flowpaths to progress. *Ecology* 85(9):2369-2379.
- Frothingham, K.M., B.L. Rhoads, and E.E. Herricks. 2002. A multiscale conceptual framework for integrated ecogeomorphological research to support stream naturalization in the agricultural Midwest. *Environmental Management*. 29(1):16-33
- Lake, P.S. 2000 Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19(4):573-592.
- Lamouroux, N., N.L. Poff, P.L. Angermeier. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology* 83(7):1792-1807.
- Lave, R. 2009. The controversy over natural channel design: Substantive explanations and potential avenues for resolution. *Journal of the American Water Resources Association* 45(6): 1519-1532.
- Leopold L.B., Wolman M.G., Miller J.P. 1964. *Fluvial Processes in Geomorphology*. Dover Publications: New York.

- Maloney, K.O., J. W. Feminella, R. M. Mitchell, S. A. Miller, P. J. Mulholland, and J. N. Houser. 2008. Landuse legacies and small streams: Identifying relationships between historical land use and contemporary stream conditions. *Journal of the North American Benthological Society* 27 (2): 280-294.
- Muotka, T., and P. Laasonen. 2002. Ecosystem recovery in restored headwater streams: The role of enhanced leaf retention. *Journal of Applied Ecology* 39 (1): 145-156.
- Palmer, M.A. 2009. Reforming watershed restoration: science in need of application and applications in need of science. *Estuaries and Coasts* 32(1):1-17.
- Poole, G.C. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology* 47:641-660.
- Poole G.C. 2010. Stream hydrogeomorphology as a physical science basis for advances in stream ecology. *Journal of the North American Benthological Society* 29(1): 12-25.
- Resh, V.H., Brown, A.V., Covich, A.P. Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., Wissmar, R.C.1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7(4):433-455.
- Rhoades, E.L., M.A. O'Neal, and J.E. Pizzuto. 2009. Quantifying bank erosion on the south river from 1937 to 2005, and its importance in assessing Hg contamination. *Applied Geography* 29(1): 125-134.
- Rosenberg RG. 1984. Handhewn ties of the Medicine Bows. *Annals of Wyoming* 56:39-53.
- Sedell, R., F.N. Leone and W .S. Duval. 1991. Water transportation and storage of logs. *American Fisheries Society Special Publication* 19:325-368.
- Sidle, R.C. and Y. Onda. 2004. Hydrogeomorphology: overview of an emerging science. *Hydrological Processes* 18:597-602.
- Stanley, E., S. Powers, and N. Lottig. 2010. The evolving legacy of disturbance in stream ecology: Concepts, contributions, and coming challenges. *Journal of the North American Benthological Society* 29 (1): 67-83.
- Sudduth, E.B., B.A. Hassett, P.Cada, and E. S. Bernhardt. 2011. Testing the field of dreams hypothesis: Functional responses to urbanization and restoration in stream ecosystems *Ecological Applications* 21(6):1972-1988.
- Thoms, M.C., and M. Parsons. 2002. Eco-geomorphology: an inter-disciplinary approach to river science. *International Association of Hydrological Sciences* 276:113-120.

- Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8(1):36-50.
- Townsend, C.R., M.R. Scarsbrook, and S. Doledec. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* 42:938-949.
- Walter, R.C. and D.J. Merritts. 2008. Natural streams and the legacy of water-powered mills. *Science* 319(5861): 299-304.
- White, P.S., S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction. Pages 3-13 in S.T.A. Pickett and P.W. White, editors. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Wohl E. 2001. *Virtual Rivers: Lessons from the Mountain Rivers of the Colorado Front Range*. Yale University Press.
- Yarnell, S.M., J.F. Mount, E.W. Larsen. 2006. The influence of relative sediment supply on riverine habitat heterogeneity. *Geomorphology* 80(3-4):310-324.
- Young, M.K., D. Haire, and M.A. Bozek. 1994. The effect and extent of railroad tie drives in streams of southeastern Wyoming. *Western Journal of Applied Forestry* 9(4): 125-130.

Figure 1.1 Conceptual diagram of approximate spatial and temporal scales of the processes included in this dissertation. Hatching indicates scales outside the scope of this research.



Chapter 2 - Disturbance legacies of historic tie-drives persistently alter geomorphology and large wood characteristics in headwater streams, southeast Wyoming

Abstract

Instream wood is an integral component of stream morphology in forested areas. However, few studies have evaluated the legacy effects of historic wood removal activities and associated impacts on channel morphology, contemporary wood loading, and recruitment. This study investigated the role of historic tie-driving, a widespread channel disturbance legacy, in shaping present-day stream channel conditions in southern Wyoming. Geomorphic and riparian surveys were used to assess the extent of disturbance and degree of recovery within three sets of paired tie-driven and non-driven study reaches. Tie-driven streams were narrower, shallower, and had low cross-sectional roughness and higher width-to-depth ratios when compared to non-driven streams. Study reaches in first-order tie-driven streams were characterized by predominantly plane-bed morphologies and an extremely low abundance of wood compared to paired, non-driven reaches. Wood loads in second-order tie-driven reaches were similar to non-driven reaches, but overall wood distribution varied and was more likely to accumulate in jams. Existing wood loads in tie-driven reaches exhibited a narrower range of geomorphic functions and were less stable overall, although the relative state of decay was similar across all reaches. Basal area, stream power, and reach slope were identified as key mechanisms driving wood retention in the study reaches. The results of this study suggest that contemporary channel morphology and wood loads continue to reflect disturbance histories but have not yet been affected by other contemporary disturbances expected to influence wood loads such as bark beetle infestations.

Introduction

While billions of dollars have been invested in stream restoration in the United States, restoration efforts may not be producing the desired ecosystem improvements, indicating a disconnect between river science and river restoration practice (Bernhardt et al., 2005; Palmer, 2009). The reliance on reference reaches to provide a baseline or target condition for restoration projects compounds other shortcomings related to restoration techniques. Reference reaches, or

minimally impaired systems that approximate characteristic stream function, are often used as templates to guide restoration projects and management initiatives. Reference reaches are chosen based on a variety of considerations including their ability to represent pre-disturbance conditions (Brookes, 1987) as well as similarities in morphology (Rosgen, 1994), physiographic qualities (Montgomery et al., 1995), and more recently, characteristics that capture process-based dynamics instead of form-based features (Downs and Simon, 2011). However, the selection of reference reaches requires an understanding of historic system conditions as well as future response trajectories. Given the spatial extent and history of human impacts on streams (Gregory, 2006), systems altered by past disturbance events (hereafter referred to as disturbance legacies) underlie much of our contemporary understanding of what constitutes natural stream function (Walter and Merritts, 2008; Burchsted et al., 2011; Downs and Simon, 2011).

One aspect of fluvial geomorphology that is often overlooked in the reference stream selection process is the role of large wood (LW). The scientific study of the functional role of LW in streams has a rich theoretical foundation in terms of channel form and of process-based implications for stream systems (e.g., Keller and Swanson, 1979; Lienkaemper and Swanson, 1987; Marston et al., 1995; Brooks and Brierley, 2002; Flores et al., 2011). The geomorphic impacts of LW are numerous and include the alteration of flow patterns (Gippel, 1995; Daniels and Rhoads, 2004), storage of organic matter and sediment (Lisle, 1995; Thompson, 1995; Montgomery et al., 2003; Daniels, 2006), and controls on bedform morphology (Montgomery et al., 1995). Considerable effort has focused on recruitment mechanisms and patterns (Downs and Simon, 2001; Webb and Erskine, 2003) as well as transport potential (Abbe and Montgomery, 1996). Longitudinal patterns of wood throughout stream networks vary based on network position and have been attributed to a variety of drivers, including channel gradient, channel width, stream power, and drainage area (Wohl and Jaeger, 2009) — although local variations in channel and valley morphology can mask these drivers (Wohl and Cadol, 2011). This body of work has served as an integral foundation for understanding ecological functions such as habitat diversity and nutrient retention (Bilby and Likens, 1980; Bisson et al., 1987; Gurnell et al., 1995). Large wood has also received attention from the management community given the significant channel responses to wood removal and additions (Piegay et al., 2005; Chin et al., 2008; Lassetre and Kondolf, 2012). Despite the recent increase in research on wood dynamics

over the last several decades, relatively little is known about wood loading in systems not subjected to pervasive historic anthropogenic disturbances.

Instream wood loads can be influenced by a multitude of factors, including geomorphic disturbances such as mass wasting events (Lancaster et al., 2003; Montgomery et al., 2003; Wohl et al., 2009), riparian disturbances (Wallace et al., 2001), as well as historic and contemporary human impacts such as beaver extirpation (Burchsted et al., 2010), timber harvesting (Gurnell et al., 2000), urbanization (Finkenbine et al., 2000; Segura and Booth, 2010), and navigation (Angradi et al., 2009; Philips and Park, 2009). In the absence of human influence, instream wood loads typically reflect a balance among input rates, species decay rates, and export rates (Benda et al., 2003), the latter of which is partly determined by the transport capacity of the stream (Swanson et al., 1976; Gurnell et al., 2000; Wohl and Goode, 2008). Headwater streams, especially in mountainous regions, are generally associated with high wood loadings because of adjacent dense riparian forests, steep slopes, and the limited transport capacity of their characteristically small channels. Wood loads in low-order streams are closely coupled to riparian and hillslope characteristics as well as geomorphic retention mechanisms, while hydrologic properties play less of a role in transport. Although determining the residence time of instream wood is difficult, several studies in the western United States have found that some pieces of wood will remain unmoved for 70-100 years, and records exist of pieces lasting in the channel for ~ 250 years (Swanson et al., 1976; Murphy and Koski, 1989). Few studies have examined wood residence time explicitly, but it is generally understood that piece dimensions relative to the size of the channel and the potential for integration within the channel influence mobility (Wohl and Goode, 2008).

This paper focuses on the legacy of tie-driving, also known as timber floating, which is an extensive, but largely unstudied, historic anthropogenic disturbance along the Front Range of the Rocky Mountains that has largely gone unstudied. As railroads reached the Rocky Mountains during the mid-1800s, streams were the primary method for transporting railroad ties, as was common throughout the United States (e.g., Sedell et al., 1991; Wohl, 2001). Timbers were harvested and cut into ties across the forested land, including riparian areas, and through all seasons. Ties were stored on floodplains and within stream channels throughout the year until the high spring flows could carry the wood loads downstream in what were referred to as tie drives (Fig. 2.1). Modifications necessary to make streams drivable included clearing riparian

vegetation for tie storage and passage; removal of existing LW, debris jams, and boulders; and construction of surge dams and feeder flumes to increase flow. Young et al. (1994) inventoried individual bedforms, censused LW (pieces ≥ 2 m long with mean diameters ≥ 15 cm), and sampled riparian vegetation (trees ≥ 20 cm diameter at breast height) to evaluate the effects of tie drives on streams in southern Wyoming. They found that stream channels that had previously been tie-driven had fewer pools, lacked LW, and were characterized by riparian forests with low stem densities and limited streamside shrub cover. Decreased wood loads owing to historic tie-driving and contemporary management activities were also observed in the Bighorn National Forest in northern Wyoming (Nowakowski and Wohl, 2008). However, detailed information regarding morphodynamic differences, the functional role of instream wood, and recruitment potential of additional wood is needed to fully articulate the extent, magnitude, and legacy effects of tie-driving.

The geomorphic implications of timber floating and associated practices such as the use of splash dams have been studied in other regions including Oregon, USA (Miller, 2010), Sweden (Dahlstrom et al., 2005), and the Italian Alps (Comiti, 2012). Study results have shown consistent channel responses to the construction of splash dams, channelization, and other structural alterations, particularly effects on channel geometry, planform, and hydraulic alterations (Table 2.1). In addition to alterations in channel structure, evidence also suggests that logging activities in the riparian area can have lasting impacts on the channel as well. In both Oregon and Washington, riparian logging has altered LW recruitment and has led to altered distribution of LW piece size classes, altered spatial distribution of LW along stream networks, increased sediment transport and channel widening, fewer and less deep pools, and increased riffle length (Czarnomski et al., 2008; Mellina and Hinch, 2009). Research along streams in coastal Maine demonstrates an overall loss in geomorphic heterogeneity associated with historic hillslope and riparian logging (Magilligan et al., 2008). The work presented here focuses on the removal of LW from the channel and investigates the effects of this legacy on contemporary channel morphology in a variety of dimensions.

Our primary research objective was to examine the geomorphic responses of low-order streams to the removal of LW associated with historic tie-driving. We used geomorphic, instream wood, and riparian surveys to evaluate differences between tie-driven and non-driven headwater stream reaches in the Medicine Bow National Forest, southeast Wyoming. We

hypothesized that tie-driven streams would be characterized by simplified channel morphology, less dense and younger stands of riparian trees, and lower instream wood loading. We addressed four response variable categories with respect to tie-driving legacies: (i) channel morphology; (ii) frequency, volume, and size of instream LW; (iii) function of instream LW; and (iv) riparian–channel wood recruitment relationships.

Regional Setting

The Medicine Bow National Forest is located in the Rocky Mountains of southern Wyoming, USA, and includes the Sierra Madre and Snowy Mountain ranges. The underlying geology of the area ranges in origin from granitic, metasedimentary, and metavolcanic rocks to glacial deposits in the higher elevations (Love and Christiansen, 1985). Elevations within the Medicine Bow National Forest boundary range from 2170 to 3640 m. 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).

The majority of annual precipitation in the region falls as snow between October and May and mean annual precipitation varies from ~ 28 cm at low elevations to 669 cm at the highest elevations. Average annual temperatures range from a low of -1.31°C to a high of 11.65°C with January typically being the coldest month and July being the warmest (PRISM Climate Group). The flow regime throughout the area is snowmelt dominated, and peak flow usually occurs in June.

Forests are typically dominated by a mixture of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and aspen (*Populus tremuloides*) that vary in relative abundance depending on elevation and aspect (Dillon et al., 2005). Published estimates of stand age suggest that within the Sierra Madre and Snowy ranges, only 15% to 30% of trees are more than 150 years old and therefore stands qualifying as old-growth (generally thought to be between 200 and 300 years old in spruce–fir dominated regimes) are very limited (Dillon et al., 2005). Stream channel morphology in the area is consistent with channel morphology in other mountainous regions (Montgomery and Buffington, 1997) and highly dependent on gradient and the geomorphic influence of instream wood (Wohl and Goode, 2008; Wohl and Merritt, 2008). Typical channel types associated with streams in the region include step–pool, plane–bed, and pool–riffle channels (Wohl and Merritt, 2008). Common

natural disturbances in the study region include wildfire, bark beetle outbreaks, and debris flows; while human disturbances range from historic activities such as removal of beaver, placer mining, and tie-driving; to present day activities related to resource management, development, and recreation (Wohl, 2001, 2006; Dillon et al., 2005).

Methods

Selection of study reaches

We adopted a paired-reach sampling design, with two pairs (four reaches) in the Snowy Range and one pair (two reaches) in the Sierra Madre (Fig. 2.2). Reach pairs were located in close proximity to control for localized differences in geology, elevation, and riparian forest structure that may confound detection of differences in channel morphology associated with disturbance conditions. Each reach-pair consists of one tie-driven reach and one non-driven reach. Because of the extensive history of human activity within the National Forest, tie-driven streams were determined on the basis of tall and decayed stumps, abandoned cabins close to the reach, and other indications of prior logging activity. None of the study reaches were located in areas where the riparian community would qualify as old-growth. Non-driven streams were determined based on the quantity and age of existing wood loads in the channel and riparian area, the presence of large boulders or knickpoints near the study reach, and any other geologic feature that would prohibit the passage of ties during high flow events. Each identified stream was cross-checked with the historical records of tie-driving compiled by Young et al. (1994). There are historical records of tie-driving that correspond with two of the non-driven reaches. However, field evidence indicated that any tie-drives occurred downstream of the chosen study reach locations based on the site selection criteria listed above. Study watersheds were evaluated for disturbances (e.g. blow-downs, fire, beaver dams) that would impact wood loading or other geomorphic processes using a combination of historic records, aerial and satellite imagery, and field reconnaissance. Selection of study reaches was further constrained by common physiographic criteria including stream order, reach slope, geomorphic characteristics of valley bottoms, and surficial geology. Paired study reaches were selected to be as physically analogous as possible, with the exception of tie-driven-related attributes.

Field methods

Along each sampling reach, we surveyed 30 evenly spaced cross sections and one centerline longitudinal profile extending 30 channel widths in length using a stadia rod and level (Simon and Castro, 2003). Reach lengths were scaled according to average bankfull width in order to account for differences in stream size. Beaver Creek, East Fork Encampment River, Flume Creek and Horse Creek each have 90 m long reaches and North Fork Rock and Trail Creeks have 210 m long reaches (Fig. 2.2). Stream reaches were sampled in July and August 2012 following peak snowmelt flows. Channel geometry was calculated for the bankfull portion of each cross section and reaches were classified following Montgomery and Buffington (1997) into categories for pool–riffle, plane–bed, step–pool, and cascade channel sequences. Each reach was also mapped at the habitat unit scale (i.e. individual, discrete bedforms). Substrate size distributions were visually estimated for each morphologic unit using a randomly placed 0.5 m x 0.5 m gridded plot (Gordon et al., 2004). The same operator performed all of the visual estimates of substrate cover to minimize observer bias (Daniels and McCusker, 2010). Riparian forest stand characteristics were sampled in 0.05-ha circular plots (2 to 4 plots per reach), which were established adjacent to the stream channel in locations that were representative of the variation in forest structure along the entire study reach. Within each plot, information recorded on all live and dead trees (≥ 5 cm diameter at breast height, DBH) included species, DBH, and evidence of bark beetle incidence and damage. Infestation by bark beetles is responsible for recent, widespread tree mortality throughout the Rocky Mountain region (Jenkins et al., 2008; Raffa et al., 2008) and was recorded in order to gain insight on the trajectories of future wood loading in the study reaches.

A wood census was completed for all pieces of LW within the bankfull channel that were longer than 1 m and at least 10 cm in diameter following the level I metrics suggested by Wohl et al. (2010). For each piece of instream wood occurring within each reach, the total length, length of the portion within the channel, and two end diameters were measured. The volume of each piece within the channel was calculated using Eq. (1) (Lienkaemper and Swanson, 1987):

$$(1) \quad Volume = \frac{\pi(D_1^2 + D_2^2)L}{8}$$

where D_1 and D_2 are end diameters (m) for each piece and L is the piece length within the channel (m). Calculated piece volumes were summed to quantify wood loads for each reach. Because the total piece lengths were not used, calculated volumes and reach wood loads do not

include the volume of wood outside of the stream channel. Instream stability, structural associations, and piece function (see Table 2.2 for category definitions) were recorded for each LW piece to compare process-based characteristics of existing wood loads between tie-driven and non-tie-driven reaches. Decay class and recruitment source were recorded to relate riparian condition with instream wood loads (see Table 2.2 for category definitions).

Data analysis

We used Analysis of Variance (ANOVA) to test for differences in channel morphology and LW piece dimensions between tie-driven and non-driven study reaches. Channel width, average depth, and cross-sectional area were scaled by watershed area to enable comparisons across watersheds. Normality was assessed using the Shapiro-Wilk test prior to running each ANOVA. The following variables were log transformed to meet assumptions of normality: channel width (scaled), average channel depth (scaled), cross-sectional area (scaled), width-to-depth ratios (W:D), average LW piece diameter, and average in-channel LW volume. Total LW piece length and in-channel piece length did not meet normality assumptions after transformation so they were compared using the Kruskal-Wallis test, a non-parametric ANOVA. To assess differences in the functional characteristics of LW, categorical variables associated with the wood census metrics were analyzed using χ^2 analyses.

We used simple linear regression analyses to evaluate relationships between wood loads and control variables representing physiographic, riparian, and geomorphic conditions that have been shown to influence LW recruitment to streams. Control and response variables used in the regression analyses are described in Table 2.3. Four variations of wood loading metrics (sensu Wohl and Jaeger, 2009) were used as response variables to examine differences in the frequency and volume of LW pieces in each study reach and to standardize those values by study reach area to account for loading differences across sites. Control variables representing physiographic, riparian, or geomorphic categories (Table 2.3) were run individually as opposed to a multiple linear regression because of the low sample size ($n = 6$). We used $\alpha = 0.05$ and $\alpha = 0.1$ to determine model significance.

Results

Study reach characteristics are summarized in Table 2.4. Of the six reaches sampled, only one pair, Trail Creek and North Fork Rock Creek, was located along second-order streams.

Riparian tree species composition reflected the dominant species in the area: lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). Approximately 39.0% to 71.6 % of the basal area (in North Fork Rock Creek and Beaver Creek, respectively) was composed of dead trees, with lodgepole pine killed by mountain pine beetle within the last 8 years and Engelmann spruce recently killed by spruce beetle (Colorado State Forest Service, 2012; Dwire et al., in press). The distribution of tree diameter size classes is indicative of uneven aged cohorts of riparian trees across non-driven and tie-driven reaches. Approximately 84% of live trees in non-driven and in tie-driven sites had DBH values of 25 cm or less, while 60% of dead trees in non-driven sites and 45% of dead trees in tie-driven sites fell in this category (Fig. 2.3).

Morphological conditions

On average, channel dimensions were similar for study reaches within the same stream order (Table 2.5). First-order reaches had bankfull widths of ~ 3 m with average depths ranging from 0.16 to 0.3 m. Second-order reaches were almost twice as wide with average depths just over 0.4 m. However, results from the ANOVA tests indicate that both scaled and unscaled metrics of channel geometry differ between tie-driven and non-driven reaches (Table 6). When scaled by watershed area and log-transformed to meet assumptions of normality, non-driven reaches were significantly wider (Fig. 2.4A; Table 6; $p < 0.001$), deeper (Fig. 2.4B; Table 6; $p < 0.001$), and had greater cross-sectional area (Fig. 2.4C; Table 6; $p < 0.001$) than tie-driven reaches. Non-driven reaches also had significantly smaller W:D ratios (Fig. 2.4D; Table 6; $p < 0.01$) and significantly higher cross-sectional roughness values (Fig. 2.4E; Table 6; $p < 0.001$). Longitudinal roughness values were not significantly different between tie-driven and non-driven streams (Fig. 2.5).

Habitat units were inventoried to assess morphological heterogeneity associated with tie-driven and non-driven reaches (Fig. 2.5; Table 2.7). Habitat units characterizing the study reaches included pools, riffles, runs, steps, and cascade morphologies. A greater proportion of tie-driven reaches were characterized by riffle or run morphologies compared to their non-driven site pairs (Table 2.7). In general, a smaller percentage of total reach area in tie-driven streams were composed of pool features compared to non-driven reaches, with the exception of Horse Creek (Table 2.7). Tie-driven reaches also had a smaller percentage of area characterized by high

gradient morphologies such as steps or cascades (Table 2.7). In East Fork Encampment River, three out of four pools are associated with wood-forced morphology while in Trail Creek, six out of nine pools are associated with wood-forced morphology (Fig. 2.5).

The substrate across all habitat units was relatively coarse and was characterized by size classes representing cobbles and boulders, with sparse patches dominated by gravels (Fig. 2.6). Differences in the distribution of grain sizes between tie-driven and non-driven reaches were not significantly different (p value > 0.1), even when morphologic unit type was taken into account (Table 2.7). Additionally, the geometric mean — which captures the central tendency of the grain size distributions while accounting for extremes in the sample distribution — did not differ between tie-driven and non-driven reaches (Table 2.7; p value > 0.1).

Characteristics of instream large wood

With the exception of Trail Creek, tie-driven reaches had substantially fewer pieces of instream wood, translating to overall lower wood loads (Table 2.8). Trail Creek and its non-driven site pair, North Fork Rock Trail Creek, are both second-order streams and had similar quantities of wood pieces within the study reaches. However, Trail Creek is somewhat unique in that it had the highest riparian basal area, which was mostly comprised by standing dead trees. The majority of instream wood found in the Trail Creek reach was concentrated in four jams that formed along recently downed trees (Fig. 2.5). In North Fork Rock Creek, instream wood was found in two jam formations; but these jams did not appear to have an impact on morphology, and most pieces were more evenly distributed throughout the reach (Fig. 2.5).

Average total piece length ranged from ~ 5 to 9 m across all reaches with fairly consistent average diameters (Table 2.8; Fig. 2.7). The exception was Horse Creek, which only had two pieces of instream wood in the study reach and also had the lowest basal area. The average diameters for the two LW pieces were 19 and 7.95 cm; however, it is difficult to accurately compare these values to the rest of the basin, given the small sample size. Normalized values of average LW piece diameter or volume of LW pieces within the channel between disturbance conditions were not significantly different (Table 2.6). The Kruskal-Wallis nonparametric test revealed that total piece length was not significantly different between non-driven and tie-driven streams; however, the length of LW within the channel of tie-driven reaches was significantly longer than pieces within the channel of non-driven reaches (Table 2.6; Fig. 2.7). Taken

together, the similarities in instream wood dimensions as represented by diameter and total length reflect the traits of the dominant riparian tree species and suggest that the primary recruitment mechanism for the study streams has been individual tree mortality (Benda et al., 2003).

Wood census metrics differed significantly between tie-driven and non-driven reaches, indicating notable differences in the functional and structural role of instream LW pieces (χ^2 tests, Fig. 2.8). The stability of wood pieces, as indicated by the number of anchored piece ends (0, 1, 2), differed significantly between disturbance conditions with more pieces in the non-driven reaches being anchored at two ends (Fig. 2.8A; $\chi^2(2, n = 138) = 7.33, p < 0.05$). Non-driven study reaches also had more pieces in a greater range of decay classes (Fig. 2.8B; $\chi^2(5, n = 138) = 12.02, p < 0.05$). In tie-driven reaches, no pieces were observed in the *rotten* decay class; and 16% of all pieces retained limbs, bark, and needles, indicating that they were recently recruited to the channel. The frequencies of piece function, which infers the morphologic role that each piece plays in the channel, were also different between non-driven and tie-driven reaches. In non-driven reaches, 33% of the pieces were acting as ramps compared to 52% in tie-driven reaches (Fig. 2.8C; $\chi^2(4, n = 138) = 17.21, p < 0.01$). Additionally, 16% of the pieces inventoried in non-driven streams were incorporated into the channel, while no incorporated pieces were inventoried for tie-driven streams. Structural associations of LW pieces indicate the types of instream features that retain wood. Pieces in non-driven reaches were associated with a wider variety of channel structures (Fig. 2.8D; $\chi^2(7, n = 138) = 20.18, p < 0.01$). In both non-driven and tie-driven reaches, the most common structural associations were stream banks (33% and 47%, respectively) and debris jams (30% and 34%, respectively). Tie-driven reaches had no log steps, while six log steps were inventoried for non-driven streams. Approximately 19% of LW pieces inventoried in non-driven reaches were identified as having structural associations other than the main categories listed in Table 2.2. These pieces were primarily ramps and bridges that were held in place by trees in the riparian area. Large wood pieces in the tie-driven reaches were associated with a wider range of channel types compared to non-driven reaches ($\chi^2(7, n = 138) = 23.75, p < 0.001$). The majority of wood pieces were associated with riffle morphologies in non-driven (77%) and tie-driven (63%) reaches. Approximately 35% of LW pieces in tie-driven reaches were found in pools compared to only 11% in non-driven reaches. Sources of LW between non-driven and tie-driven reaches were not significantly different. In non-driven

streams, 11% of the pieces were contributed from the hillslope, 37% were from the riparian area, and 42% of pieces were from unknown sources. In tie-driven reaches, 28% of the pieces were contributed from the hillslope, 36% were from the riparian area, and 36% of pieces were from unknown sources.

Relations among wood loads, riparian and geomorphic variables

Basal area was significantly correlated with the total number of instream wood pieces ($Piece_{Tot}$; $p < 0.1$, $R^2 = 0.48$) and total wood volume (Vol_{tot} ; $p < 0.05$, $R^2 = 0.61$) across all study reaches (Table 2.9). Basal area was the only riparian variable that explained a significant portion of the variation for these LW metrics. Stream power (W ; $p < 0.1$, $R^2 = 0.43$) and reach slope (S ; $p < 0.1$, $R^2 = 0.49$) were correlated with total volume of instream wood for each study reach (Table 2.9). Reach slope was the only control variable significantly related to total volume standardized by unit area (Vol_{Load} ; $p < 0.05$, $R^2 = 0.64$). No variables were significantly correlated with wood load per reach area ($Piece_{Load}$; Table 2.9).

Discussion

Comparisons between non-driven and tie-driven stream reaches indicate that tie-driven reaches are significantly more narrow and shallow and have lower cross-sectional areas compared to non-driven reaches. Additionally, they are characterized by significantly lower cross-sectional roughness and higher width to depth ratios. Non-driven reaches were significantly wider, deeper, and had a larger cross-sectional area and greater cross-sectional roughness values compared to tie-driven pairs. The variety of habitat units across sites reflects the range of morphologic types expected of mountain streams (Montgomery and Buffington, 1997). However, tie-driven streams were dominated by runs or riffles and had proportionally fewer pools compared to non-driven streams, although substrate conditions were similar. Overall, tie-driven streams were associated with lower wood loads and altered load characteristics. Although the dimensions of individual wood pieces are similar, LW in tie-driven streams tends to be younger than those in non-driven streams, and the majority of wood is arranged as ramps. The lack of bedforms associated with LW incorporated in the channel such as log steps and the predominance of plane-bed features found in tie-driven reaches are consistent with Young et al. (1994). Their results indicate that tie-driven channels were largely dominated by plane-bed features with fewer discrete channel units than non-driven reaches (Young et al.

1994). They also identified instream wood as a morphologic control for pool formation in their reference (non-driven) reaches and note the lack of log steps in tie-driven reaches. Direct comparisons between the frequency of channel units and specific riparian stand parameters could not be made because of differences in channel inventory and riparian sampling methods.

Morphologic conditions

The simplified channel morphology associated with tie-driven reaches, as represented by altered channel geometry, lower cross-sectional roughness, and low diversity of bedforms typify the result of adjustments made over the course of decades following the practice of tie-driving. Previous studies examining the effects of LW removal on stream channels have found increases in water velocity (Gregory and Davis, 1992), enhanced scouring of fine sediments (Beschta, 1979), and decreased frequency and size of pools (Lisle, 1986; Richmond and Fausch, 1995; Diez et al., 2000). Increases in velocity and bedload movement that result from wood removal can lead to the straight, featureless bed characteristics of plane-bed morphologies as the channel adjusts between transport-limited and supply-limited phases of sediment loading (Heede, 1985; Montgomery and Buffington, 1997). Reaches characterized as pool-riffle have transitioned to plane-bed channels following events of increased sediment supply, although plane-bed channel morphology is ultimately associated with sediment supply-limited conditions such as bed armoring (Lisle, 1995; Wohl and Cenderelli, 2000). The heightened transport capacity associated with extended plane-bed reaches has been shown to impact rates of wood removal and increase wood recruitment in downstream reaches (Downs and Simon, 2001). The presence of instream wood is an important morphological control on sediment storage, particularly finer size classes (Diez et al., 2000; Montgomery et al., 2003), so a lack of wood can exacerbate armoring and facilitate the export of fine sediment. Given the geomorphic parameters, the present condition of tie-driven streams is characterized as wood supply-limited channels that provide little resistance during times of high flow. This increased transport capacity likely prolongs channel recovery under normal sediment delivery conditions as material is flushed out during peak flows.

Characteristics of instream large wood

In the Medicine Bow National Forest, the number and volume of instream wood pieces remains remarkably low in first-order tie-driven streams and is accumulating in jams in the second-order tie-driven reach. Without human influence, instream LW removal rates reflect

wood decay rates, mechanical breakdown through abrasion and fragmentation, and the overall transport capacity of the channel. Mountain headwater streams are often associated with high wood loads because of their limited transport capacity (Jones et al., 2011) and are frequently characterized by reaches of log step sequences and wood incorporated in the channel (Hyatt and Naiman, 2001). The total volume and volume per unit area of LW in tie-driven streams is low, suggesting that wood-loading patterns reflect the impact of wood removal necessary for tie-driving. However, the limited wood present in tie-driven channels seems to have a larger geomorphic contribution than wood in the non-driven reaches. Localized transitions in habitat units within tie-driven channels were more frequently associated with the presence of wood, as indicated by the difference in the pools associated with wood in tie-driven reaches. The presence of wood in tie-driven reaches results in localized but distinct differences in morphology. In non-driven reaches, wood is more evenly distributed so that the introduction of new pieces into the channel does not influence channel form as noticeably.

Extensive investigations of wood loads in streams of the Colorado Front Range suggest that despite local and basin scale variability, predictable patterns of wood loading correspond to network position (Wohl and Jaeger, 2009). Rates of wood input coupled with geomorphic characteristics combine to create zones of transport limitation where wood loads are high, supply limitation where wood loads are low, and transition areas characterized by high frequencies of jams (Wohl and Jaeger, 2009). However, in Medicine Bow National Forest the practice of tie-driving was so widespread that almost every major drainage basin was affected and has resulted in conditions that contradict this framework. Differences in piece stability and decay class between tie-driven and non-driven reaches indicate that wood in non-driven streams is less mobile, which is consistent with expected transport-limited conditions. Large wood in tie-driven streams is less stable and younger, on average. In our study, much of the LW in older decay classes in tie-driven reaches were pieces located in the various jams in Trail Creek (Fig. 2.8B). The accumulation of wood in these jams, in a second-order tie-driven reach, suggests that the legacy of wood removal upstream may result in more effective wood transport than might be expected. Channel banks were the most common structural association for LW pieces in tie-driven and in non-driven streams, which is likely an artifact of the narrow channels relative to the length of many recruited wood pieces. Bank associations do not necessarily imply stability as shorter and thinner pieces can move under high flow conditions unless additional structures

are present such as riparian vegetation or boulders that can retain the piece. Given the prevalence of tie-driving in the area, it is possible that many headwater streams are effectively supply-limited systems that actively export a portion of recruited wood.

Previous studies of wood loads in Rocky Mountain Front Range streams indicate that larger quantities of wood are associated with increases in watershed area (Richmond and Fausch, 1995). However, wood loads in our reaches did not correspond to this pattern and overall were on the low end of those found in streams of the Colorado Front Range and Wyoming (Table 2.10). Instream wood is a more significant geomorphic mechanism in non-driven reaches as shown by the higher proportion of pieces incorporated in the channel and found in jam formations. While log steps and jams have been identified as the primary wood-based mechanisms inducing channel adjustments in mountain streams (Wohl and Goode, 2008; Beckman and Wohl, 2014), ramp formations were the predominant mechanism contributing to the variety of bedforms in tie-driven reaches. Ramps, or LW pieces that are partially in the channel, were prevalent in tie-driven reaches, yet they represent a limited influence on channel morphology overall. However, ramps deflect flow, help break up bed armoring in localized areas, and contribute to the development of jams. They also represent the initial stage of wood reintroduction following the recovery of the riparian area (Vaz et al., 2013).

Relations among wood loads, riparian and geomorphic variables

Wood recruitment mechanisms in mountain streams are dominated by topography and operate at episodic (landslides, blowdowns, etc.) or continuous (bank erosion, tree mortality) rates (Downs and Simon, 2001; Jones et al., 2011). Large-scale controls on wood recruitment can be categorized as forest characteristics, hydrological processes, geomorphic controls, and management activities (Gurnell et al., 2000). In headwater streams, forest structure and geomorphic controls are the predominant influences on wood recruitment as flow is usually not powerful enough to transport existing pieces. Generally, the frequency of instream wood decreases as channel width increases because of lower storage capacity and the decreased transport potential of the channel (Montgomery et al., 1995; Baillie et al., 2008). However, we observed that the largest wood loads were associated with the widest reach in tie-driven streams. This pattern further corroborates the observation that first-order tie-driven streams may be effective at LW transport despite their relatively small size.

Similarities in piece length and diameter between tie-driven and non-driven reaches suggest that tree mortality is an important recruitment process as most of the LW pieces sampled represented mature tree size classes. The positive correlation between basal area and the total number of pieces (Table 2.9) supports the relationships associated with wood recruitment to the stream channel. Increases in the volume of LW loads is related to the tree size within the adjacent riparian area. When larger scale recruitment controls are considered, a variety of riparian and geomorphic controls influence wood frequency and volume. Basal area and metrics of transport potential (stream power and slope) were much stronger predictors of wood recruitment than physiographic controls representing basin conditions. However — in other studies investigating wood loads — recruitment sources, stand age, and local channel and valley morphology have been identified as dominant controls (Wohl and Cadol, 2011). In this study, no significant relationship between wood load per channel area and drainage area was found, which contradicts expected wood loading relationships associated with position in the network (Table 2.2; Table 2.9). Previous work has shown that lower order streams are associated with greater wood loads per area because of transport limitations associated with smaller channels (Wohl and Jaeger, 2009). The tie-driven streams in this study reflect the opposite: the first-order reaches had less wood when compared to the second-order reaches. Given the pervasiveness of tie-driving, wood loads throughout the Medicine Bow National Forest are undoubtedly altered from what would be considered an undisturbed state.

Investigations into wood loads in the Rocky Mountain Front Range indicate that local variability is a stronger determinant of LW piece frequency at the reach-scale than at the basin-scale controls (Wohl and Cadol, 2011). In this study, the number of LW pieces and local channel roughness in the cross-sectional and longitudinal directions were not significantly related. While channel roughness was significantly different between non-driven and tie-driven reaches, the lack of a direct linear relationship between wood loading and roughness suggests that roughness is likely a secondary factor regulating channel transport capacity and wood retention. Stream power and reach slope were both found to have strong correlations with metrics of wood storage (Table 2.9), particularly as they relate to piece volume. Stream power and reach slope both influence the transport capacity of the channel.

Interestingly, the riparian variables that were not significantly related to wood loads (Table 2.2) across study reaches suggest that LW recruitment dynamics lags behind forest

recovery in the riparian area and the recovery of wood loads within the channel (Benda et al., 2003). The wood loads presented here fall well below many of the estimates made for streams within old growth riparian conditions (Table 10), which may indicate a disruption in wood recruitment. Wood loads were not correlated with stem density, the basal area of standing dead trees, or the proportion of standing dead trees in the riparian area. The lack of relationship between stem density and wood loads indicates that channel condition and transport processes are determining wood retention. The lack of relationship between instream wood loads and the dead basal area or proportion of dead riparian trees attributed to beetle-caused mortality is striking (Table 2.8; Fig. 2.3). These results show that wood recruitment in the study streams has not yet responded to the recent bark beetle infestations in the area, consistent with results found in northern Colorado (Ryan et al., 2014).

Legacies and implications of tie-driving across the Medicine Bow Mountains

The legacies of historic tie-driving within the study area include altered system components such as geomorphic forms, wood loading, and riparian conditions throughout the study region. Tie-driving has not occurred in this region since the 1940s, and in some areas since the early 1900s, yet channel adjustments and wood loading are still in the early stages of recovery. Like other pervasive historic stream disturbances such as mill dams in the northeast (Walter and Merritts, 2008) and logging in coastal Maine (Magilligan et al., 2008) and in the Pacific Northwest (Bilby and Ward, 1991), tie-driving has altered the dominant channel forms and processes characterizing streams in the Medicine Bow Mountains. The alteration of these ecosystems is notable given the area's role as a significant location for recreation and its history of management within the twentieth century. Reference streams that exhibit non-driven conditions may be of little use as targets for management objectives on tie-driven streams. Differences in morphology, and associated processes such as sediment and wood transport, will complicate channel manipulations conducted at the reach scale. For example, engineered log steps are frequently used to promote pool development and habitat heterogeneity. However, placement within a tie-driven reach could result in local scouring and the eventual undercutting of the structure. Management decisions regarding fish passage, habitat availability, and sediment control must be made with the understanding that many streams in the forest may not respond as

expected to strategies implemented at the reach scale, particularly if tie-driving legacies are pervasive across the network in question.

Looking forward, channel response rates in the region may increase given the prevalence of bark-beetle-caused tree mortality throughout the area. The mountain pine beetle and spruce beetle are responsible for the vast majority of tree mortality in the area (Colorado State Forest Service, 2012). In this study, the proportion of standing dead trees attributed to beetle kill in the riparian areas sampled ranged from 41% to 89% (in Beaver Creek and Flume Creek, respectively). This constitutes a large source of recruitable wood in the near future and may represent a reset in terms of wood recruitment to streams at a large scale (Dwire et al., in press). Once LW recruitment begins to occur, future wood loads and channel response may very well obscure the legacies of tie-driving with the coming decades.

Conclusions

Tie-driving represents a pervasive and long-lasting disturbance to stream channel morphology and wood loading and continues to influence the ability of affected channels to retain LW. Tie-driven channels in the Medicine Bow National Forest display simplified morphology as characterized by extensive plane-bed reaches and low abundance of instream wood loads. Evidence of the impacts associated with tie-driving is supported by significant differences in channel geometry, wood loads, and wood recruitment potential. The degree of channel response and recovery of wood loading appears to occur at different rates depending on stream order; first-order tie-driven streams are characterized by supply limitation, while second-order systems are accumulating wood. Despite the extensive literature examining the role of instream wood, this study is one of few studies that addresses channel response following extensive historic disturbance related to tie-driving, including wood load removals and channel simplification.

References

- Abbe, T.B., Montgomery D.R., 1996. Large woody debris jams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers: Research and Management* 12,201-221.
- Angradi, T.R., Bolgrien, D.W., Jicha, T.M., Pearson, M.S., Taylor, D.L., Hill, B.H., 2009. Multispatial-scale variation in benthic and snag-surface macroinvertebrate assemblages in mid-continent US great rivers. *Journal of the North American Benthological Society* 28(1),122-141.
- Baillie, B. R., Garrett, L. G., Evanson, A. W., 2008. Spatial distribution and influence of large woody debris in an old-growth forest river system, New Zealand. *Forest Ecology and Management*, 256(1), 20-27.
- Beckman, N.D., Wohl, E., 2014. Carbon storage in mountainous headwater streams: The role of old-growth forest and logjams. *Water Resources Research* DOI:10.1002/2013WR014167.
- Benda, L., D. Miller, J. Sias, D. Martin, R. Bilby, C. Veldhuisen, and T. Dunne. 2003. Wood recruitment processes and wood budgeting. Pages 49-73 in S.V. Gregory, K.L. Boyer, and A.M. Gurnell, editors. *The ecology and management of wood in world rivers*. American Fisheries Society, Symposium 37, Bethesda, Maryland.
- Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. C Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G.M. Kondolf, P.S. Lake, R. Lave, J.L. Meyer, T.K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. *Science* 308: 636-637.
- Beschta, R. L. 1979. Debris removal and its effects on sedimentation in an Oregon Coast Range stream. *Northwest Science*, 53(1), 71-77.
- Bilby, R.E., Likens, G.E., 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 61(5),1107-1113.
- Bilby, R. E., Ward, J. W., 1991. Characteristics and function of large woody debris in streams draining old-growth, clearcut, and second-growth forests in southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 2499-2508.
- Bisson P.A., R.E. Bilby, M.D. Bryant, C.A. Dolloff, G.B. Grette, R.A. House, M.L. Murphy, K.V. Koski and J.R. Sedell. 1987. Large woody debris in forested streams in the Pacific

- Northwest: past, present and future. In: *Streamside Management: Forestry and Fishery Interactions*. (Eds E.O. Salo & T.W. Cundy), pp. 143–190. Proceedings of the Symposium, February 12–14, 1986, Seattle, Washington, College of Forest Resources, Contribution 57. University of Washington, Washington.
- Brookes, A. 1987. Restoring the sinuosity of artificially straightened stream channels. *Environmental Geology and Water*. 10(1):33-41.
- Brooks, A. P., Brierley, G. J., 2002. Mediated equilibrium: the influence of riparian vegetation and wood on the long-term evolution and behaviour of a near-pristine river. *Earth Surface Processes and Landforms*, 27(4), 343-367.
- Burchsted, D., Daniels, M.D., Thorson, R. and Vokoun, J., 2010. The river discontinuum: Applying beaver modifications to baseline conditions for restoration of forested headwaters. *Bioscience* 60 (11), 908-922.
- Chin, A., Daniels, M.D., Urban, M.A., Piegay, H., Gregory, K.J., Bigler, W., Boyer, K., Butt, A., Grabel, J., Gregory, S.V., LaFrenz, M., Laurencio, L.R., and Wohl, E., 2008. Perceptions of Wood in Rivers and Challenges for Stream Restoration in the United States. *Environmental Management*. 41 (6), 893-903.
- Colorado State Forest Service 2012. 2012 Report on the Health of Colorado’s forests: Forest Stewardship through Active Management. Available from csfs.colostate.edu/pages/pub-csfs2.html [accessed 5 Feb 2014].
- Comiti, F. 2012. How natural are Alpine mountain rivers? Evidence from the Italian Alps. *Earth Surface Processes and Landforms* 37(7):693-707.
- Connell, J.H. 1978. Diversity in Tropical Rain Forests and Coral Reefs. *Science* 199(4335):1302-1310.
- Czarnomski, N.M., Dreher, D.M., Snyder, K.U., Jones, J.A., Swanson, F.J., 2008. Dynamics of wood in stream networks of the western Cascades Range, Oregon. *Canadian Journal of Forestry Research* 38,2236-2248, doi:10.1139/X08-068.
- Dahlstrom, N., Jonsson, K., Nilsson, C. 2005. Long-term dynamics of large woody debris in a managed boreal forest stream. *Forest Ecology and Management* 210(1-3):363-373.
- Daniels, M.D. 2006. Distribution and dynamics of large woody debris and organic matter in a low-energy meandering stream. *Geomorphology*, 77(3-4), 286-298.

- Daniels, M. D., McCusker, M. H. 2010. Operator bias characterizing stream substrates using Wolman pebble counts with a standard measurement template. *Geomorphology*, 115(1), 194-198.
- Daniels, M.D., Rhoads., B.L., 2004. Effect of LWD configuration on spatial patterns of three-dimensional flow in two low-energy meander bends at varying stages. *Water Resources Research*, 40 (11) W11302, doi:10.1029/2004WR003181.
- Díez, J. R., Larrañaga, S., Elozegi, A., Pozo, J. 2000. Effect of removal of wood on streambed stability and retention of organic matter. *Journal of the North American Benthological Society*, 621-632.
- Dillon, G.K., Knight, D.H., Meyer, C. B., 2005. Historic range of variability for upland vegetation in the Medicine Bow National Forest, Wyoming. RMRS-GTR-139, Fort Collins, CO; USDA Forest Service, Rocky Mountain Research Station. 85 pages.
- Downs, P.W., Simon, A., 2001. Fluvial geomorphological analysis of the recruitment of large woody debris in the Yalobusha River network, Central Mississippi, USA. *Geomorphology* 37(1-2),65-91.
- Dwire, K.A., Hubbard, R., Bazan, R. In press. Comparison of riparian and upland forest stand structure and fuel loads in beetle infested watersheds, southern Rocky Mountains. Submitted to *Forest Ecology and Management*
- Finkenbine, J.K., Atwater, J.W., Mavinic, D.S., 2000. Stream health after urbanization. *Journal of the American Water Resources Association*. 36(5),1149-1160.
- Flores, L., Larranaga, A., Diez, J., Elozegi, A., 2011. Experimental wood addition in streams: effects on organic matter storage and breakdown. *Freshwater Biology*, 56(10), 2156-2167.
- Gardeström, J., Holmqvist, D., Polvi, L.E., Nilsson, C., 2013. Demonstration restoration measures in tributaries of the Vindel river catchment. *Ecol. Soc.* 18 (3), 8. <http://dx.doi.org/10.5751/ES-05609-180308>.
- Gippel, C.J. 1995. Environmental hydraulics of larger woody debris in streams and rivers. *Journal of Environmental Engineering*, 121(5), 388-395.
- Gordon, N.D., McMahon, T.A., Finlayson, B.L., Gippel, C.J., Nathan, R.J., 2004. *Stream Hydrology: An Introduction for Ecologists* John Wiley and Sons, West Sussex, England.
- Gregory, K.J. 2006. The human role in changing river channels. *Geomorphology* 79(3-4):172-191.

- Gregory, K. J., Davis, R. J., 1992. Coarse woody debris in stream channels in relation to river channel management in woodland areas. *Regulated Rivers: Research & Management*, 7(2), 117-136.
- Gurnell, A.M., Gregory, K.J., Petts, G.E., 1995. The role of coarse woody debris in forest aquatic habitats: implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5, 143-166.
- Gurnell, A.M., Petts, G.E., Harris, N., Ward, J.V., Tockner, K., Edwards, P.J. Kollmann, J., 2000. Large wood retention in river channels: The case of the Fiume Tagliamento, Italy. *Earth Surface Processes and Landforms* 25,255-275.
- Heede, B.H. 1985. Channel adjustments to the removal of log steps: an experiment in a mountain stream. *Environmental Management* 9:427-432.
- Helfield, J.M., Capon, S.J., Nilsson, C., Jansson, R. Palm, D. 2007. Restoration of rivers used for timber floating: Effects on riparian plant diversity. *Ecological Applications* 17(3):840-851.
- Hyatt, T.L. Naiman, R.J. 2001. The residence time of large woody debris in the Queets River, Washington, USA. *Ecological Applications* 11(1):191-202.
- Jenkins MJ, Herbertson E, Page W, Jorgensen CA. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management* 254:16-34.
- Jones, T. A., Daniels, L. D., Powell, S. R., 2011. Abundance and function of large woody debris in small, headwater streams in the Rocky Mountain foothills of Alberta, Canada. *River research and applications*, 27(3), 297-311.
- Keller, E.A., Swanson, F.J., 1979. Effects of large organic material on channel form and fluvial processes. *Earth Surface Processes and Landforms* 4 (4), 361–380.
- Lancaster, S.T., Hayes, S.K., Grant, G.E., 2003. Effects of wood on debris flow runout in small mountain watersheds. *Water Resources Research* 39(6), doi: 10.1029/2001WR001227.
- Lassette, N.S., Kondolf, G.M., 2012. Large woody debris in urban stream channels: Redefining the problem. *River Research and Applications* 28(9),1477-1487. DOI: 10.1002/rra.1538.
- Lienkaemper, G.W., Swanson, F.J., 1987. Dynamics of large woody debris in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* 17,150-156.

- Lisle, T. E., 1986. Effects of woody debris on anadromous salmonid habitat, Prince of Wales Island, southeast Alaska. *North American Journal of Fisheries Management*, 6(4), 538-550.
- Lisle, T.E. 1995. Effects of coarse woody debris and its removal on a channel affected by the 1980 eruption of Mount St. Helens, Washington. *Water Resources Research* 31(7), 1797-1808.
- Love, J. D., Christiansen, A. C., 1985. *Geologic Map of Wyoming*. US Geological Survey.
- Lowham, H. W. *Techniques for Estimating Flow Characteristics of Wyoming Streams*. Cheyenne: U.S. Geological Survey, Water Resources Division, 1976. Print.
- Magilligan, F.J., Nislow, K.H., Fisher, G.B., Wright, J., Mackey, G. Laser, M., 2008. The geomorphic function and characteristics of large woody debris in low gradient rivers, coastal Maine, USA. *Geomorphology* 97,467-482.
- Marston, R. A., Girel, J., Pautou, G., Piegay, H., Bravard, J. P., & Arneson, C., 1995. Channel metamorphosis, floodplain disturbance, and vegetation development: Ain River, France. *Geomorphology*, 13(1), 121-131.
- Mellina, E., Hinch, S.G., 2009. Influences of riparian logging and instream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. *Canadian Journal of Forestry Research* 39,1280-1301, doi:10.1139/X09-037.
- Miller, R.R. 2010. *Is the past present? Historical splash-dam mapping and stream disturbance detection in the Oregon coastal province*. Thesis. Oregon State University.
- Montgomery, D.R., Buffington, J.M., 1997. Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* 109(5),596-611.
- Montgomery, D.R., Buffington, J.M., Smith, R.D., Schmidt, K.M., Pess, G.,1995. Pool spacing in forest channels. *Water Resources Research* 31(4),1097-1105.
- Montgomery, D.R., Massong, T.M., Hawley, S.C.S., 2003. Influence of debris flows and log jams on the location of pools and alluvial channel reaches, Oregon Coast Range. *Geological Society of America Bulletin* 115,78-88.
- Murphy, M.L., Koski, K.V., 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. *North American Journal of Fisheries Management* 9,427-436.

- Nilsson, C., Lepori, F., Malmqvist, B., Tornlund, E., Hjerdt, N., Helfield, J.M., Palm, D., Ostergen, J., Jansson, R., Brannas, E., Lundqvist, H. 2005. Forecasting environmental response to restoration of rivers used as log floatways: An interdisciplinary challenge. *Ecosystems* 8(7):779-800.
- Nowakowski, A.L., Wohl, E., 2008. Influences on wood load in mountain streams of the Bighorn National Forest, Wyoming, USA *Environmental Management* 42: 557-571.
- Palmer, M.A. 2009. Reforming watershed restoration: Science in need of application and applications in need of science. *Estuaries and Coasts* 32(1):1-17.
- Philips, J.D., Park, L., 2009. Forest blowdown impacts of Hurricane Rita on fluvial systems. *Earth Surface Processes and Landforms* 34:1069-1081, DOI: 10.1002/esp.1793.
- Piégay, H., Gregory, K. J., Bondarev, V., Chin, A., Dahlstrom, N., Eloegi, A., Gregory, S.V., Joshi, V., Mutz, M., Rinaldi, M., Wyzga, B., Zawiejska, J., 2005. Public perception as a barrier to introducing wood in rivers for restoration purposes. *Environmental Management* 36(5),665-674.
- PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 9 Sept 2013.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58 (6): 501-517.
- Richmond, A.D., Fausch, K.D., 1995. Characteristics and function of large woody debris in mountain streams of northern Colorado. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1789-1802.
- Rosgen, D.L. 1994. A classification of Natural Rivers. *Catena* 22(3),169-199.
- Ryan, S.E., Bishop, E.L, Daniels, J.M., 2014. Influence of large wood on channel morphology and sediment storage in headwater mountain streams, Fraser Experimental Forest, Colorado. *Geomorphology* 217, 73-88.
- Sedell, R., Leone, F.N., Duval, W.S., 1991. Water transportation and storage of logs. *American Fisheries Society Special Publication* 19,325-368.
- Segura, C., Booth, D.B., 2010. Effects of geomorphic setting and urbanization on wood, pools, sediment storage, and bank erosion in Puget Sound streams. *Journal of the American Water Resources Association* 46(5),972-986.

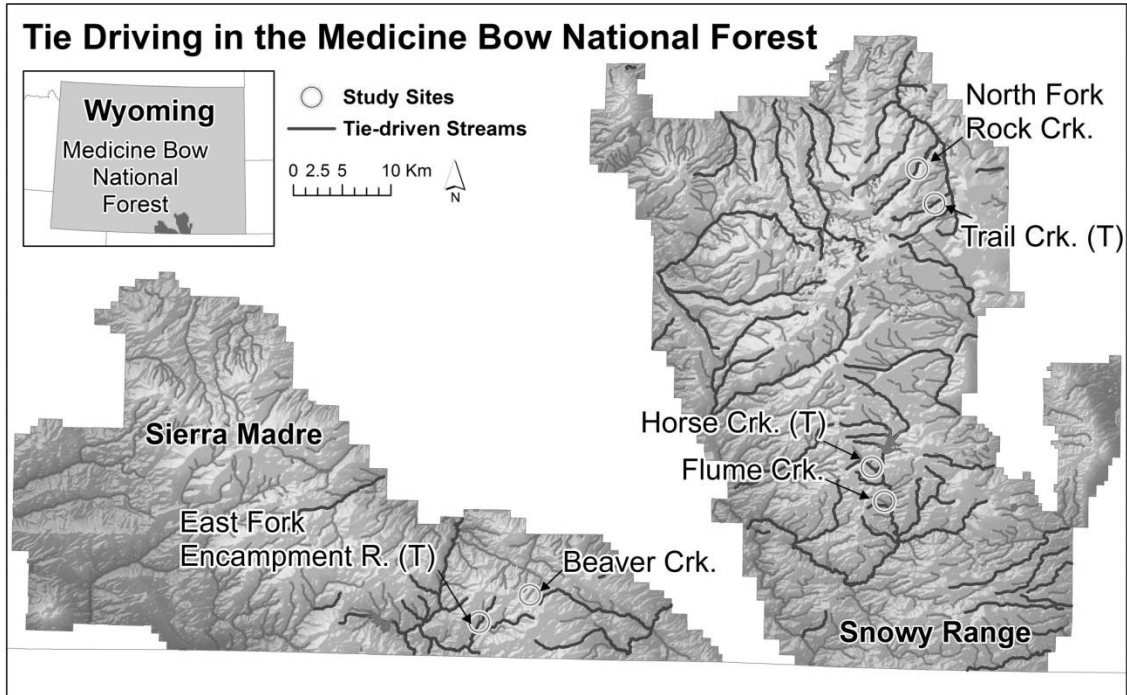
- Simon, A., Castro, J., 2003. Measurement and analysis of alluvial channel form. In: G.M. Kondolf and H. Piégay (eds), *Tools in Fluvial Geomorphology*.
- Swanson, F. J., Lienkaemper, G. W., Sedell, J. R., 1976. History, physical effects, and management implications of large organic debris in western Oregon streams. U.S. For. Serv. Gen. Tech. Rep. PNW-56.
- Thompson, D. M., 1995. The effects of large organic debris on sediment processes and stream morphology in Vermont. *Geomorphology* 11(3): 235-44.
- Vaz, P.G., Merten, E.C., Warren, D. R., Robinson, C.T., Pinto, P., Rego, F.C., 2013. Which stream wood becomes functional following wildfires? *Ecological Engineering* 54,82-89.
- Wallace, J. B., Webster, J. R., Eggert, S. L., & Meyer, J. L. 2001. Small wood dynamics in a headwater stream. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen*, 27(3), 1361-1365.
- Walter, R.C., Merritts, D.J. 2008. Natural streams and the legacy of water-powered mills. *Science* 319(5861):299-304.
- Webb, A.A., Erskine, W.D., 2003. A practical scientific approach to riparian vegetation rehabilitation in Australia. *Journal of Environmental Management* 68(4),329-341.
- Wohl, E., 2001., *Virtual Rivers: Lessons from the Mountain Rivers of the Colorado Front Range*. Yale University Press.
- Wohl, E., 2006. Human impacts to mountain streams. *Geomorphology* 79(3-4),217-248.
- Wohl, E., Cadol, D. 2011. Neighborhood matters: Patterns and controls on wood distribution in old-growth forest streams of the Colorado Front Range, USA. *Geomorphology*, 125(1), 132-146.
- Wohl, E., Cenderelli, D.A. 2000. Sediment deposition and transport patterns following a reservoir sediment release. *Water Resources Research* 36(1):319-333.
- Wohl, E., Goode, J.R. 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. *Water Resources Research* 44(W09429),1-14.
- Wohl, E., Jaeger, K. 2009. A conceptual model for the longitudinal distribution of wood in mountain streams. *Earth Surface Processes and Landforms*, 34(3), 329-344.
- Wohl, E., Merritt, D., 2008. Reach-scale channel geometry of mountain streams. *Geomorphology* 93 (3-4), 168-85.

- Wohl, E., Ogden, F.L., and Goode, J.R., 2009. Episodic wood loading in a mountainous neotropical watershed. *Geomorphology* 111,149-159.
- Wohl, E., Cenderelli, D. A., Dwire, K. A., Ryan-Burkett, S. E., Young, M. K., Fausch, K. D. 2010. Large in-stream wood studies: a call for common metrics. *Earth Surface Processes and Landforms*, 35(5), 618-625.
- Young, M.K., Haire, D., Bozek, M.A., 1994. The effect and extent of railroad tie drives in streams of southeastern Wyoming. *Western Journal of Applied Forestry* 9(4), 125-130.
- Zelt, R.B., Wohl, E. 2004. Channel and woody debris characteristics in adjacent burned and unburned watersheds a decade after wildfire, Park County, Wyoming. *57(3-4):217-233.*

Figure 2.1 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.



Figure 2.2 Location of tie-driven streams and study reaches in the Medicine Bow National Forest, southeast Wyoming. Heavy lines indicate all known tie-driven streams. The photographs compare tie-driven and non-driven conditions for each pair of study reaches.



East Fork Encampment R. (Tie-driven)



Horse Crk. (Tie-driven)



Trail Crk. (Tie-driven)



Beaver Crk. (Non-driven)



Flume Crk. (Non-driven)



North Fork Rock Crk. (Non-driven)

Figure 2.3 Density (stems ha⁻¹, live and dead, ≥ 10 cm DBH) for stems of all species by diameter class (5-cm increments) for non-driven and tie-driven riparian plots. Species sampled include subalpine fir, lodgepole pine, and Engelmann spruce.

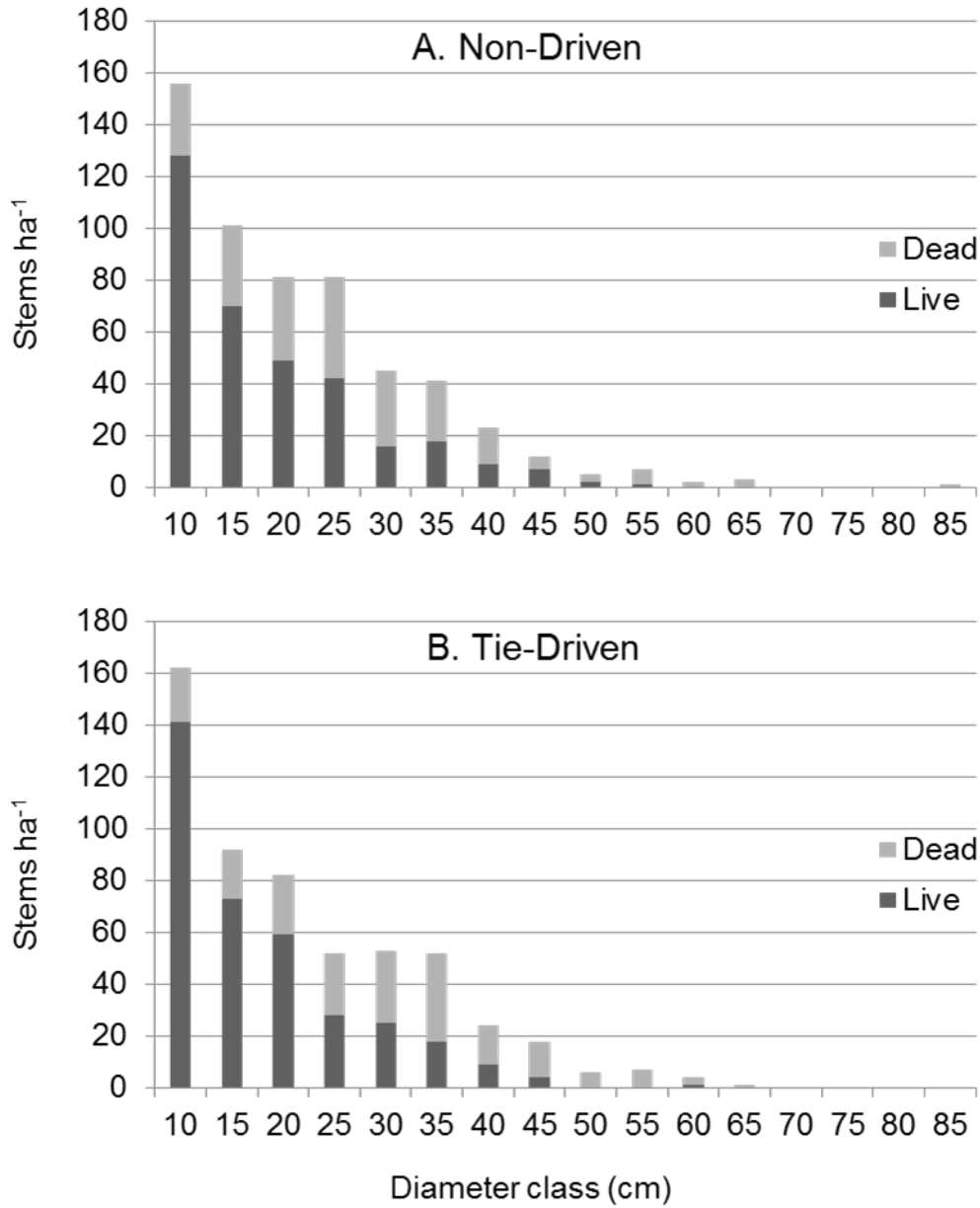


Figure 2.4 Box plots comparing scaled values of (A) channel width, (B) average depth, and (C) cross-sectional area as well as (D) width-to-depth ratios (W:D) and (E) cross-sectional roughness values between non-driven and tie-driven sites. Roughness was calculated as the standard deviation of surveyed bed elevations. Grey boxes signify the non-driven reach within the study pair.

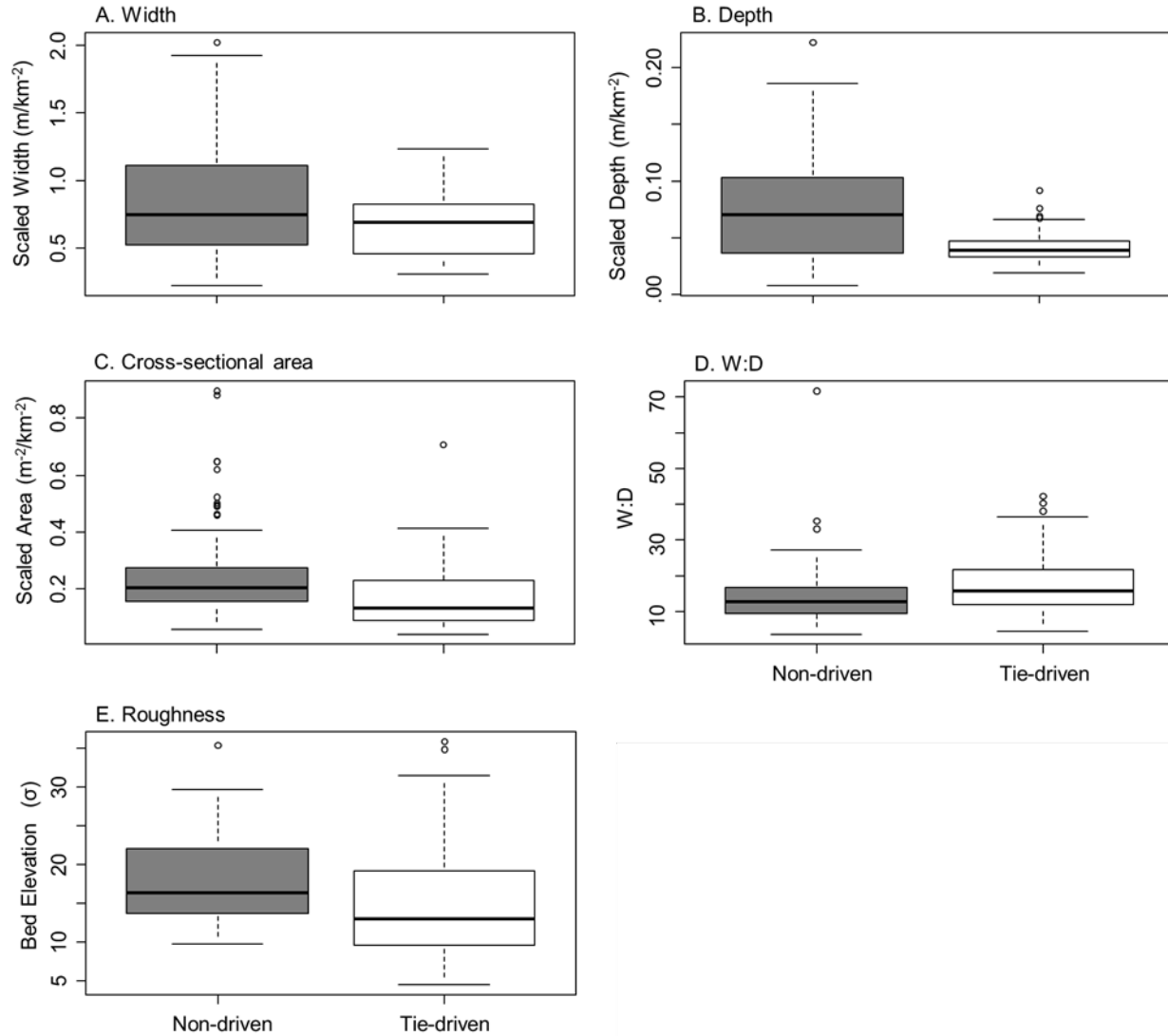


Figure 2.5 Longitudinal profiles of all reaches with cumulative accumulation of all inventoried in-channel wood. Bed elevations are shown with a solid black line, water surface elevations are shown with a gray dotted line, and cumulative frequencies of wood loads are shown with a black dashed line. Because of the low number of pieces ($n = 2$) for Horse Creek, the locations of each piece are shown instead of cumulative frequency. Habitat units are identified at the top of the graph, and wood-forced morphologies are denoted with an underline. Codes for habitat units are as follows: C = cascade, P = pool, R = run, Ri = riffle, S = step.

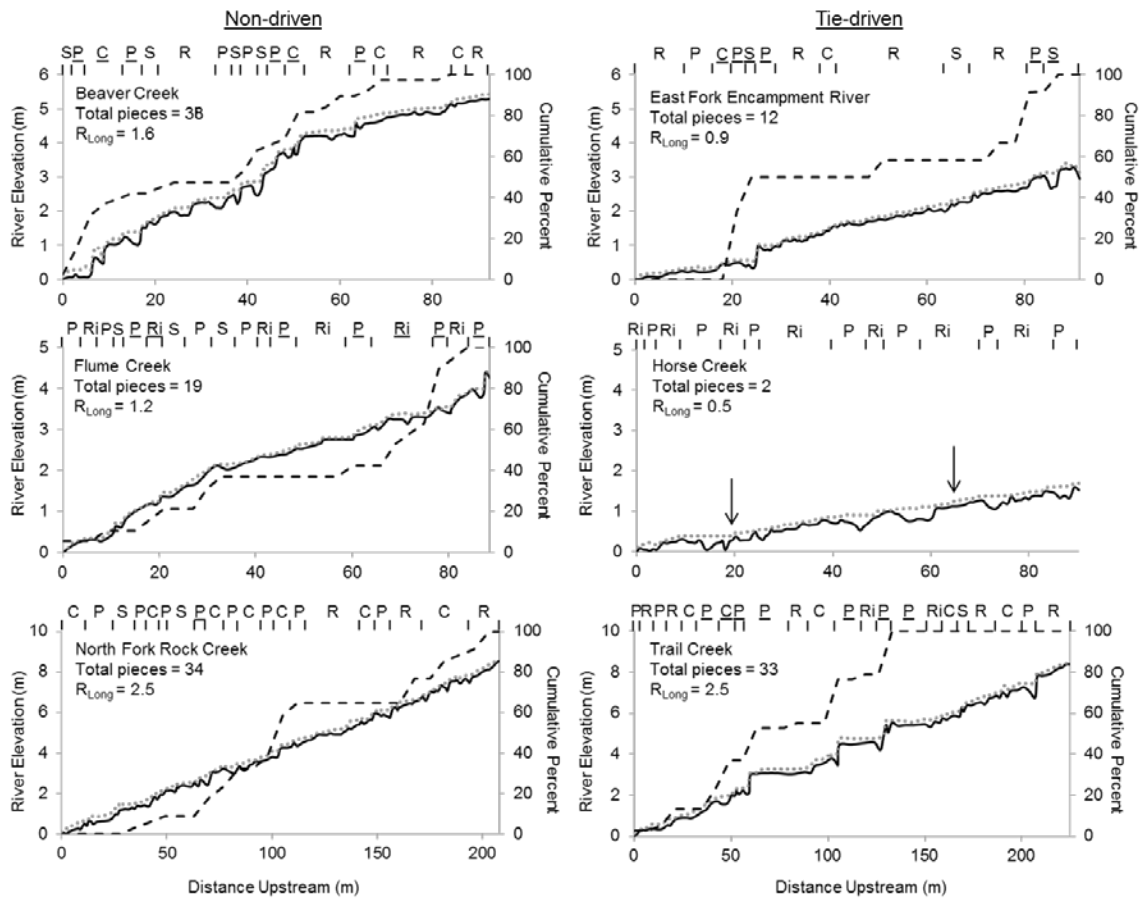


Figure 2.6 Box plots displaying grain size distributions per habitat unit for paired reaches. Grey boxes signify grain size distributions for the non-driven reach within the study pair. The dark black line within the box plots denotes D_{50} .

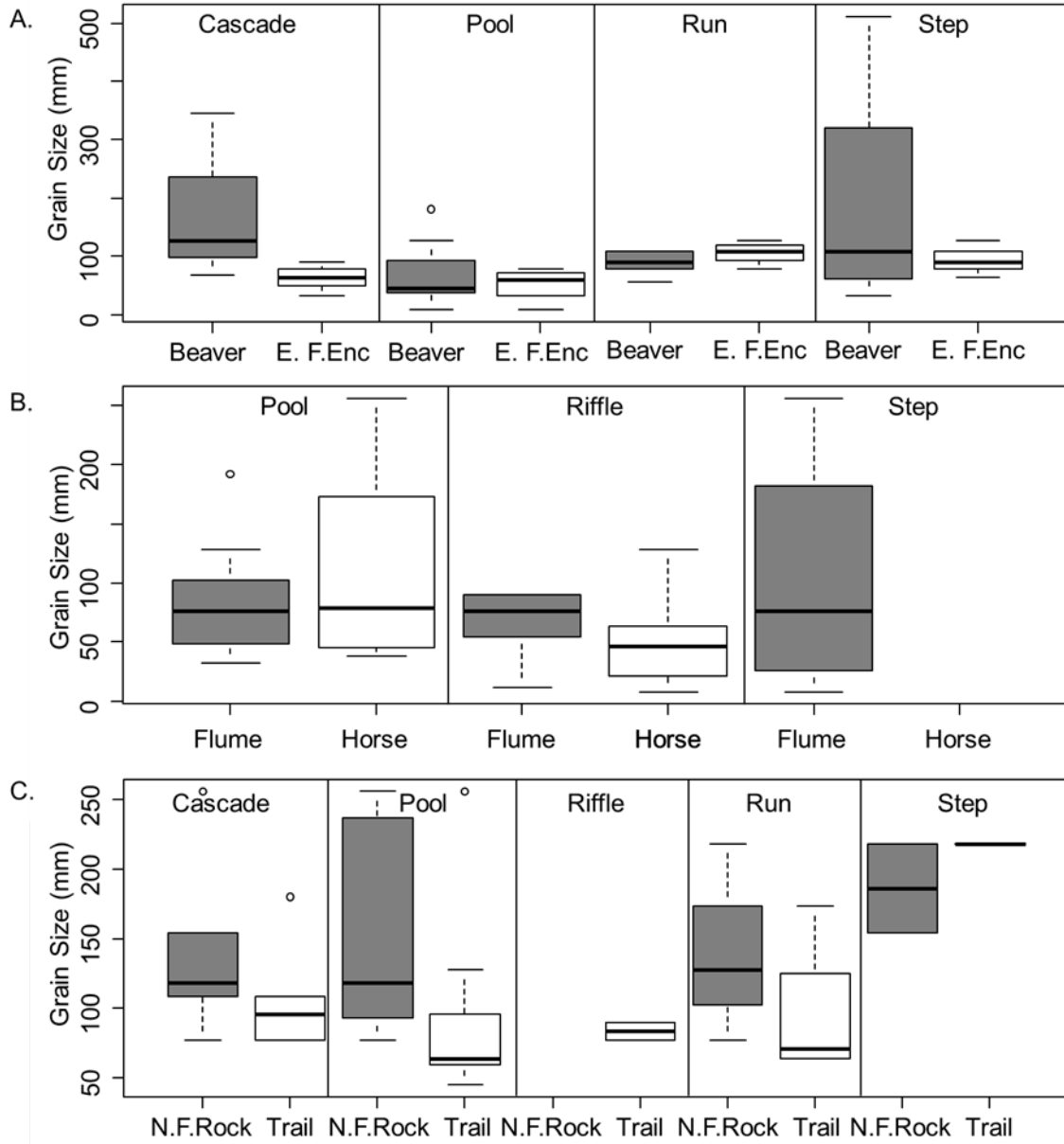


Figure 2.7 Box plots of (A) mean piece diameter and (B) total piece length by study reach. Boxes with grey shading correspond to non-driven reaches, while white boxes correspond with tie-driven reaches. Mean diameter is the average of the two measured end diameters for each piece. Raw values are plotted for Horse Creek ($n = 2$) because only two pieces were found in the study reach. Average diameter and total length between tie-driven and non-driven reaches were not significantly different between tie-driven and non-driven reaches.

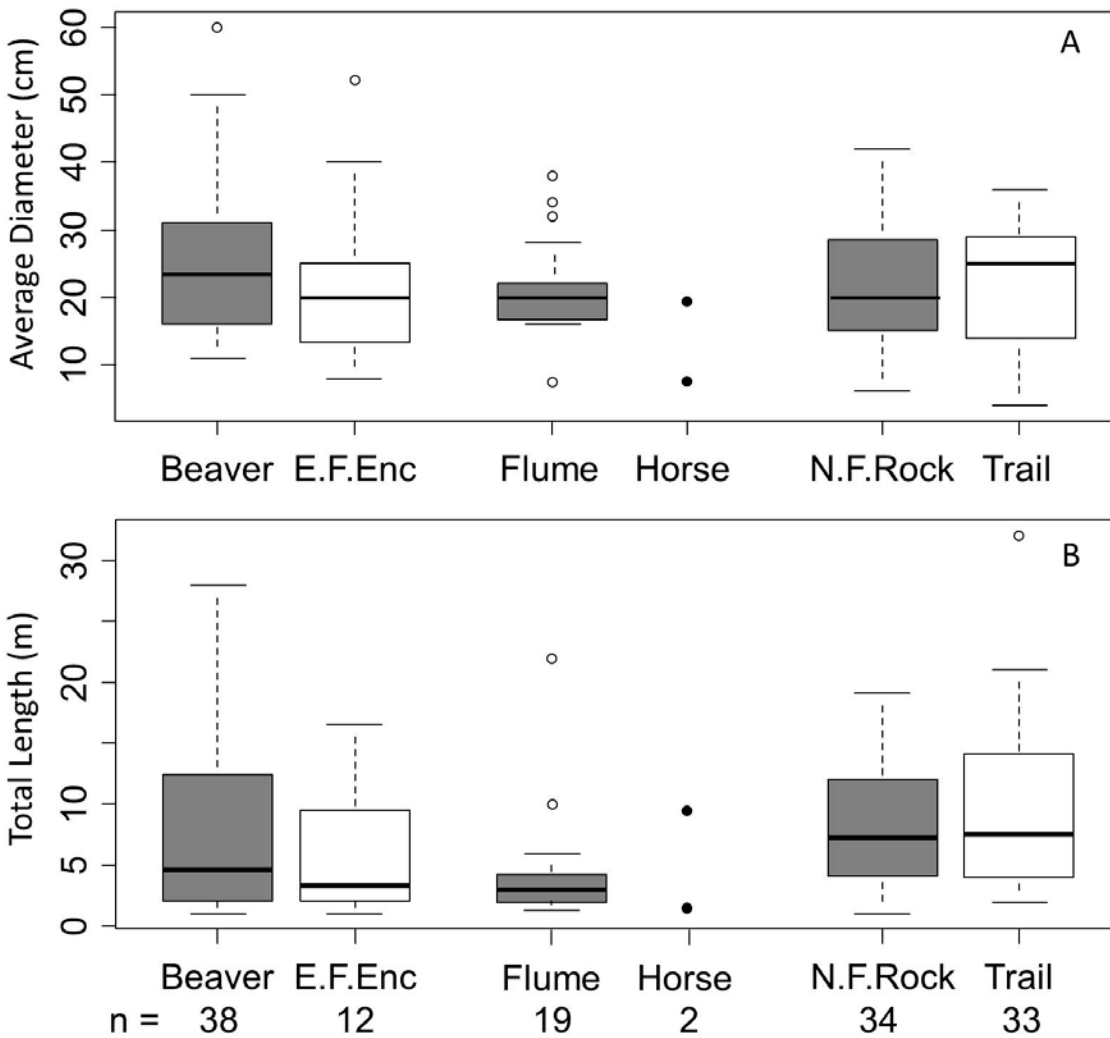


Figure 2.8 Piece frequencies for instream wood characteristics for tie-driven and non-tie-driven study reaches. All p -values represent the results of χ^2 analyses on group difference.

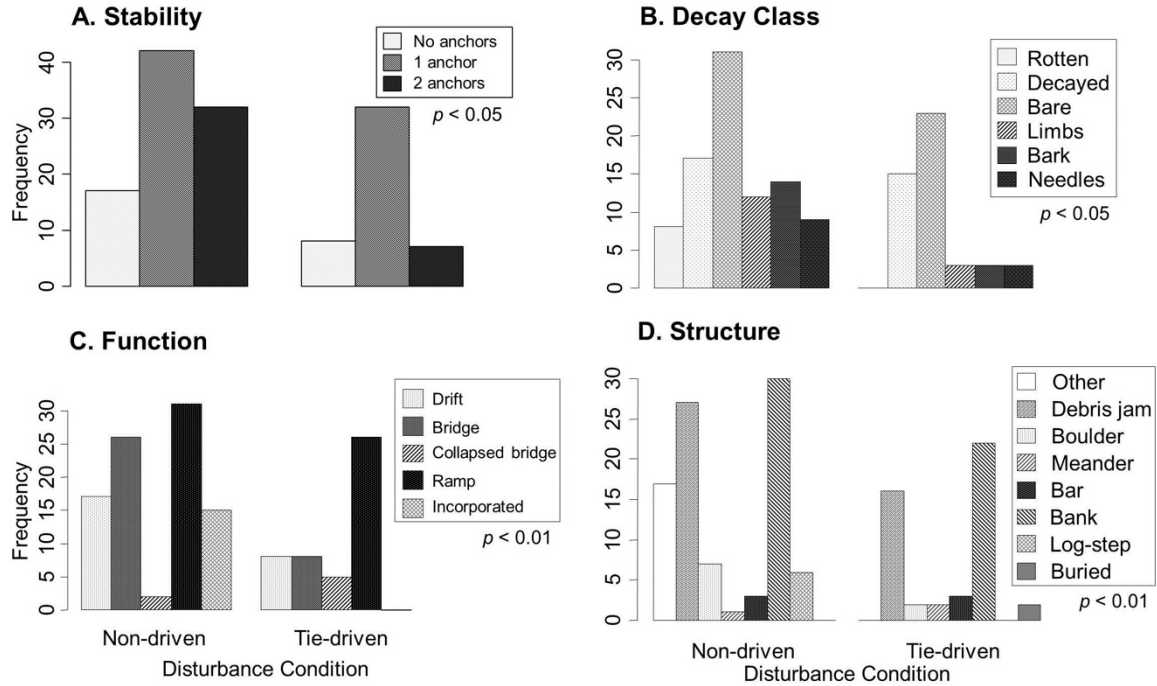


Table 2.1 Observed responses in channel geomorphology to channel modifications related to timber floating activities.

Modification	Longitudinal	Cross-sectional	Planform	Sediment Properties	Hydraulics
In-channel wood removal		- widening and aggradation ^a	- lower diversity of bedforms ^a		
Splash dams		- channel incision ^a -decreased floodplain connectivity ^c	- Fewer pools -lower diversity of bedforms ^{abce} - decreased sinuosity ^e -inundated riparian area ^e	- Increased erosion and scouring ^b - bed armoring ^a -decreased range of sediment sizes ^b	- increased flooding upstream of dam ^e -altered flow regime downstream of dam ^e
Feeder flumes			- decreased sinuosity ^e		- Reduced hyporheic exchange ^e -dewatering of backwaters, side channels, or other reaches ^e - altered flow regime downstream of flume inlet and outlet ^e
Boulder removal	-reduced channel roughness ^e	-homogenous channel depth ^e -reduced channel roughness ^e			

Channelization	-reduced channel roughness ^e	- reduced channel width ^d -decreased floodplain connectivity ^d	- decreased sinuosity ^d -homogeneity of bedforms ^{c, d}	-loss of fine grain sediment ^d	-altered flow regimes and decreased flood frequencies ^{c,e} -increased flow velocity ^d
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Table 2.2 Variables recorded for each piece of instream large wood (LW; from Wohl et al. 2010).

Variable	Categories	Description
Stability: potential mobility of piece, as defined by number of anchor points	0 - no ends	neither end of the wood is anchored in a bank or other structure
	1 - one end	one end is anchored in the bank or other structure
	2 - two ends	both ends are anchored in place
Decay class: qualitative assessment of piece age	0 -rotten	soft wood that can be broken apart easily
	1 - decayed	soft wood that cannot be pulled apart easily
	2 - bare	little to no bark present
	3 - limbs	limbs are intact and may have some or most of the bark intact
	4 - bark	bark is intact
	5 - needles	green or brown needles or leaves still attached
Function: process based descriptor of the geomorphic contribution of the piece	0 - drift	sitting on a bar with both ends within active channel
	1 - bridge	both ends above active channel, center suspended above
	2 - collapsed bridge	two ends on bank, broken in the middle
	3 - ramp	one end in channel, other end out of active channel
	4 - incorporated	portion of wood is buried in channel (may or may not be a step)
Structure: individual channel feature that contributes to the retention of the piece	1 - Debris Jam	part of a jam of 3 or more pieces
	2 - Tree/Rootwad	associated with a living tree or rootwad
	3 - Boulder	associated with a boulder in the stream
	4 - Meander	caught on the outside of a meander
	5 - Bar	sitting on a point or mid-stream bar
	6 - Bedrock	caught on bedrock
	7 - Beaver Dam	part of a beaver dam
	8 - Bank	imbedded in the bank, buried by soil or bank materials
	9 - Log step	forms a step in the stream
	10 - Buried in bed	portion of log is buried in channel bed, but is NOT functioning as a step
	0 - None/Other	something else (specify)
Channel Type: the larger morphologic unit where the piece is found	1 - pool	flat surface, deep with a downstream control
	2 - riffle	shallow, finer grained 1-2% slope
	3 - glide	between pool and riffle, no downstream control
	4 - rapid	(plane bed) 2.5 - 4 % slope, poorly defined steps, moderately steep
	5 - step/pool	well defined step pool structure
	6 - cascade	very steep, fall, irregular step-pool morphology
	7 - other	explain in comments area

Source: assessment of recruitment source	0 - unknown	source of wood cannot be determined
	1 - riparian	source of wood appears from relatively flat surface adjacent to stream channel
	2 - hillslope	wood originates from steeper landform -- either a depositional feature (moraine) or valley wall
	3 - floated	origin of wood is from upstream and has been transported into place
	4 - avalanche	wood appears to have been transported by moving snow
	5 - other	other clearly defined source -- explain in comments section

Table 2.3 Description of control and response variables used in the multiple regression analyses. Control variables are grouped by category.

Response Variables			
	Variable	Description (units)	
	Piece _{Tot}	Number of pieces per study reach (#)	
	Piece _{Load}	Number of pieces/channel area (m ²)	
	Vol _{Tot}	Total volume of wood per study reach (m ³)	
	Vol _{Load}	Total volume/channel area (m ³ /m ²)	
Control Variables			
Physiographic	Abbreviation	Variable (units)	Description
	Drive	Drive	Categorical (non-driven=1, tie-driven=2)
	Elev	Elevation (m)	Continuous; derived from 10 m resolution digital elevation models
	Area	Drainage area (km ²)	Continuous; watershed area upstream from study reach delineated using 10 m resolution digital elevation models
Riparian	StDe	Stem density (stems ha ⁻¹)	Continuous; calculated from riparian plot data
	BaArea	Basal area (m ² ha ⁻¹)	Continuous; calculated from riparian plot data and includes all trees sampled
	BaDead	Basal area of dead trees (m ² ha ⁻¹)	Continuous; calculated from riparian plot data and includes only dead trees sampled
	PDead	Proportion of dead trees (%)	Continuous; Percentage of dead trees within sampled plots
Geomorphic	ChW	Average channel width (m)	Continuous; Calculated from surveyed cross-sections
	R	Roughness (σ_z)	Continuous; standard deviation of bed elevation measurements obtained from surveyed cross-sections
	W	Total Stream Power	Continuous; Calculated from the equation $W=gQ_2S$ where g is the specific weight of water (9800 N/m ²), Q_2 is the peak flow rate with a 2-year return frequency, and S is reach slope (m/m). Values of Q_2 were estimated using regional regression equations (Lowham 1976).
	S	Reach Slope	Continuous; Obtained from surveyed longitudinal profile (m/m)

Table 2.4 Study reach characteristics^a.

Reach (Pair)	Disturbance condition	Stream Order	Riparian Plots (no.)	A _{Basin} (km ²)	E (m)	A _{Reach} (m ²)	L (m)
Beaver Creek (A)	Non	1	2	2.66	2884	336.0	92.3
East Fork Encampment River (A)	Tie	1	2	4.27	2728	305.3	91.4
Flume Creek (B)	Non	1	2	3.47	2698	231.0	88.5
Horse Creek (B)	Tie	1	2	7.28	2835	275.3	90.25
North Fork Rock Creek (C)	Non	2	3	14.24	2948	1476.8	208.0
Trail Creek (C)	Tie	2	4	8.26	2991	1478.0	225.0

^a A_{Basin} =contributing drainage area; E=elevation; A_{Reach} = area of reach calculated from reach length and average bankfull width; L=reach length

Table 2.5 Mean channel geometry metrics. Reach values represent averages over 30 surveyed cross-sections for each study reach (n=30).^a

Reach (Pair)	Disturbance condition	S (m/m)	W (m)	D (m)	Area (m ²)	W:D	R _{XS}	R _{LONG}
Beaver Creek (A)	Non	0.06	3.64±0.15 (2.2-5.38)	0.3±0.02 (0.16-0.59)	1.003±0.1 (0.4-2.38)	13.25±0.92 (5.78-26.91)	16.94±0.98 (10.57-29.67)	1.6
East Fork Encampment River (A)	Tie	0.04	3.34±0.1 (2.03-4.6)	0.16±0.01 (0.08-0.25)	0.503±0.03 (0.22-0.82)	22.73±1.47 (12.86-42.33)	9.19±0.50 (4.52-15.84)	0.9
Flume Creek (B)	Non	0.02	2.61±0.12 (1.5-4.08)	0.29±0.02 (0.14-0.57)	0.630±0.05 (0.2-1.29)	10.02±0.66 (3.7-19.98)	16.02±0.82 (9.7-26.85)	1.2
Horse Creek (B)	Tie	0.02	3.05±0.1 (2.25-4.1)	0.27±0.02 (0.14-0.55)	0.69±0.04 (0.3-1.14)	12.41±0.82 (4.52-21.76)	14.46±0.86 (8.36-27.41)	0.5
North Fork Rock Creek (C)	Non	0.04	7.1±0.28 (3.15-12.4)	0.42±0.03 (0.11-0.72)	2.814±0.22 (0.81-5.79)	20.13±2.15 (4.4-71.76)	20.17±1.04 (9.88-35.28)	2.5
Trail Creek (C)	Tie	0.04	6.54±0.3 (3.4-10.2)	0.41±0.02 (0.23-0.76)	2.401±0.16 (1.02-5.85)	17.38±1.36 (7.27-38.17)	21.70±1.19 (12.27-35.85)	2.5

S= channel gradient obtained from surveyed longitudinal profiles; W=average bankfull channel width; D=average bankfull depth; A=average cross-section area; W:D= average width to depth ratio; R_{XS} =average cross-sectional roughness represented as the standard deviation of surveyed bankfull depths; R_{LONG} = longitudinal channel roughness represented as the standard deviation of depths surveyed along the thalweg.

Table 2.6 Results of ANOVA and Kruskal-Wallis tests testing differences in geomorphologic variables between tie-driven and non-driven study reaches. The ANOVA was run on log transformed variables to meet assumptions of normality.

ANOVA			
	Ndf, Ddf	F	Pr(>F)
<u>Morphology</u>			
LogWidth_Scaled	1, 178	12.16	0.0006**
LogDepth_Scaled	1, 178	28.73	0.0006**
LogArea_Scaled	1, 178	23.33	0.0006**
LogW:D	1, 178	9.419	0.002*
LogRough	1, 178	14.07	0.0002**
<u>LW Dimensions</u>			
Diameter _{Avg}	1, 136	1.593	0.209
Volume _{Channel}	1, 136	0.092	0.763
Kruskal-Wallis			
	Ndf	Chi-squared	Pr(>F)
<u>LW Dimensions</u>			
Length _{Total}	1	1.1601	0.2814
Length _{Channel}	1	4.1055	0.0427^

*** indicates significance at the $p < 0.001$ level, * at the $p < 0.01$ level, and ^ at the $p < 0.05$ level.

Table 2.7 Habitat unit characteristics for each study reach. ^a

Site	F	A	A%	D ₁₆	D ₅₀	D ₈₄	D _g
Beaver Creek (A: Non-driven)							
cascade	4.3	20.5 (±5.9)	19.2	95.8 (±17.5)	180.5 (±33.6)	316.0 (±40.0)	172.8 (±27.0)
pool	6.5	10.4 (±1.4)	22.7	17.0 (±3.8)	69.9 (±14.1)	128.4 (±14.0)	44.7 (±7.3)
run	4.3	34.1 (±3.1)	53.1	37.1 (±2.1)	87.9 (±5.3)	142.1 (±11.2)	71.2 (±3.5)
step	4.3	4.1 (±0.3)	5.1	49.1 (±5.8)	190.5 (±50.0)	236.5 (±42.5)	105.0 (±15.0)
E.F. Encampment River (A: Tie-driven)							
cascade	2.2	15.0 (±3.4)	13.1	33.2 (±3.0)	62.0 (±7.8)	160.1 (±16.7)	72.8 (±7.0)
pool	4.4	10.0 (±1.7)	11.6	29.5 (±4.2)	50.9 (±8.0)	148.6 (±19.4)	59.5 (±3.5)
run	4.4	55.8 (±8.1)	65.2	59.8 (±6.4)	105.8 (±5.7)	236.5 (±49.8)	117.1 (±18.1)
step	4.4	11.5 (±2.4)	10.0	22.2 (±3.4)	94.0 (±8.6)	155.1 (±11.5)	55.6 (±5.1)
Flume Creek (B: Non-driven)							
pool	10.1	6.8 (±1.3)	32.9	31.4 (±4.0)	86.0 (±13.8)	157.7 (±21.5)	66.2 (±7.3)
riffle	6.7	12.3 (±1.8)	50.8	23.8 (±5.3)	66.8 (±7.5)	123.1 (±4.7)	48.7 (±4.4)
step	3.4	5.9 (±1.6)	16.3	81.9 (±28.3)	104.5 (±26.5)	176.2 (±16.5)	106.1 (±24.8)
Horse Creek (B: Tie-driven)							
pool	8.8	16.9 (±3.0)	39.6	66.5 (±20.0)	111.0 (±20.2)	181.3 (±17.5)	100.5 (±17.1)
riffle	8.8	25.7 (±6.6)	60.4	24.4 (±3.8)	49.9 (±9.6)	148.3 (±22.6)	58.6 (±8.8)
N.F. Rock Creek (C: Non-driven)							
cascade	2.9	114.7 (±20.8)	46.2	65.6 (±3.3)	138.8(±14.4)	192.9 (±13.0)	111.3 (±5.3)
pool	3.8	38.6 (±4.0)	20.7	91.1 (±18.1)	153.8 (±17.6)	203.0 (±12.1)	130.4 (±15.6)
run	1.4	150.6 (±11.9)	30.3	100.1 (±16.2)	141.0 (±16.4)	205.7 (±20.0)	140.8 (±16.7)
step	1.0	20.8 (±4.5)	2.8	127.8 (±17.0)	186.0 (±10.4)	218.0 (±12.3)	165.6 (±16.0)
Trail Creek (C: Tie-driven)							
cascade	2.2	97.9 (±7.3)	34.2	51.3 (±3.2)	107.8 (±9.3)	192.0 (±3.6)	98.7 (±3.6)
pool	3.6	22.6 (±2.3)	12.6	66.2 (±17.1)	92.4 (±15.4)	144.9 (±12.7)	93.1 (±15.0)

riffle	0.8	69.1 (± 2.8)	9.7	64.0 (± 0)	83.5 (± 2.0)	116.6 (± 3.5)	86.3 (± 1.3)
run	1.7	143.5 (± 19.9)	40.1	47.0 (± 3.3)	94.5 (± 11.5)	163.3 (± 15.6)	87.4 (± 7.2)
step	0.9	24.5 (± 1.8)	3.4	139.4 (± 3.5)	218.0 (± 0)	256.0 (± 0)	188.8 (± 2.4)

F=frequency of each habitat unit in reach per 100 m of channel length; A= average area of habitat units (m²); A_% = cumulative percent of area occupied by each respective unit; D₁₆= grain size for the 84 percentile; D₅₀=median grain size; D₈₄=grain size for the 84 percentile; D_g=geometric mean, computed as [(D₁₆)(D₈₄)]^{0.5}

Table 2.8 Reach averages of existing instream wood loads. Jams are defined as having a minimum of three LW pieces that are in contact with one another.

Site (Pair)	Disturbance condition	Stream Order	Piece Total	Proportion in jam (%)	Wood _{Load}	Total Wood _L	Channel Wood _L
Beaver Creek (A)	Non	1	38	26.3	0.11	7.11 ± 1.1 (1.0 – 27.9)	2.95 ± 0.39 (1-10.7)
East Fork Encampment River (A)	Tie	1	12	0	0.04	5.62 ± 1.42 (1.0-16.5)	3.12 ± 0.79 (0.5-9.1)
Flume Creek (B)	Non	1	19	31.5	0.08	4.62 ± 1.12 (1.2-22)	2.32 ± 0.28 (0.5-6.2)
Horse Creek (B)	Tie	1	2	0	0.01	1.95; 9.5*	1.95; 4*
North Fork Rock Creek (C)	Non	2	34	32.3	0.02	8.36 ± 0.87 (1.0-19.1)	3.62 ± 0.47 (0.5-11.2)
Trail Creek (C)	Tie	2	33	48.5	0.02	9.24 ± 1.2 (1.9-32.2)	4.27 ± 0.48 (1.4-13.1)

Wood_{Load}= number of pieces per m²; Total Wood_L=average total piece length (m); Channel Wood_L= average piece length within the bankfull channel (m). *Total Wood_L and Channel Wood_L for Horse Creek are raw piece dimensions.

Table 2.9 Linear models assessing relationships relating wood loading metrics (response variables) to geomorphic and riparian control variables.

Response Variable	Control Variable	<i>p</i> -Value	Adj. R ²
Piece _{Tot}	BaArea	0.08 [^]	0.48
Piece _{Load}	n/a		
Vol _{Tot}	BaArea	0.04*	0.61
	W	0.1 [^]	0.43
	S	0.07 [^]	0.49
Vol _{Load}	S	0.03*	0.64

* indicates significance at $p < 0.05$; [^]indicates significance at $p < 0.1$

Table 2.10 Summary of wood loads in other Rocky Mountain streams. Type designations refer to descriptors of riparian condition used in the original publication.

Region	Type	Pieces/100 m	Source
Yellowstone National Park and Shoshone National Forest, Wyoming	Undisturbed	63	Zelt and Wohl 2004
	Disturbed	61	
Bighorn National Forest, Wyoming	Managed	13	Nowakowski and Wohl 2008
	Unmanaged	42	
	Combined	27	
	Combined	17	
Arapaho and Roosevelt National Forests, Colorado	Oldgrowth	18	Richmond and Fausch 1995
	Oldgrowth	50	
	Oldgrowth	24	
	Oldgrowth	33	
	Oldgrowth	46	
	Oldgrowth	54	
	Oldgrowth	37	
	Oldgrowth	32	
	Oldgrowth	59	
	Oldgrowth	60	
	Oldgrowth	64	
	Disturbed	22	
	Disturbed	26	
	Disturbed	16	
Disturbed	2		
This Study	Tie-driven	13	
	Tie-driven	2	
	Tie-driven	15	
	Non-driven	41	
	Non-driven	21	
	Non-driven	16	

Chapter 3 - Carbon pools in stream-riparian corridors: legacy of disturbance along mountain streams of southeastern Wyoming

Abstract

Streams and their accompanying riparian environment are intrinsic components of terrestrial carbon cycling. However, they have been understudied in terms of the magnitude of their storage components as well as 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 instream components of carbon including fine and coarse particulate organic matter and instream large wood. Biomass was also measured for riparian components including standing trees (live and dead), regenerating conifers, shrubs and herbaceous vegetation, downed coarse and fine wood, and litter and duff layers. Biomass was converted to carbon for all components and differences in storage were compared between tie-driven and non-driven reaches. 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 was similar between disturbance conditions, the amount of carbon stored in large instream 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.

Introduction

Despite significant progress in revealing the mechanisms that regulate terrestrial C cycling (Schimel et al. 2001), stream systems 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 have been identified as 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 physical landscape rivals that of other geomorphic agents (Hooke 1999). Headwater streams are closely coupled with adjacent riparian and hill slope environments 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 and how alterations may cascade to 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 instream OM dynamics are sensitive to riparian manipulations (e.g. Hall et al. 2000; Eggert et al. 2012). However, organic matter 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 allochthonous OM subsidies (Figure 3.1; Gregory 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), and controls on bedforms (Montgomery et al. 1995) as well as ecological functions such as nutrient transformation and retention and habitat diversity (Bilby and Likens 1980; Gurnell et al. 1995). Coarse downed wood (CDW) stored on the forest floor is considered to be in a similar size class as instream LW and has been estimated to account for 10-20% 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 and fine particulate organic matter (CPOM and FPOM) to instream aquatic communities partially 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

(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 and duff accumulate and decompose 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 have been estimated to comprise an average of approximately 6% of stored C in forests while C stored in soils comprises an average of 50% of total stored C in the same ecosystems (Turner et al 1995). Estimates of dissolved organic matter (DOM) within stream reaches vary widely with respect to the riparian environment as well as seasonal moisture availability, although they are consistently a large component of instream 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) following the harvest and transport of large loads of wood downstream are examples of an anthropogenic disturbance legacies. These removal activities have altered contemporary regional instream wood loads and impacted geomorphic heterogeneity through increased sediment transport, channel widening, and habitat simplification (Magilligan et al. 2008; Czarnomski et al. 2008; Mellina and Hinch 2009). Ample empirical evidence links riparian and geomorphic mechanisms with OM dynamics, yet to our knowledge there is no published research that quantifies contemporary C pools in both the stream channel and the adjacent riparian zone within the context of a disturbance legacy.

Streams in the Rocky Mountain region have also undergone extensive, yet understudied, historic wood removal known as tie-driving (Figure 3.2; 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 28-40 cm diameter at breast height (DBH; Anonymous 1916; Rosenberg 1984). Harvests occurred across the forest, including riparian areas, and through all seasons. Railroad ties were stacked, frequently along the channel floodplains, until high flows following snowmelt could transport loads of ties 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., in press), yet it remains unclear how tie-driving has influenced contemporary C storage in stream-riparian corridors. 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 evaluate the role of historic tie-driving on instream and riparian carbon pools for six headwater stream segments in the Medicine Bow National Forest, Wyoming, United States. We define the riparian corridor in these headwater systems as the terrestrial environment within 25 meters of the top of the stream bank during bankfull conditions. This width relates to the approximate height of mature trees and thus captures the potential sources of LW and smaller allochthonous material within the riparian area that is available to the stream channel. Also, many low-order streams in the area were glaciated, and streams developed between lateral moraines, resulting in fairly narrow conifer-dominated floodplains. We created a partial organic matter budget to quantify differences in instream and riparian carbon pools and capture potential differences in carbon dynamics 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 will be lower in tie-driven reaches than non-driven reaches because of combined factors related to the legacy of timber harvest and instream wood removal.

Study Area and Site Description

The study sites are located in the in the Sierra Madre and Snowy Range of Medicine Bow National Forest in southern Wyoming (Figure 3.3). Elevations within the Sierra Madre range from approximately 2200 to 3600 m above sea level; elevations within Snowy Range range from 2500 to 3640 m above sea level. The underlying geology of the area is primarily Precambrian granite and gneiss although there are isolated areas of metasedimentary and metavolcanic rocks as well as glacial deposits in the higher elevations of both ranges (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).

The majority of annual precipitation in the region falls as snow during the months of October through May. Mean annual precipitation increases from approximately 28 cm at lower elevations to 669 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 lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*). The western portion of the Sierra Madres 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 Merritt 2008; Wohl and Goode 2008). 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 prior 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 3.1; Figure 3.3). Reach pairs were located in close proximity to control for localized differences in geology, elevation, and riparian vegetation that may confound detection of differences in channel morphology associated with disturbance conditions. Site pairs were chosen so that each reach pair shared the following physiographic criteria: stream order, reach slope, valley bottom morphology, and surficial geology.

Significant geomorphologic differences associated with tie-driving were identified along these reaches in a previous study (Ruffing et al., in press). Overall, tie-driven channels were narrower and shallow, had smaller cross-sectional areas, greater width to depth ratios, and lower roughness values compared to non-driven reaches, although stream widths were similar. 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., in press).

Methods

Instream C Components

Instream large wood

Large instream wood is characterized as any piece longer than 1 m and at least 10 cm in diameter that is contained at least partially within the bankfull portion of the stream channel.

Within each study reach, the total length of each piece of large wood as well as the length of the portion within the channel was measured. Diameters were measured at both ends of each piece. Volume was calculated separately for the portion of each piece within the channel (LWC) and the portion on the riparian floodplain (LWF) using equation 1 (Lienkaemper and Swanson 1987):

$$(1) \quad Volume = \frac{\pi(D_1^2 + D_2^2)L}{8}$$

where D_1 and D_2 are end diameters (m) for each piece and L is the piece length (m). We assumed an average density of 400 kg m^{-3} and used a multiplication factor of 0.5 (Forest Products Laboratory 2010) to estimate the C content of each piece. The mass and C content were summed and standardized by area for each reach and then averaged for tie-driven and non-driven reaches.

CPOM and FPOM standing stocks

Instream OM samples were collected along each study reach during July 2013 following peak flow and therefore represent mid-season standing stocks. Sample collections were stratified by habitat unit within each reach with seven separate sampling locations for each reach. One m wide transects were established across the channel perpendicular to the direction of flow and organic matter was collected by dislodging present stocks and collecting material 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 lab, 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 until they reached constant weight. 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, % AFDM was applied to the total mass of the sample. Both CPOM and FPOM sample masses were standardized by the area of each habitat unit sampled.

The dried CPOM subsamples were ground to a fine powder before being analyzed for C content on a Carlo Erba NA 1500 Analyzer (Carlo Erba; Thermo Electron Corp., Milan, Italy). Total C is reported as a percentage of dry mass and percentage were applied to the total AFDM of respective CPOM samples in order to calculate the C content of each sample. Because the size

of the FPOM samples was so small, the C content was estimated to be equivalent to the organic fraction of the sample.

Riparian Components

Forest canopy and understory

Riparian vegetation included live and dead standing trees, conifer regeneration in the understory, shrubs, herbaceous plants and roots of live plants. Riparian vegetation was sampled in 0.05-ha circular plots. The number of plots per reach varied (2-5) depending on reach length, with at least one plot located on each side of the channel. Plot-center locations 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 diameter at breast height (DBH) were recorded on all live and dead trees (≥ 5 cm DBH). Evidence of mountain pine beetle (MBP) incidence and damage was recorded for each standing lodgepole pine tree (*Pinus contorta* Dougl. var. *latifolia* Engelm., live or dead); similarly, spruce beetle (SB) incidence was recorded for each standing Engelmann spruce (*Picea engelmannii* (Parry) Engelm., live or dead). Information recorded on live saplings in two diameter classes (stems ≥ 2.5 cm and < 5 cm DBH; and stems < 2.5 cm DBH) 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 and height class (< 0.5 m or ≥ 0.5 m). Percent cover of shrubs, herbaceous vegetation, and litter was visually estimated for each plot.

Downed wood and riparian floor

Within each plot, we conducted a complete tally of coarse downed wood (> 8.0 cm in diameter); length and two end diameters were measured on each piece — or portion of each piece — that occurred within the plot perimeter. For each stump located within the sampled plots, the height, basal diameter (above the root swell), and diameter at the cut surface were measured. Decay status of each downed large wood piece and stump was noted as either sound or rotten. Three transects (12.63 m in length) were established in each plot starting from plot center and extending to the perimeter on randomly selected bearings to sample fine downed wood, litter, and duff. Fine downed wood loads were estimated using the planar intercept method for characterizing fuel loads in three size classes (Brown 1974). Along each transect, the

smallest size class (piece diameter: 0 – 0.6 cm) was tallied for the first 6.3 m and the two larger size classes (piece diameter 0.6-2.5 cm and 2.5 - 8.0 cm) 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 (12 depths per transect; 36 depths per plot; 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.

Riparian C pools

Aboveground (AG) biomass for all stems ≥ 2.5 cm was calculated using genera-specific published allometric equations, which account for tree boles, branches of all sizes, and foliage (Jenkins et al. 2003). For dead trees, calculated AG biomass was reduced by 30%. For trees and understory stems, belowground (BG) biomass was estimated at 20% of AG biomass (Jenkins et al. 2003). For saplings (<2.5 cm DBH) and seedlings, plants over a representative height range were harvested, dried and weighed, and equations for calculating biomass were developed by regressing dry weights against measured plant heights. Aboveground biomass for shrubs and herbaceous vegetation was calculated using allometric equations previously determined for dominant species (Turner et al. 2004; Wohl et al. 2012). Biomass of trees was converted to C content using a multiplication factor of 0.48 (Lamton and Savidge, 2003). Biomass of saplings, seedlings, shrubs and herbaceous plants was converted to C content using multiplication factors from 0.42 to 0.52, depending on the biomass component (Lamton and Savidge, 2003). Soils were collected with a split-core sampler of known volume.

Dimensions of each downed wood piece (diameter ≥ 8.0 cm) were used to calculate piece volume in cubic meters, approximating the piece as a cylinder following equation 1. Total 'sound' and 'rotten' wood volumes were summed for each plot in cubic meters. Biomass of wood volume was then calculated for each plot, assuming a wood density of 400 kg m^{-3} for sound pieces, and 300 kg m^{-3} for rotten pieces (Forest Products Laboratory 2010). For each plot, FDW biomass was calculated according to Brown (1974) by averaging the values for the three transects. Biomass 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. 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). Soil samples were sieved at 2 mm to remove rocks and litter, homogenized, and dried to a constant weight. A subsample was then analyzed for carbon content using a Costech ECS 4010 Elemental Analyzer with Zero Blank Autosampler. We then applied the resulting percentages of C to the entire sample to determine the amount of C stored in soils.

Data Analysis

Instream C components were LWC, LWF, CPOM, and FPOM. C values for AG and BG tree biomass were summed so that estimates of C represented total tree biomass for both live and dead trees. C estimates for both size classes of saplings were combined with C estimates for seedlings to make one component reflecting regenerating conifers. Other discrete components included in riparian C estimates were shrubs, herbaceous vegetation, sound and rotten CDW, FDW, stumps, litter, duff, and soil. Average total C pools representing each stream and riparian component were summed for each study reach and compared using independent t-tests to evaluate the effects of tie-driving on C pools. 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). We used a significance criterion of $P \leq 0.1$ due to the small sample size ($n = 6$ study reaches).

Results

Instream C Components

Historic tie-driving activity was associated with lower quantities of CPOM (1.62 g AFDM m^{-2} in tie-driven reaches and 6.74 g AFDM m^{-2} in non-driven reaches) as well as fewer pieces of large wood stored within the channel ($n = 47$ total pieces in tie-driven reaches and $n = 97$ total pieces in non-driven reaches) and on the floodplain ($n = 28$ total pieces in tie-driven reaches and $n = 59$ total pieces in non-driven reaches). However, midseason standing stocks of FPOM were similar between historic disturbance conditions (0.02 g AFDM m^{-2} in tie-driven reaches and 0.03 g AFDM m^{-2} in non-driven reaches).

Relative to C stored in other instream components, FPOM and CPOM represented minimal amounts of overall total C storage (Table 3.2). 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 (0.07 Mg ha⁻¹) and lowest in both North Fork Rock Creek (non-driven) and Horse Creek (tie-driven; 0.003 Mg ha⁻¹). Although average total C values for the CPOM component varied widely among the non-driven sites (Fig. 3.4 A), they did not differ between disturbance conditions. The quantity of C contained in FPOM was highest in non-driven North Fork Rock Creek (0.0028 Mg ha⁻¹) and lowest in non-driven Beaver Creek (0.0004 Mg ha⁻¹), and averages of total C for this compartment were similar across disturbance conditions (Fig. 3.4 B). Large wood, both in the channel and on the floodplain, were the largest components of instream C. Horse Creek (tie-driven), which only had two pieces of large wood within the reach, had the lowest amount of C stored in LW components while Beaver Creek (non-driven) had the largest amount of C (Table 3.2). On average, a larger amount of C is stored in the portion of pieces on the floodplain compared to portions within the channel. Tie-driven reaches had lower values of C attributed to LW, although this difference was not statistically significant (Figure 3.4 C and D).

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 3.5). This pattern 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. While subalpine fir had relatively high basal area along non-driven stream segments, this skewed pattern reflects the stand characteristics at Beaver Creek (non-driven), where approximately 52% of the trees sampled were subalpine fir (live and dead). For lodgepole pine and Engelmann spruce, the distribution of live versus dead trees reflects the recent MPB and SB epidemics in the region (Dwire et al., in press). The current size class distribution of trees differs between tie-

driven and non-driven stream segments (Figure 3.6). Tie-driven reaches have a larger proportion of mature (DBH > 25 cm) lodgepole pine trees than non-driven reaches.

Live tree biomass was greatest in North Fork Rock Creek while dead tree biomass was greatest in Beaver Creek, both non-driven stream segments. Horse Creek (tie-driven) had the lowest total tree biomass (live and dead). Dead AG biomass exceeded live AG biomass in four of the six study reaches; exceptions were non-driven North Fork Rock and tie-driven Trail Creek (Table 3.2). In comparing average total tree C (AG + BG) between disturbance conditions, both live and dead C content is greater in non-driven reaches, but only the difference in C content of live trees was significant ($P = 0.0686$, $t=2.413$; Figure 3.7). Despite the similarities in C stored in standing dead trees, it is worth noting that the species distributions of the standing dead trees were significantly different. 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.

Understory vegetation

Understory vegetation components, including regenerating conifers, shrubs, and herbaceous cover contributed relatively little to plot-level biomass compared to live and dead trees and large downed wood. Biomass of shrubs and herbaceous vegetation was relatively consistent across sites. Flume Creek (non-driven) had the greatest biomass for regenerating conifers (stems < 5 cm DBH) while Beaver Creek (non-driven) had the lowest biomass (Table 3.2). No significant differences were found in carbon pools for shrubs, herbaceous cover, or regenerating conifers (Figure 3.8) between the two disturbance types.

Stumps and downed wood

Next to trees, coarse and fine downed wood comprised the second largest component of biomass within the sampled riparian areas. The biomass of rotten CDW and FDW was highest in Flume Creek (non-driven) while North Fork Rock Creek (non-driven) had the largest amount of sound CDW (Table 3.2). Stumps were a relatively large component of measured biomass in East Fork Encampment River (tie-driven), but overall were relatively minor for other study reaches (Table 3.2). 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 C content of rotten coarse downed wood and fine downed wood was significantly greater in non-driven riparian reaches compared to tie-driven reaches ($P = 0.0107$, $t=3.671$ and $P = 0.0208$, $t=2.958$; Figure 3.9, C and E). Sound CDW was also higher in non-driven reaches although not significantly different. Stumps were the only component of C storage representing woody vegetation where non-driven reaches were lower than tie-driven reaches although this difference was not significant (Figure 3.9 D).

Forest Floor

Litter and duff each contributed less than 0.2% of total riparian biomass although together these components accounted for more biomass than shrubs and herbaceous vegetation combined. The average depth of the litter layer 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, these differences were not significant. 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. Non-driven riparian plots had significantly greater duff depths compared to tie-driven plots ($P = 0.035$, U-statistic=1261.0). The organic matter of soils was larger than the biomass of litter and duff combined and contributed roughly 2% of total riparian biomass.

The estimated C content of litter was slightly higher for tie-driven reaches but not significantly different from non-driven reaches (Figure 3.9 A). On average, duff represented a larger C component than litter and was slightly higher in non-driven reaches although not significantly different than tie-driven reaches (Figure 3.9 B). Soils represented the smallest component of C on the forest floor and were also not significantly different between reaches (Figure 3.9 C).

Total C in Stream and Riparian Corridors

Combined total instream C pools ranged from 0.77 Mg ha⁻¹ in tie-driven Horse Creek to 126.91 Mg ha⁻¹ in non-driven Beaver Creek (Table 3.2), but did not differ significantly between tie-driven and non-driven reaches. Large wood in both the channel and the floodplain constitutes 99.97-99.98% of instream C in all study streams (Fig. 3.10). Pools of C stored in riparian components were much larger than those stored in the stream across all study reaches and ranged from 64.91 Mg ha⁻¹ in Horse Creek to 231.36 Mg ha⁻¹. Average total riparian C pools were

higher in non-driven reaches but not significantly different from tie-driven reaches. Total tree biomass (AG + BG, live + dead) represents the largest proportion of C and although the biomass of live trees was significantly higher in non-driven streams, the overall quantities of live and dead tree biomass did not differ between disturbance types (Fig. 3.11). Downed wood, the second largest compartment of riparian C next to trees, was also higher in non-driven reaches compared to tie-driven reaches especially amounts of rotten CDW and FDW (Fig. 3.11). When instream and riparian pools were combined, Horse Creek still ranked lowest in overall C storage at 65.68 Mg ha⁻¹. Beaver Creek had the largest overall C storage at 358.27 Mg ha⁻¹.

Non-driven reaches had greater total quantities of C for stream, riparian, and combined ecosystem components compared to tie-driven reaches, although these differences were not significant. Of the small pools (Fig. 3.11), C stored in soils was the largest component and there were no significant differences in quantity of C stored in small pools across sites. Of the large pools (Fig. 3.12), non-driven streams had significantly more C stored in rotten downed wood, fine downed wood, live trees, and wood stored on the floodplain compared to non-driven sites. In summary, live and dead standing trees represented the largest C pool followed by LW, CDW and FDW. Overall contributions to C pools for other components were minimal but tree regeneration represented the largest of these pools followed by, litter and duff, stumps, shrubs and herbaceous vegetation, CPOM and FPOM. The relative magnitude of these pools was consistent between non-driven and tie-driven streams.

Discussion

More C was stored in non-driven streams and riparian areas compared to tie-driven streams and riparian areas. Across sites there was 55-99% more C stored in the riparian area compared to the stream channel. The strongest legacies of tie-driving were differences in total C stored in large instream wood and downed wood on the floodplain. Non-driven reaches had approximately twice the amount of C stored in LW and FDW. Standing trees represented the largest component of C and while differences in total C do not directly reflect the history of tie-driving, species composition suggests some correlation to tie-driving activity.

Our estimates of total C as well as individual C components are conservative. Even though C stored in soils and DOM has been identified as the largest pools for both environments (Wagener et al. 1998), they are regulated by a variety of controls which likely confound

differences due to legacy disturbances. The amount of C stored as FPOM was underestimated because of the lower limit of the size class we used and both CPOM and FPOM travel long distances during times of high flow (Webster et al. 1999). The snowmelt driven flow regime of the area likely resets standing stocks that have accumulated during the year. Sampling during mid-summer was necessary for logistical reasons (site access and safety) yet this period likely corresponds with the lower limit of overall standing stocks during the year. Our estimates for C storage of LW in non-driven streams are 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 LWC and LWF compartments for tie-driven streams were much lower than other reported values (Chen et al. 2005).

Our plot level estimates for C storage in riparian components are among the most complete yet published (see Sutfin et al, in review). 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 (Figure 3.10). Although C content of sound CDW did not differ between disturbance reach types, we interpret the lower abundance of rotten CDW along tie-driven reaches as another disturbance legacy.

Feedbacks between riparian and instream 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 1999; Myneni et al 2001; Fang 2014). The large number of lodgepole pine in different size classes likely reflects both the growth release of small uncut trees and the understory forest regeneration that followed removal of the lodgepole overstory trees 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 2012, Beckman and Wohl 2014), few studies have explicitly linked forest characteristics and instream C storage. C 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., in press). Debris dams, channel morphology, 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 instream 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. While 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 temporal scale at which the magnitude of C pools between tie-driven and non-driven stream reaches represents an important difference in stream-riparian C storage. Allochthonous OM drives aquatic food webs in headwater streams and OM inputs and turnover generally occur over seasonal or annual time scales. While midseason standing stocks of CPOM were not significantly different between tie-driven and non-driven stream reaches, FDW on the floodplain, which corresponds to the same size class as CPOM, was significantly higher in non-driven streams. The small size of these components represents a class of C storage which will be turned over at relatively short timescales due to decomposition and export from the system.

In contrast, C stored in wood that is either in the channel, on the floodplain adjacent to the channel, or on the riparian floor is relevant at much longer time scales. 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 large wood 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 large wood (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 the intermountain west (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. in press).

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. 2013). Eventually, C stored in standing dead trees will shift to detrital or instream 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 and it is expected that up to 90% of infested trees will fall within 10-15 years (Mitchell and Priesler 1998). 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. in press).

Conclusion

Tie-driving is a notable disturbance that has shaped contemporary C storage in stream-riparian corridors. Tie-driven streams store less C in both in the channel and riparian areas. Differences in the quantity of C stored in downed wood in the stream and on the floodplain were notable. 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. Tree mortality due to bark beetles will likely shape future C dynamics in this region as trees continue to die and standing dead trees begin to fall. Incorporating geomorphic and riparian mechanisms of C storage with ecological metrics quantifying fluxes between systems would improve 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 capture the effect of a historic disturbance on C pools within this type of ecosystem.

References

- Anonymous. 1916. Timber sale contract, Medicine Bow National Forest, 8/11/16. Grand Encampment Museum, Encampment Wyoming.
- Aufdenkampe AK, Mayorga E, Raymond PA, Melack JM, Doney SC, Alin SR, Aalto RE, Yoo K. 2011. Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere. *Frontiers in Ecology and the Environment* 9(1):53-60.
- Battin TJ, Kaplan LA, Findlay S, Hopkinson CS, Marti E, Packman AI, Newbold JD, Sabater F. 2008. Biophysical controls on organic carbon fluxes in fluvial networks. *Nature Geoscience* 1(2):95-100.
- Beckman ND, Wohl E. 2014. Carbon storage in mountainous headwater streams: The role of old-growth forest and logjams, *Water Resources Research* 50:2376–2393.
- Bilby RE, Likens GE. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 61(5):1107-1113.
- Bilby RE, Ward JW. 1991. Characteristics and function of large woody debris in streams draining old-growth, clearcut, and second-growth forests in southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 48:2499-2508.
- Brookshire ENJ, Dwire KA. 2003. Controls on patterns of coarse organic particle retention in headwater streams. *Journal of the North American Benthological Society* 22(1): 17-34.
- Brown S. 2002. Measuring carbon in forests: current status and future challenges. *Environmental Pollution*. 116(3):363-372.
- Brown JK. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT-16.
- Chen XY, Wei XH, Scherer R. 2005. Influence of wildfire and harvest on biomass, carbon pool, and decomposition of large woody debris in forested streams of southern interior British Columbia. *Forest Ecology and Management* 208(1-3):101-114.
- Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Duarte CM, Kortelainen P, Downing JA, Middelburg JJ, Melack J. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10(1):171-184.

- Collier KJ, Bowman EJ. 2003. Role of wood in pumice-bed streams - I: Impacts of post-harvest management on water quality, habitat and benthic invertebrates. *Forest Ecology and Management* 177(1-3):243-259.
- Czarnomski NM, Dreher DM, Snyder KU, Jones JA, Swanson FJ. 2008. Dynamics of wood in stream networks of the western Cascades Range, Oregon. *Canadian Journal of Forestry Research* 38:2236-2248.
- Dalzell BJ, Filley TR, Harbor JM. 2007. The role of hydrology in annual organic carbon loads and terrestrial organic matter export from a midwestern agricultural watershed. *Geochimica Et Cosmochimica Acta* 71(6):1448-1462.
- Daniels MD. 2006. Distribution and dynamics of large woody debris and organic matter in a low-energy meandering stream. *Geomorphology*, 77(3-4), 286-298.
- Daniels M.D., Rhoads., B.L., 2004. Effect of LWD configuration on spatial patterns of three-dimensional flow in two low-energy meander bends at varying stages. *Water Resources Research*, 40 (11) W11302, doi:10.1029/2004WR003181.
- Dillon GK, Knight DH, Meyer CB. 2005. Historic range of variability for upland vegetation in the Medicine Bow National Forest, Wyoming. Gen. Tech. Rep. RMRS-GTR-139. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 85 p.
- Dwire KA, Hubbard R, Bazan R. 2015. Comparison of riparian and upland forest stand structure and fuel loads in beetle-infested watersheds, southern Rocky Mountains. *Forest Ecology and Management* 335: 194-206. DOI: 10.1016/j.foreco.2014.09.039
- Eggert SL, Wallace JB, Meyer JL, Webster JR. 2012. Storage and export of organic matter in a headwater stream: responses to long-term detrital manipulations. *Ecosphere* 3(9) DOI: 10.1890/ES12-00061.1.
- Fang JY, Kato T, Guo ZD, Yang YH, Hu HF, Shen HH, Zhao X, Kishimoto-Mo AW, Tang YH, Houghton RA. 2014. Evidence for environmentally enhanced forest growth. *Proceedings of the National Academy of Sciences of the United States of America* 111(26): 9527-9532.
- Forest Products Laboratory. 2010. Wood Handbook: Wood as an Engineering Material. USDA Forest Products Laboratory, General Tech Report FPL-GTR-190, Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory.

- Freudenberger L, Hobson PR, Schluck M, Ibisch PL. 2012. A global map of the functionality of terrestrial ecosystems. *Ecological Complexity* 12:13-22.
- Gippel CJ. 1995. Environmental hydraulics of larger woody debris in streams and rivers. *Journal of Environmental Engineering*. 121(5):388-395.
- Gregory SV, Swanson F, McKee A, Cummins K., 1991. An ecosystem perspective of riparian zones. *BioScience* 41:540–550.
- Gurnell AM, Gregory KJ, Petts GE. 1995. The role of coarse woody debris in forest aquatic habitats: implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5:143-166.
- Hall RO, Wallace JB, Eggert SL. 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* 81(12):3445-3463.
- Hicke JA, Johnson MC, Hayes JL, Preisler HK. 2012. Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management* 271:81-90.
- Hooke RL. 1999. Spatial distribution of human geomorphic activity in the United States: Comparison with rivers. *Earth Surface Processes and Landforms* 24(8):687-692.
- Houghton RA, Hackler JL, Lawrence KT. 1999. The U.S. Carbon Budget: Contributions from Land-Use Change. *Science* 285(5427):574-578.
- Jenkins MJ, Herbertson E, Page W, Jorgensen CA. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management* 254:16-34.
- Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49:12-35.
- Kulakowski D, Veblen TT, Bebi P. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *Journal of Biogeography* 30(9):1445-1456.
- Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452(7190):987-990.
- Lamloom SH, Savidge RA. 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. *Biomass and Bioenergy* 25, 381-388.

- Law BE, Turner D, Campbell J, Sun OJ, Van Tuyl, Ritts WD, Cohen WB. 2004. Disturbance and climate effects on carbon stocks and fluxes across Western Oregon USA. *Global Change Biology* 10(9):1429-1444.
- Liang L, Chen Y, Hawbaker, TJ, Zhu ZL, Gong P. 2014. Mapping Mountain Pine Beetle Mortality through Growth Trend Analysis of Time-Series Landsat Data. *Remote Sensing* 6(6):5696-5716.
- Lienkaemper GW, Swanson, FJ, 1987. Dynamics of large woody debris in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* 17,150-156.
- Love JD, Christiansen AC. 1985. Geologic Map of Wyoming. US Geological Survey.
- Lutes D C, Keane RE, Caratti JF, Key CH, Benson NC, Sutherland S, Gangi LJ. 2006. FIREMON: Fire effects monitoring and inventory systems. Gen Tech. Rep. RMRS-GTR-164-CD. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Magilligan FJ, Nislow KH, Fisher GB, Wright J, Mackey G, Laser M. 2008. The geomorphic function and characteristics of large woody debris in low gradient rivers, coastal Maine, USA. *Geomorphology* 97,467-482.
- Marcus WA, Rasmussen J, Fonstad MA. 2011. Response of the Fluvial Wood System to Fire and Floods in Northern Yellowstone. *Annals of the Association of American Geographers* 101(1):21-44.
- Mellina, E, Hinch, SG, 2009. Influences of riparian logging and instream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. *Canadian Journal of Forestry Research* 39,1280-1301, doi:10.1139/X09-037.
- Mitchell RG, Preisler HK. 1998. Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. *Western Journal of Applied Forestry* 13, 23–26.
- Montgomery DR, Buffington JM, Smith RD, Schmidt KM, Pess G. 1995. Pool spacing in forest channels. *Water Resources Research* 31(4),1097-1105.
- Montgomery DR, Buffington JM. 1997. Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* 109(5),596-611.
- Myneni RB, Dong J, Tucker CJ, Kaufmann RK, Kauppi PE, Liski J, Zhou L, Alexeyev V, Hughes MK. 2001. A large carbon sink in the woody biomass of Northern forests.

Proceedings of the National Academy of Sciences of the United States of America 98
(26):14784-14789

- Naiman RJ, Bilby RE, Schindler DE, Helfield JM. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5(4):339-417.
- Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H, 2013. *Vegan: Community Ecology Package*. R package version 2.0-8. <http://CRAN.R-project.org/package=vegan>
- Pawson RR, Evans MG, Allott TEHA. 2012. Fluvial carbon flux from headwater peatland streams: significance of particulate carbon flux. *Earth Surface Processes and Landforms* 37(11):1203-1212.
- RStudio. 2012. RStudio: Integrated development environment for R (Version 0.96.122) [Computer software]. Boston, MA. Retrieved May 20, 2012.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58(6):501-517.
- Riccardi C.L. [et al.]. 2007. Quantifying physical characteristics of wildland fuels using the Fuel Characteristic Classification System. *Canadian Journal of Forestry* 37:2413-2420.
- Rosenberg RG. 1984. Handhewn ties of the Medicine Bows. *Annals of Wyoming* 56:39-53.
- Ruffing, C., Daniels MD, Dwire, KA. Disturbance legacies of historic tie-drives persistently alter geomorphology and large wood characteristics in headwater streams, southeast Wyoming (in revision for *Geomorphology*).
- Schimel DS, House JI, Hibbard KA, Bousquet P, Ciais P, Peylin P, Braswell BH, Apps MJ, Baker D, Bondeau A, Canadell J, Churkina G, Cramer W, Denning AS, Field CB, Friedlingstein P, Goodale C, Heimann M, Houghton RA, Melillo JM, Moore B, Murdiyarso D, Noble I, Pacala SW, Scholes RJ, Steffen WL, Wirth C. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* 414(6860):169-172.
- Sedell R, Leone FN, Duval WS. 1991. Water transportation and storage of logs. *American Fisheries Society Special Publication* 19,325-368.
- Stevens MHH, Cummins KW. 1999. Effects of long-term disturbance on riparian vegetation and in-stream characteristics. *Journal of Freshwater Ecology* 14(1):1-17.

- Sutfin N, Wohl E, Dwire KA. Banking carbon: A review of organic carbon reservoirs in river systems (in review for *Earth Surface Processes and Landforms*).
- Tank JL, Rosi-Marshall EJ, Griffiths NA, Entekin SA, Stephen ML. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society*. 29(1):118-146.
- Thompson DM. 1995. The effects of large organic debris on sediment processes and stream morphology in Vermont. *Geomorphology* 11(3): 235-44.
- Turner DP, Koerper GJ, Harmon ME, Lee JJ. 1995. A Carbon Budget for Forests of the Conterminous United States. *Ecological Applications* 5:421–436.
- Turner MG, Tinker DB, Romme WH, Kashian DM, Litton CM. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7: 751-775
doi:10.1007/s1002-004-0011-4.
- Wagener SM, Oswald MW, Schimel JP. 1998. Rivers and soils: Parallels in carbon and nutrient processing. *Bioscience*. 48(2):104-108.
- Webster JR, Benfield EF, Ehrman TP, Schaeffer MA, Tank JL, Hutchens JJ, D'Angelo DJ. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology* 41(4):687-705.
- Wohl E. 2001. *Virtual Rivers: Lessons from the Mountain Rivers of the Colorado Front Range*. Yale University Press.
- Wohl E. 2006. Human impacts to mountain streams. *Geomorphology* 79(3-4),217-248.
- Wohl E, Jaeger K. 2009. A conceptual model for the longitudinal distribution of wood in mountain streams. *Earth Surface Processes and Landforms*, 34(3), 329-344.
- Wohl E, Goode JR. 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. *Water Resources Research* 44(W09429),1-14.
- Wohl E, Merritt D, 2008. Reach-scale channel geometry of mountain streams. *Geomorphology* 93 (3-4), 168-85.
- Wohl E, Dwire K, Sutfin N, Polvi L, Bazan R. 2012. Mechanisms of carbon storage in mountainous rivers. *Nature Communications* 3:1623 DOI: 10.1038/ncomms2274
- Young MK, Haire D, Bozek MA, 1994. The effect and extent of railroad tie drives in streams of southeastern Wyoming. *Western Journal of Applied Forestry* 9(4), 125-130.

Figure 3.1 Conceptual diagram of riparian and instream carbon pools (after Gregory et al. 1991). Pools in italics were not directly measured as part of this study. Abbreviations are as follows: herbaceous vegetation (Herb. veg.), coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), dissolved organic matter (DOM).

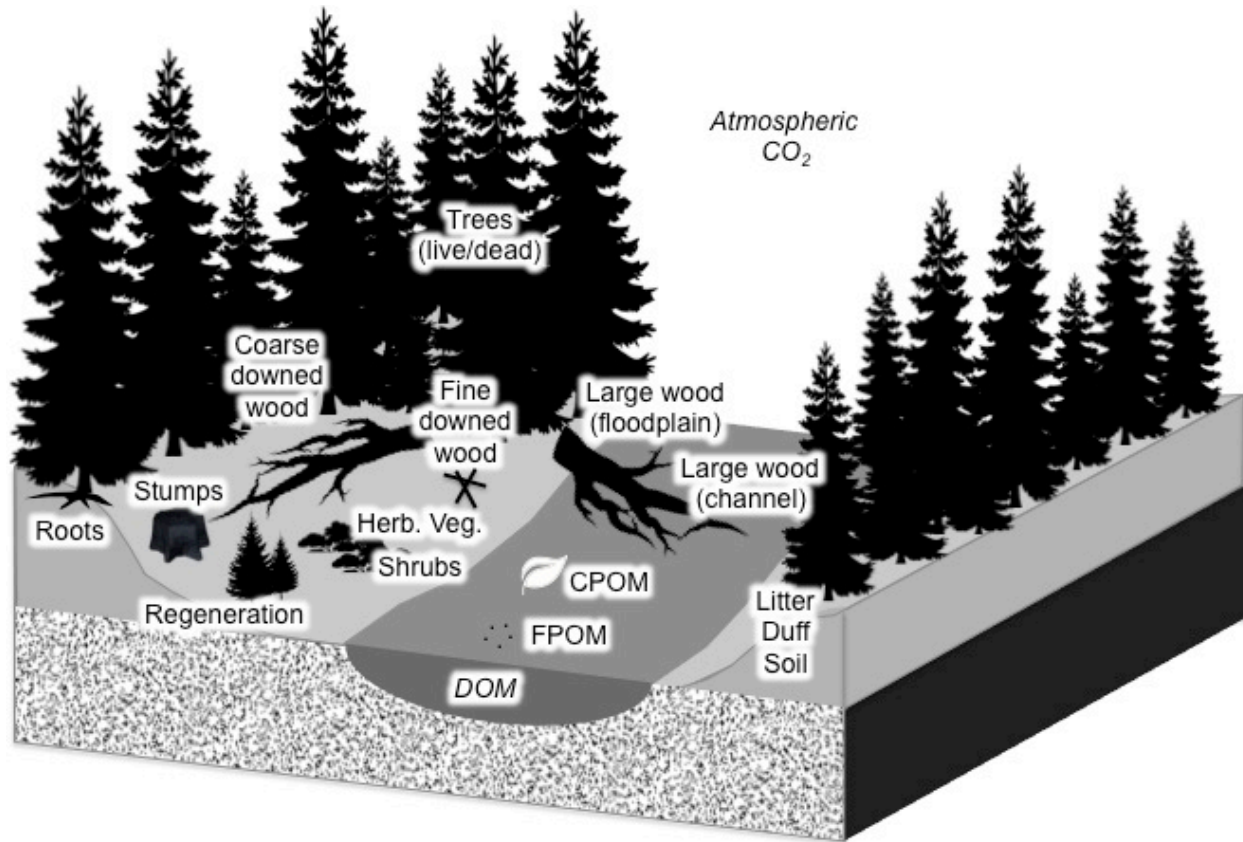


Figure 3.2 Tie driving in the Medicine Bow National Forest, southeast Wyoming. (A) Railroad ties were cut and stored in the riparian area adjacent to the stream channel. (B) Ties were floated downstream following peak flow. (C) Extensive tie jams were a routine event during drives. (D) Ultimately, tie drives accumulated in larger rivers to be delivered to processing centers downstream. Photographs courtesy of the Grand Encampment Museum.



Figure 3.3 Location of tie-driven streams and study reaches in the Medicine Bow National Forest, southeast Wyoming. Heavy lines indicate all known tie-driven streams.

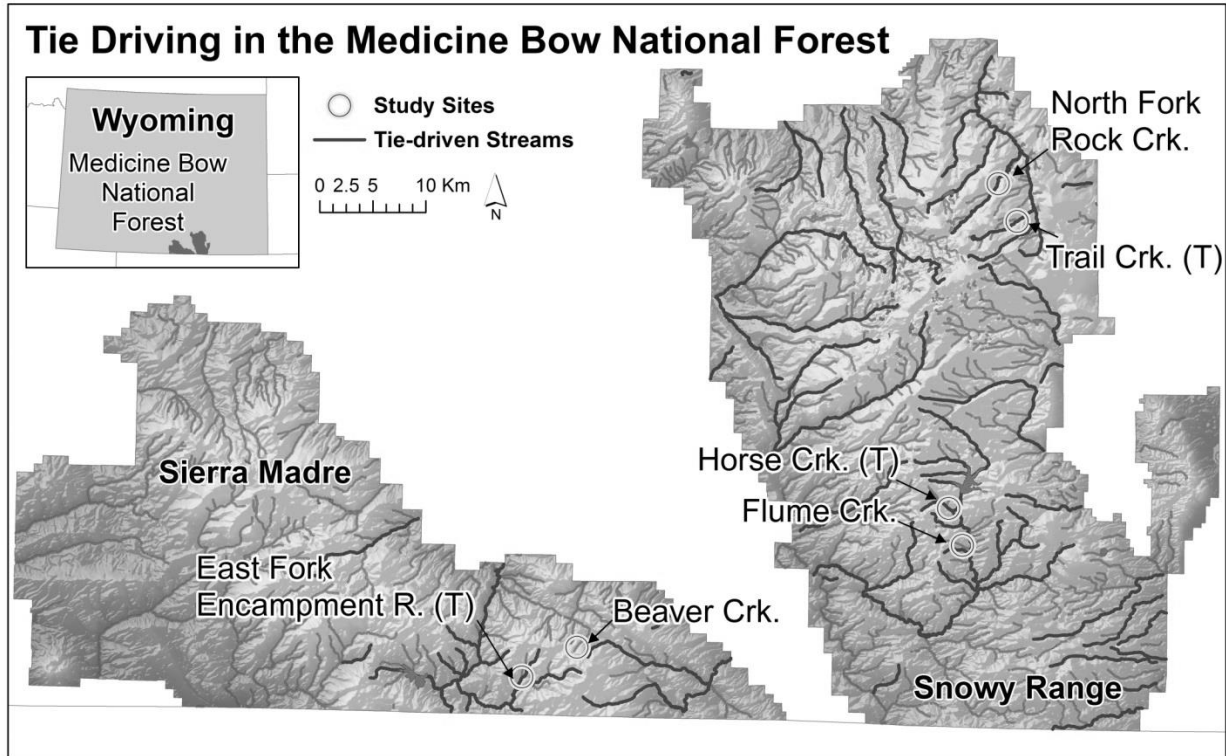


Figure 3.4 Measured average instream C pools in non-driven and tie-driven reaches for coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), in-channel large wood (LWC) and the portion of in-channel large wood stored on the floodplain (LWF). Significant differences with P values < 0.1 are indicated by ‘*’.

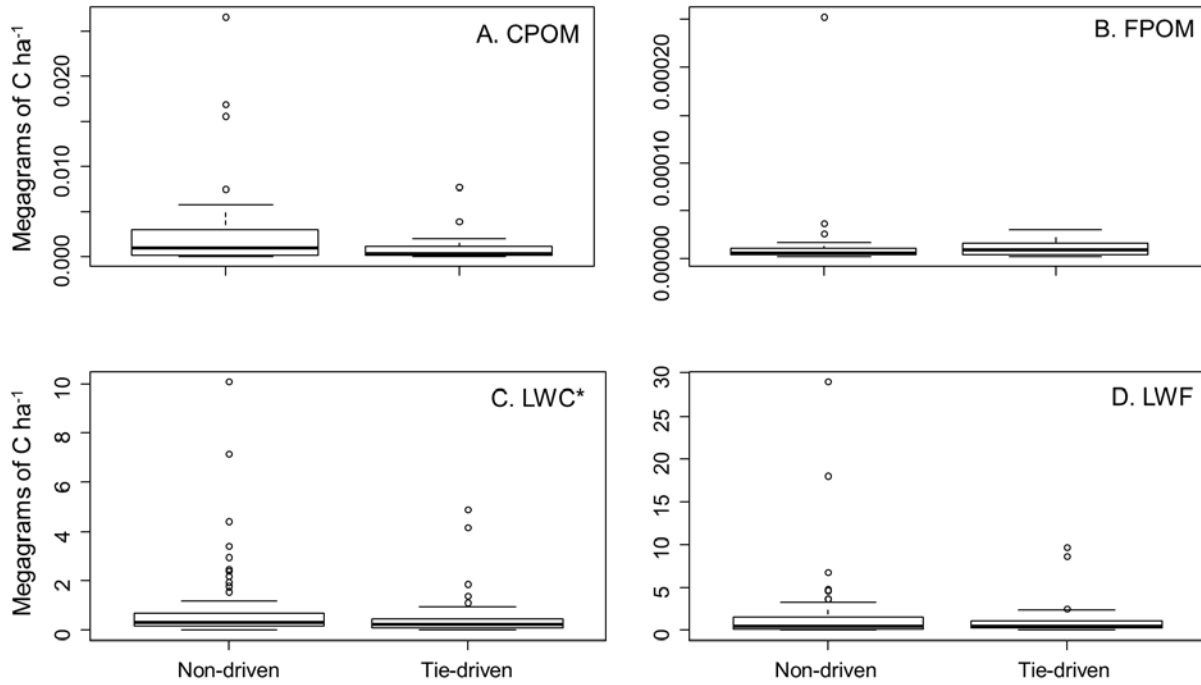


Figure 3.5 Live and dead basal area (m² ha⁻¹) for subalpine fir, lodgepole pine, and Engelmann spruce in non-driven and tie-driven riparian plots.

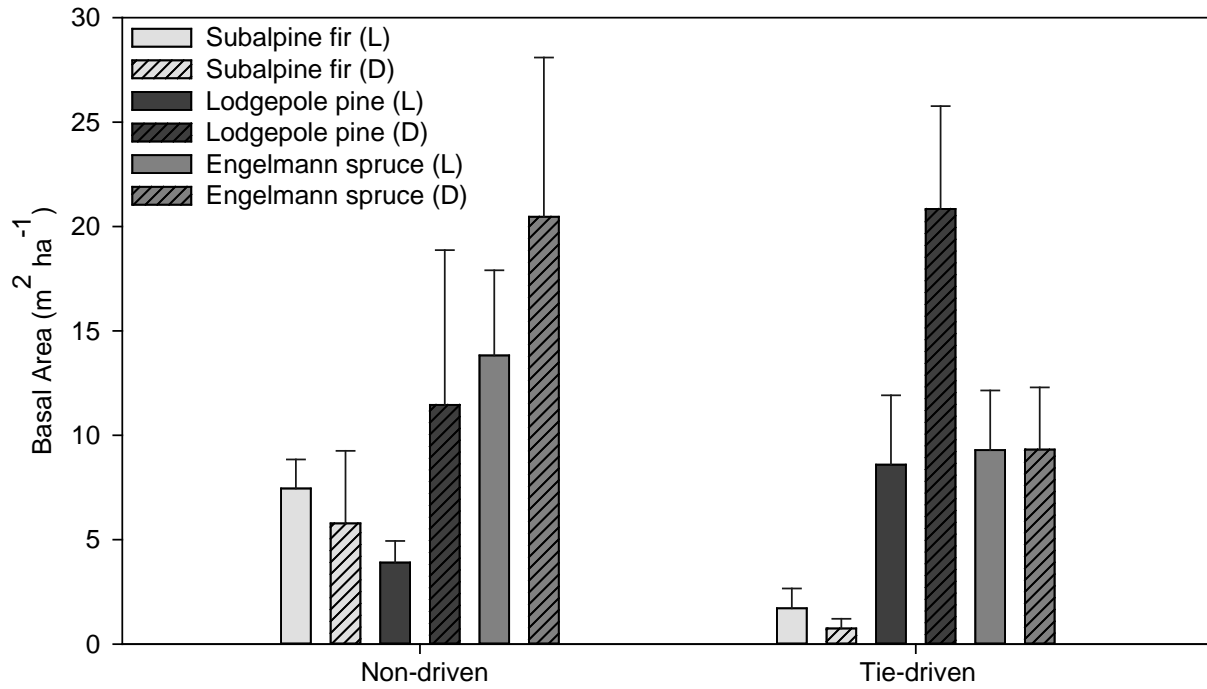


Figure 3.6 Density (stems ha⁻¹, live and dead, ≥ 10 cm DBH) of subalpine fir, lodgepole pine, and Engelmann spruce stems by diameter class (5 cm increments) for non-driven and tie-driven riparian plots.

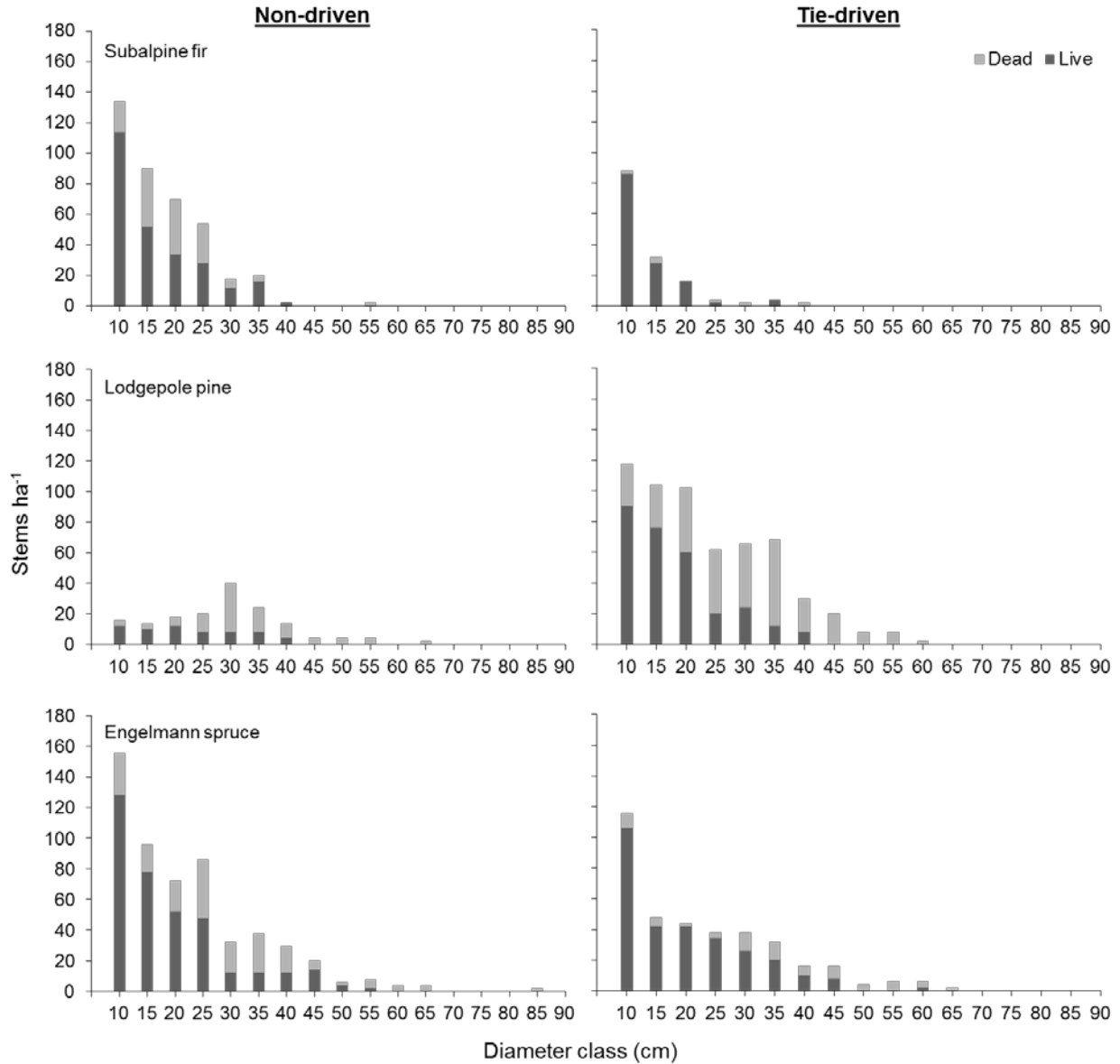


Figure 3.7 Measured C stored in total tree biomass of live and dead trees in non-driven and tie-driven reaches. Significant differences with P values < 0.1 are indicated by ‘*’.

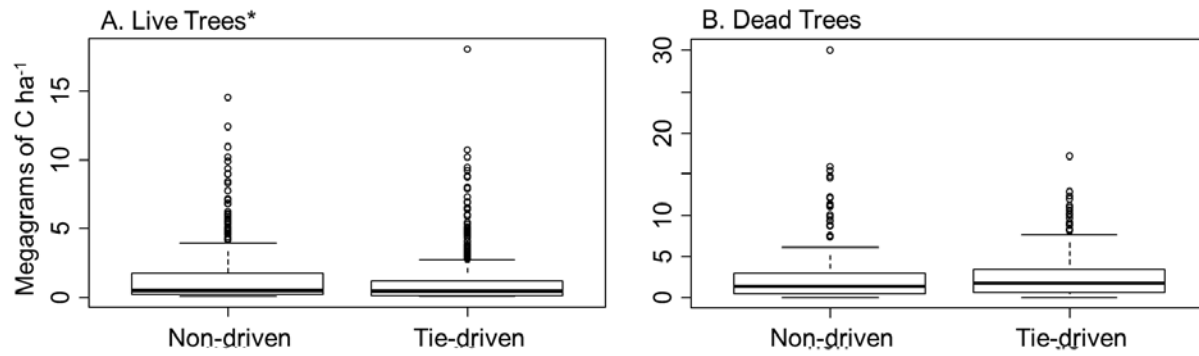


Figure 3.8 Comparison of average total carbon stored in understory vegetation in non-driven and tie-driven reaches.

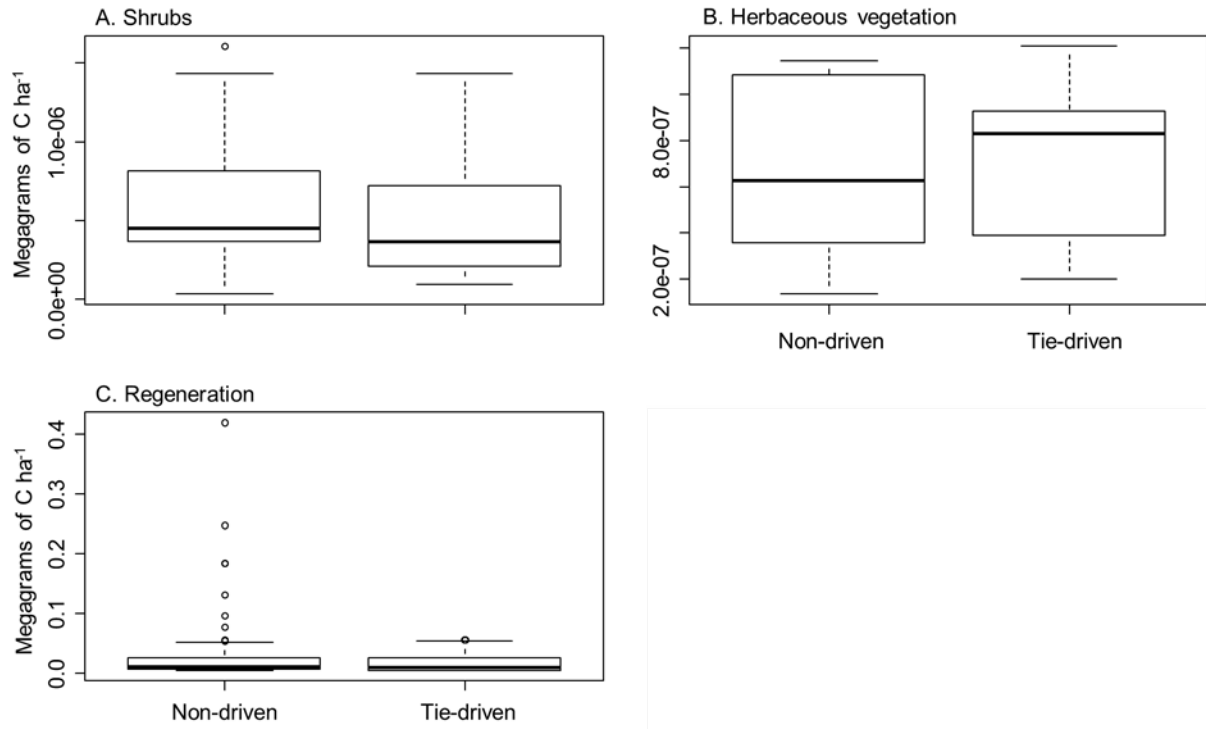


Figure 3.9 Measured C stored in riparian forest floor components in non-driven and tie-driven reaches. Significant differences with P values < 0.1 are indicated by ‘*’.

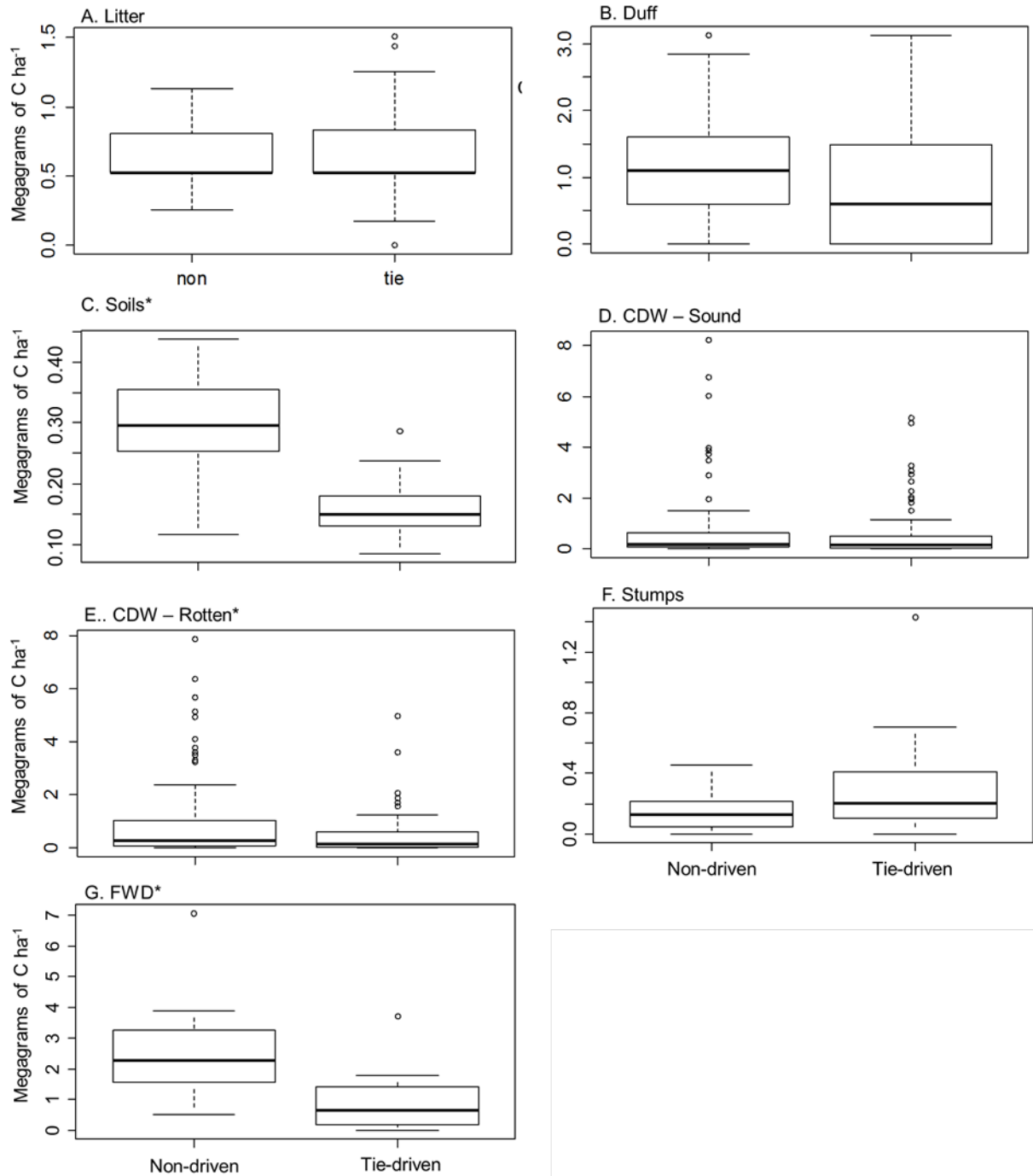


Figure 3.10 Average total carbon pools of the largest ecosystem components for tie-driven and non-driven streams. Significant differences with P values < 0.1 are indicated by '*'. Quantities of carbon in coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) as well as stumps, conifer regeneration, herbaceous vegetation and shrubs are too small to be visible and were not included on the figure.

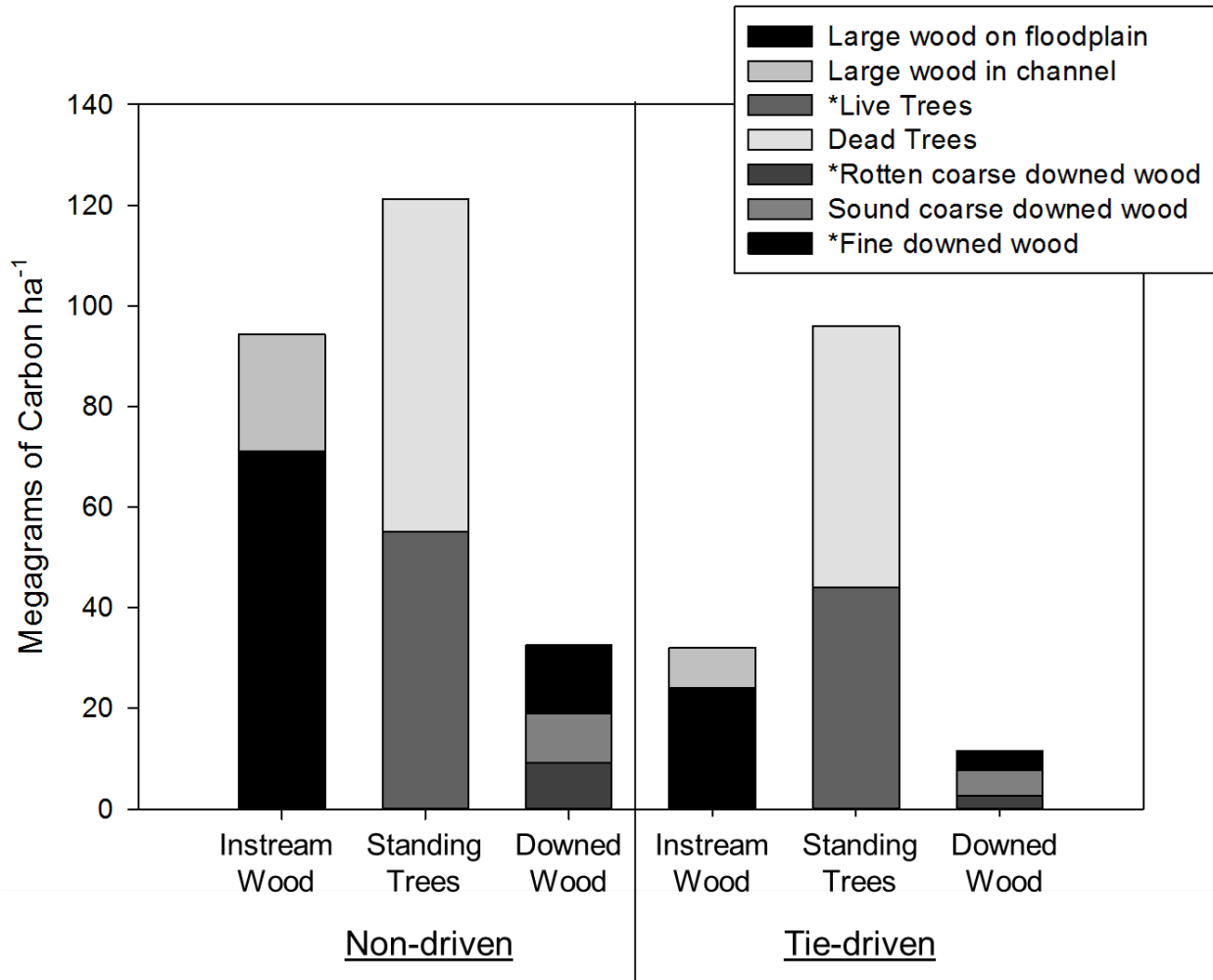


Figure 3.11 Small C pools measured across tie-driven and non-driven sites. The small pools account for approximately 5% of total C stored in stream-riparian corridors of both non-driven and tie-driven streams.

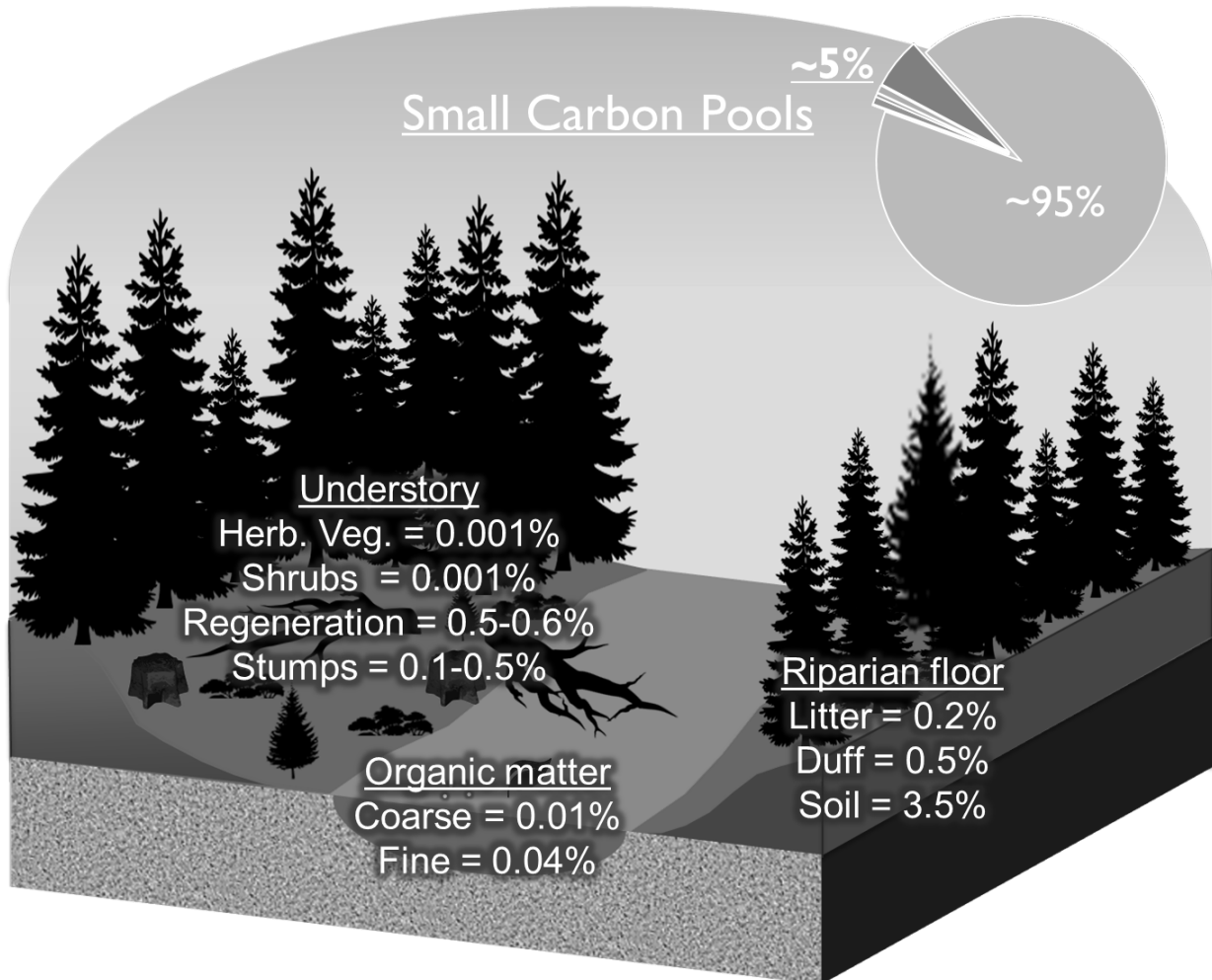


Figure 3.12 Large C pools measured across tie-driven and non-driven sites. The large pools account for approximately 95% of total C stored in stream-riparian corridors of both non-driven and tie-driven streams. An ‘*’ denotes pools which were significantly different.

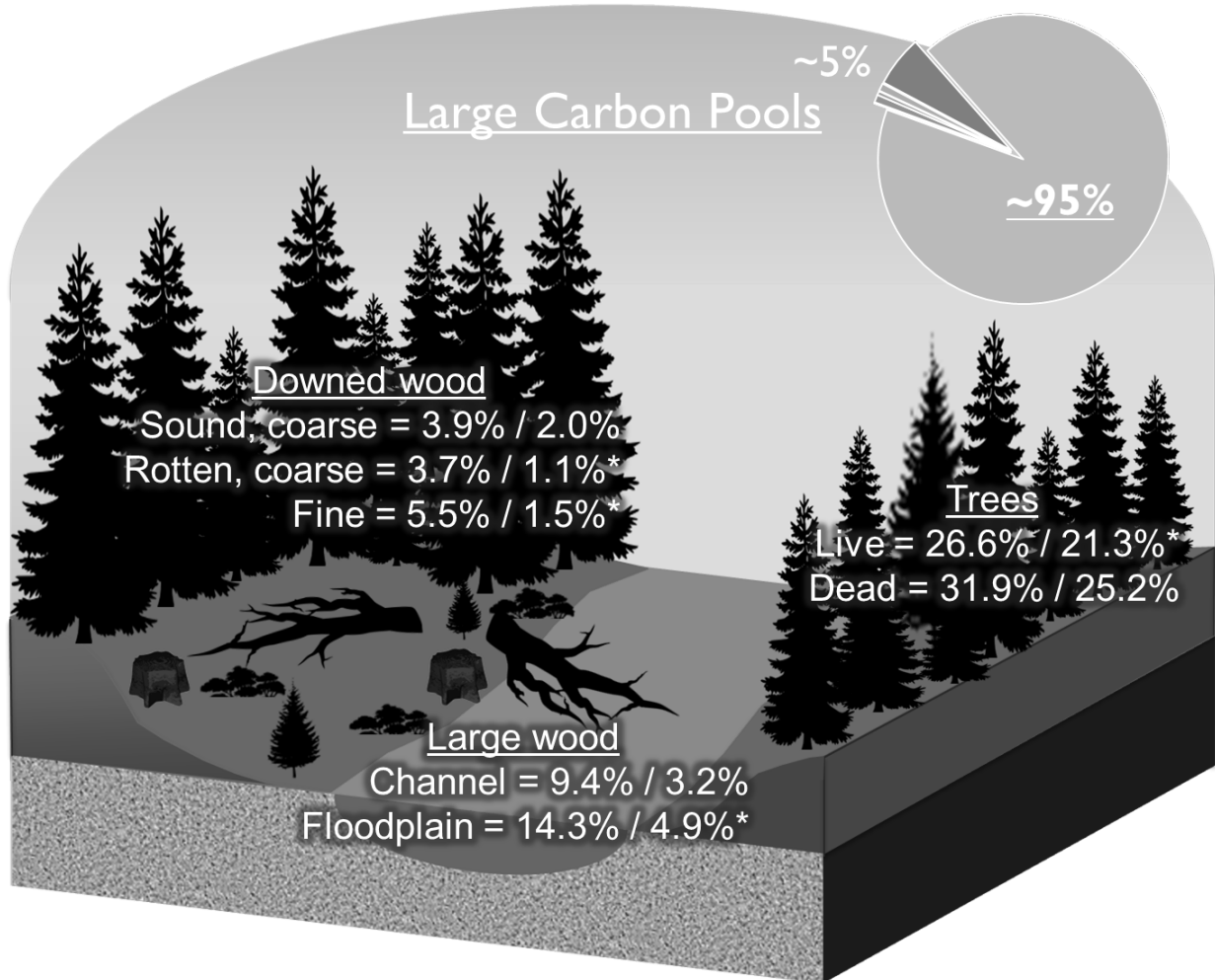


Table 3.1 Study reach characteristics

Stream (Pair)	Drive	Stream Order	Reach Length (m)	Basin Area (km ²)	Elevation (m)	Gradient (m/m)	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

Table 3.2 Measured carbon pools for instream and riparian components of study reaches. Data are means, SE, and range 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 - AG	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 - BG	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 - AG	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 - BG	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
AG Regen ≥ 2.5 cm - < 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
BG Regen ≥	Biomass	0.002	0.16 ± 0.02	0.01 ± 0.002	0.02	0.04 ± 0.01	0.07 ± 0.05

2.5 cm - < 5 cm	(Mg ha ⁻¹)						
	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
AG 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
BG 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
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

Chapter 4 - Influence of stream channel disturbance legacies on ecosystem metabolism in headwater streams, southeast Wyoming

Abstract

Geomorphic properties of streams are linked to ecosystem function through processes related to storage, transport, and other drivers influencing biogeochemical conditions. Here we investigate how tie-driving, a widespread historic channel disturbance legacy, where mountain streams were cleared so logs could be floated downstream during spring runoff, impacts contemporary rates of ecosystem metabolism in southern Wyoming. Metabolic rates were compared along with geomorphic and riparian properties to assess the extent of disturbance and degree of recovery within three sets of paired tie-driven and non-driven study reaches. Whole stream metabolism was measured using a two-station, diurnal approach and rates were compared between disturbed and reference reaches. Gross primary productivity (GPP) was significantly greater in tie-driven reaches than non-driven reaches, although rates of ecosystem respiration (ER) and net ecosystem productivity (NEP) were not significantly different. Aeration rates (k) were strongly correlated with wood loads, a direct link of the disturbance legacy to potential rates of gas exchange with the atmosphere. Results of this research contribute to the current understanding of feedbacks between stream channels and ecosystem function at both historic and contemporary time scales while informing management efforts and restoration initiatives.

Introduction

Streams are closely coupled to their catchments and thus are particularly sensitive to disturbance (defined here as discrete events associated with human activity that disrupt the ecosystem; Resh et al. 1988). Disturbances and disturbance regimes directly shape ecological patterns and processes in streams and leave lasting impacts on the physical environment that can cause cascading impacts to ecosystems (Fisher 1997). Despite the progress made in understanding disturbance in stream environments (e.g. Lake 2000; Dodds et al. 2004; Dewson et al. 2007), little is known about how multiple drivers within a system may interact following disturbances, especially in relation to feedbacks between geomorphic conditions and metrics of ecosystem function (Elosegi et al. 2010) or recovery time (Valett et al. 2002). Disturbance legacies, or contemporary system states derived from past disturbance events, provide a context

for studying integrative ecosystem interactions in streams through the comparison of altered yet stable conditions with reference systems. Few documented investigations have explored stream disturbance legacies, but existing work shows that historic land use practices have been associated with impacts on contemporary measures of biodiversity (Harding et al. 1998), community assemblage (Burcher and Benfield 2006), and stream water chemistry (Maloney et al. 2008). However, it is still unclear how legacy disturbances might manifest themselves in regards to ecosystem function and whether such legacies might contribute to altered system states or regime shifts.

Ecosystem metabolism encompasses a set of integrative metrics of ecosystem function that link the consumption of organic carbon across different trophic levels of the aquatic community with the energy being produced and stored in algal and aquatic plant communities. Metabolism is a function of two component rates, gross primary productivity (GPP) and ecosystem respiration (ER). The net difference between them is net ecosystem production (NEP). Rates of GPP and ER reflect autotrophic and heterotrophic conditions, respectively, and therefore ratios between the two metrics (GPP/ER; also referred to as GPP/ER) are indicative of trophic characteristics by revealing the balance of autochthonous and allochthonous energy pathways within streams (Dodds 2006). Ecological principles and empirical evidence support the role of light, temperature, hydrology, organic matter, and nutrients in driving GPP and ER; however, these relationships can vary greatly and potential responses to disturbances are not well understood. As the call for incorporating metrics of ecosystem function into stream management and monitoring grows (Young et al. 2008; Bunn et al. 2010), it becomes even more critical to quantify relationships between physical drivers and metabolic responses in order to assess ecosystem impairment and recovery.

Numerous studies have explored the influence of controlling variables on GPP and the most commonly found controlling driver is light, generally measured as photosynthetically active radiation (PAR). Variability in canopy cover due to seasonal changes (Hill 1996), riparian community characteristics (Mulholland et al. 2001), and degree of riparian canopy closure (Bott et al. 2006) have all been associated with altered rates of GPP. Additionally, channel geometry can influence light availability through bank shading (Julian et al. 2011) and variations in discharge have been linked to light variability as well (Acuña et al. 2011). Other factors that may impact rates of GPP include the influence of flow variability in regulating light and

substrate stability (Uehlinger and Naegeli 1998) and temperature, mainly as mediated by metabolic activity of algal communities (Acuña et al. 2011).

The effects of various drivers on ER are less clear although relationships have been found between rates of ER and supply of organic matter (Sinsabaugh 1997; Mulholland 2001; Meyer et al. 2007), nutrient concentrations (Mulholland et al. 2001; Bernot et al. 2010), and hydrologic variability associated with hyporheic exchange (Grimm and Fisher 1984; Naegeli and Uehlinger 1997; Fellows et al. 2001; Acuña et al. 2011). Additionally, a positive relationship between temperature and ER has been found in a variety of environments (Sinsabaugh 1997). Because ER reflects the consumption of organic carbon by all organisms in the system (including primary producers), an improved understanding of the effects of disturbance on drivers of ER would reveal potential bottom-up effects on the stream food web.

Even though GPP and ER are characterized by spatial and temporal variability, the tight coupling between the physical stream template and metabolic processes is evident in the response of GPP and ER to disturbances such as flow variations (Uehlinger 2000, 2003; Dodds et al. 2004) and wildfire (Betts and Jones 2009). However, the effects of anthropogenic disturbances to the stream channel itself and associated impacts on ecosystem metabolism have not been studied extensively. Additionally, alterations to the stream template resulting from disturbances can persist for varying degrees of time (McTammany et al. 2007). For example, historic agricultural practices and military land use activities have been found to have significant negative effects on ER through increased streambed instability, lack of in-channel wood, and low availability of labile organic carbon even though results on GPP are mixed in the same study systems (Houser et al. 2005). As metabolic rates become a more common management indicator of ecosystem function in stream ecosystems (Young et al. 2008), the need to understand impacts of both contemporary and legacy disturbances on metabolism, especially as they relate to altered channel morphology will continue to grow.

The role of large, in-channel wood represents an important aspect of channel morphology that has been well studied for decades (e.g. Keller and Swanson 1979; Lienkaemper and Swanson 1987; Marston et al. 1995; Brooks and Brierley 2002; Flores et al. 2011). Large wood alters flow patterns (Gippel 1995; Daniels and Rhoads 2004), is responsible for organic matter and sediment storage (Lisle 1995; Thompson 1995; Montgomery et al. 2003; Daniels 2006), and provides important controls on bedform morphology in many forested systems (Montgomery et

al. 1995). The body of work exploring the role of large instream wood has provided an integral foundation for understanding ecological functions such as habitat diversity and nutrient retention (Bilby and Likens 1980; Bisson et al. 1987; Gurnell et al. 1995) although relationships with GPP and ER are not characterized as well.

Historic wood removal activities in select regions, most notably the Pacific Northwest (Bilby and Ward 1991) and coastal Maine (Magilligan et al. 2008), represent significant geomorphic disturbances. Streams in the Rocky Mountain region have also been subject to extensive wood removal associated with timber floating, although this particular disturbance legacy is largely overlooked (Wohl 2006). As railroads reached the Rocky Mountains in the mid-1800s, streams were used as the primary method for transporting railroad ties, as was common throughout the United States (e.g. Sedell et al. 1991). Timbers were cut into ties and stored throughout the year until the high spring flows following snow melt could carry the load downstream in what was referred to as tie drives (Fig. 4.1). To make streams drivable, debris jams and boulders were removed and surge dams and feeder flumes were built to increase flow. The effects of these tie drives on the streams of the area have led to simplified stream channels, depauperate wood loads, and reduced riparian canopies (Young et al. 1994; Ruffing et al., in press).

The objective of this study was to evaluate differences in GPP, ER, and NEP across tie-driven and non-driven stream reaches in order to test for relationships between metabolic characteristics and a variety of physical controls influenced by the disturbance. We hypothesized that (1) GPP will be greater in tie-driven reaches compared to non-driven reaches because of increased light related to thinner riparian canopy cover and higher width to depth (W:D) ratios; (2) ER will be lowest in tie-driven reaches compared to non-driven reaches because of decreased organic matter standing stocks related to decreased channel storage capacity; and (3), all study reaches will be net heterotrophic as evidenced by higher rates of ER compared to GPP but tie-driven reaches are expected to be less heterotrophic than non-driven reaches due to overall higher rates of GPP compared to ER. We expected that the physical controls driving differences in metabolism would include reduced canopy cover, higher width to depth ratios (W:D), and decreased channel roughness in tie-driven reaches.

Methods

Study Area and Site Selection

The streams for this study were located in the Sierra Madre and Snowy Mountain ranges within Medicine Bow National Forest in southern Wyoming, USA (Fig. 4.1 E). The underlying geology of the Medicine Bow Mountains ranges from granitic, metasedimentary and metavolcanic rocks to glacial deposits in the higher elevations (Love and Christiansen 1985). Elevations within the Medicine Bow National Forest boundary range from 2170 to 3640 m. Forests in these areas are montane pine forests dominated by lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), as well as isolated areas of aspen (*Populus tremuloides*) (Dillon et al. 2005). Mean annual precipitation varies throughout both ranges but typically ranges from approximately 28 cm at low elevations to 669 cm at the highest elevations. Average annual temperatures range from a low of -1.31°C to 11.65°C with January typically being the coldest month and July being the warmest (PRISM Climate Group). Hydrologic regimes in both ranges are snowmelt dominated and peak flows usually occur in June.

Stream channel morphology in the area, like that of mountain streams in general, is highly dependent on gradient and the geomorphic influence of in-channel wood (Montgomery and Buffington 1997; Wohl and Merritt 2008; Wohl and Goode 2008). Typical channel types associated with area streams include step-pool, plane-bed, and pool-riffle channels in addition to other unique wood-forced morphologies (Wohl and Merritt 2008). Given the prevalence of tie-driving, altered channel morphologies devoid of wood are found throughout the area (Fig. 4.1E). Young et al. (1994) found that tie-driven stream reaches had less channel complexity as evidenced by a lack of instream large wood and pools and also had less dense riparian vegetation. Other natural disturbances which are common in this region include flooding, fire, and debris flows (Wohl 2006).

Study reaches were selected using a paired-reach sampling design, with two pairs in the Snowy Range and one pair in the Sierra Madre. Each reach pairing (Fig. 4.1 E) consists of one tie-driven reach and one non-driven reach, each extending approximately 30 times the average channel width. Pairs were located in close proximity to one another to help control for localized variations in geology, elevation, and riparian forest structure. Tie-driven streams were identified

by the presence of tall and decayed stumps and abandoned cabins close to the reach as well as other indicators of past logging activity. Non-driven streams were identified based on lack of past logging activity and were typified by high quantity and old age of existing wood loads in the channel and riparian area, the presence of large boulders or knickpoints near the study reach, and other permanent geologic or morphologic features which would prohibit the passage of ties during high flow events. Each reach identified was cross-checked with the historical records of tie-driving compiled by Young et al. (1994). While historical records of tie-driving exist for two of the non-driven reaches (North Fork Rock Creek and Flume Creek), field evidence suggests that historic tie-drives occurred downstream of the study reach locations.

The selection of study reaches was further constrained by common physiographic criteria including stream order, reach slope, geomorphic characteristics of valley bottoms, and surficial geology so that site pairs would be as physically analogous as possible, with the exception of tie-driven-related attributes (Table 4.1; Fig. 4.2). Significant morphologic differences associated with tie-driving were identified in a previous study (Ruffing et al., in press). Overall, tie-driven channels are more shallow, have a smaller cross-sectional area, greater width to depth ratios (W:D), and lower roughness values when compared to non-driven reaches, although stream widths are not significantly different. First order tie-driven streams have significantly lower wood loads than first order non-driven reaches, however, wood has accumulated in second order tie-driven reaches. First order tie-driven reaches are dominated by riffle and run morphologies while the second order tie-driven reach has a large proportion of wood-forced pools caused by wood jams. Inorganic substrate conditions across all sites are relatively coarse and dominated by size classes representing cobbles and boulders, with sparse patches dominated by gravels. With the exception of Trail Creek, tie-driven reaches have substantially fewer pieces of instream wood, translating to overall lower wood loads. Trail Creek and its non-driven site pair, North Fork Rock Trail Creek, are both second order streams and had similar quantities of wood pieces within the study reaches (Ruffing et al., in press).

Ecosystem Metabolism Field Procedures

Rates of GPP and ER were estimated using the 2-station open-system exchange technique (Odum 1956, Young and Huryyn 1998) in July and August of 2013. Diel O₂ and temperature curves were measured at the upstream and downstream ends of each reach. This technique uses

changes in O₂ measured over a minimum of 24 hours as a proxy for metabolic activity and relies on the assumption that all changes in O₂ are driven by photosynthesis, respiration and gas exchange with the atmosphere (aeration, Bott 2006).

YSI ProODO data loggers (Yellow Springs Instruments, Yellow Springs, Ohio) were positioned in the thalweg of the stream at stations corresponding to the upstream and downstream end of each reach and set to log temperature and dissolved O₂ continuously at 15 minute intervals. Photosynthetically active radiation (PAR) was logged at the same 15 minute intervals at each station using Odyssey integrating PAR sensors (Dataflow Systems PTY Limited) placed directly above the ProODO loggers in order to capture light available for instream primary producers. Data loggers were deployed simultaneously for each reach pair so that metabolism was estimated under similar atmospheric conditions. Before deployment at reach stations, data loggers were calibrated to water saturated air and then deployed simultaneously at a single station for a minimum of 45 minutes to ensure consistent measurements between data loggers.

Reach lengths were obtained from channel surveys and upstream and downstream reaches were located at permanently monumented cross-sections (see Ruffing et al., in press for detailed survey methods). Once loggers were deployed, wetted widths, depths, and canopy cover were measured throughout the reach. Canopy cover was measured using a spherical densiometer. The conservative tracer Rhodamine was used to measure velocity and calculate discharge during the period of deployment. Rhodamine was pumped into the stream with a peristaltic pump (Fluid Metering, Inc.) at a constant rate. Fluoresence was measured using a handheld Aquaflo fluorometer (model 8000-010; Turner Designs, Sunnyvale, California) at consistent time intervals in order to directly capture travel time.

Metabolism Calculations and Modeling

We applied a curve-fitting model based on Holtgrieve et al. (2010) and Riley and Dodds (2013) which uses depth, temperature, barometric pressure and PAR to drive estimates of GPP, ER and aeration as they influence predicted fluctuations in O₂ over the course of at least 24 hours. The contribution of GPP, ER, and aeration to changes in O₂ over time and between stations can be determined using average wetted width, average depth, temperature, barometric pressure and PAR in addition to average velocity and discharge. The curve fitting procedure is a

capability of the Solver tool available in Microsoft Excel (version 2010; Microsoft Corporation, Redmond Washington) which was employed to find the best fit between measured and modeled O₂ values through minimizing the sum of squared errors (SSE) between observed and modeled changes in O₂ values across the measurement reaches by changing values of GPP, ER, and aeration. Temperature and O₂ values from the downstream station were offset by travel time so that the initial time step for metabolism estimates was the same between the two stations. The two-station model was used for the longest continuously logged time period coincident between both stations. One-station models were run for the downstream stations to compare the results of the two-station model calculations, and confirm that we could use a one station value in a case where the upstream probe failed. The single station method is based on similar calculations (Dodds et al. 2013) but relies on measurements logged at one downstream station.

We calculated the change in O₂ (mg/L) from GPP as a function of temperature for each time step using equations developed by Jassby and Platt (1976) and Parkhill and Gulliver (1999) as

$$\Delta O_2 \text{ GPP}_T = P_{max} 1.036^{T_{avg}-20} \tanh\left(\frac{\alpha [1.036^{T_{avg}-20}] PAR}{P_{max} [1.036^{T_{avg}-20}]}\right) t_{travel} \quad [1]$$

where P_{max} is the maximum photosynthetic rate per unit area (mg/L/min⁻¹ estimated at 20°C), α is the initial slope of the relationship between GPP and PAR. The T_{avg} variable is the average temperature (°C) between both stations and is used to correct GPP for temperature. The t_{travel} variable is the travel time (min) between the two stations.

Changes in O₂ from ER for each time step were also temperature-corrected and calculated using the formula from Parkhill and Gulliver (1999) as

$$\Delta O_2 \text{ ER}_T = -R_T (1.045^{T_{avg}-20}) t_{travel} \quad [2]$$

where -R_T is the respiration rate mg O₂/L/ min at the average temperature.

Changes in O₂ from aeration (k) were calculated using equations from Riley and Dodds (2013) as

$$\Delta O_2 \text{ k}_T = -O_{2avg} + \left(\frac{O_{2avg}}{\frac{O_{2\%sat}}{100}}\right) k_T t_{travel} \quad [3]$$

where O_{2avg} represents the average O₂ concentration between both stations, O_{2%sat} is the percent O₂ percent saturation at each time step, and k_T is a temperature-corrected aeration constant.

Aeration values were modeled using a non-linear curve fitting approach within the metabolism

model and compared to published values of aeration in mountain streams (Riley and Dodds 2013; Table 4.2).

The final modeled values for changes in O₂ were calculated for each time step as

$$\frac{\Delta O_{2\text{Modeled}}}{\Delta t} = \frac{\Delta O_{2\text{GPP}_T}}{\Delta t} + \frac{\Delta O_{2\text{ER}_T}}{\Delta t} + \frac{\Delta O_{2k_T}}{\Delta t} \quad [4]$$

The Solver tool then adjusted the values for P_{max}, α, R_T, and k_T so that the SSE between measured values of ΔO₂ and ΔO_{2Modeled} were minimized. Resulting curves showed model fits that were consistent with observed diel trends. The averages for ΔO₂GPP_T and ΔO₂ER_T were converted to m⁻² and scaled per day to calculate GPP_{Daily} and ER_{Daily}. Values for NEP_{Daily} represent the difference between rates of GPP_{Daily} and ER_{Daily}. Values for k_T were scaled per day (k_{O2} d⁻¹) as well as by area (k_{O2} m⁻²) to compare gas flux at both temporal and spatial scales.

Each reach was modeled continuously using two stations for the entire length of the logging period when possible (Table 4.4). The two station models using the entire continuously logged data series for Horse Creek and Trail Creek records performed poorly because of fluctuations in barometric pressure and light throughout the week so those records were subdivided, modeled separately, and averaged to account for this variation. The upstream ProODO in North Fork Rock Creek was tampered with by wildlife so metabolism in North Fork Rock Creek was modeled using a single station model with the data logged at the downstream station. Comparisons between the one and two station models provided consistent results so values for mean daily GPP, ER, k, and NEP rates and mean areal k rates were taken from the results of the two-station models except in situations where an upstream probe failed in which case we used the downstream probe with a one station model.

Statistical Analysis

Differences in stream temperature between stations and across sites were assessed using Analysis of Variance (ANOVA). A Shapiro-Wilk test confirmed normality, thus temperature data was not transformed prior to analysis. We used a paired Student's t-test to test for significant differences in discharge, mean daily rates of GPP, ER, k, and NEP, and mean areal rates of k between tie-driven and non-driven reaches. We used linear regressions to evaluate relationships between daily rates of GPP, ER, and NEP and independent variables representing abiotic controls on these rates (Table 4.3). Control variables were grouped into physiographic, riparian, or geomorphic categories and analyzed individually in the regression analyses because

the low sample size ($n=6$) limited the number of variables allowed in the models. Pearson correlation matrices were used to ensure that control variables were independent.

Results

Physical Conditions

Bankfull and wetted widths were similar within stream orders ($p > .10$). First order reaches had bankfull widths of approximately 3 m and depths ranging from 0.16 to 0.3 m. Second order reaches were almost twice as wide with average depths slightly over 0.4 m. Average stream temperature across sites ranged from 6.05°C (SE ± 0.04) in Beaver Creek to 11.2°C (SE ± 0.09) in North Fork Rock Creek. During the data collection period, discharge ranged from 2.45 m³/m in Flume Creek to 16.38 m³/m in Trail Creeks. Discharge was not significantly different between disturbance conditions ($p > .10$). Stream temperature was not significantly different between upstream and downstream stations ($p > .10$), among sites ($p > .10$), or between disturbance conditions ($p > .10$; Fig. 4.3). Non-driven reaches had significantly more dense riparian canopies compared to non-driven streams ($p < 0.05$). Diel swings in O₂ and temperature, necessary for successful modeling, were recorded at all sites. Across all stations, peaks in O₂ occurred during night when temperatures were the lowest (Fig. 4.4).

Metabolism Models

Gross Primary Productivity

Overall, rates of GPP were low across all sites, ranging from 0.02 g O₂ m⁻² d⁻¹ in Flume Creek to 0.19 g O₂ m⁻² d⁻¹ in Horse Creek, both of which are non-driven reaches (Table 4.4). Average values of GPP were greater for tie-driven sites (p value < 0.05 ; Fig. 4.5 A) but did not differ between stream orders or reach pairs. Within site pairs, rates of GPP were 56% higher in East Fork Encampment River (tie-driven) compared to Beaver Creek, 13% higher in Flume Creek compared to Horse Creek (tie-driven) and 40% higher in Trail Creek (tie-driven) compared to North Fork Rock Creek.

Ecosystem Respiration

Values for ER ranged from a low of $0.05 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in Horse Creek to a high of $5.44 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in Trail Creek, both tie-driven reaches (Table 4.4). Beaver Creek and North Fork Rock Creek, both non-driven reaches, had lower average rates of ER than their tie-driven pairs (23% and 46%, respectively) while ER rates in Flume Creek were 99% higher than in Horse Creek. There were no significant differences in rates of ER between disturbance conditions (Fig. 4.5 B), stream orders, or reach pairs.

Net Ecosystem Metabolism

All streams were net heterotrophic except for Horse Creek which was slightly autotrophic with an NEP rate of $0.09 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Table 4.4). In comparison, the reach pair Flume Creek was more heterotrophic with a rate of $-3.68 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$. Trail and East Fork Encampment River, both tie-driven sites, were more heterotrophic than their non-driven reach pairs 46% and 21%, respectively. Despite these differences, rates of NEP were not significantly different between disturbance conditions (Fig. 4.5 C), stream orders, or reach pairs. Ratios of GPP to ER (P/R; Table 4.4) were less than 1 for all sites except Horse Creek, which is consistent with net heterotrophy. However, there were no significant differences between disturbance conditions, sites, or reach pairs.

Abiotic Controls on Ecosystem Metabolism

Structural variables (Table 4.3) representing site, geomorphic, wood, riparian, and organic matter characteristics were not significant in predicting variations in ER or NEP (Table 4.5). However, the results of regression analyses indicate that riparian canopy density was the strongest predictor variable explaining variations in GPP ($p < 0.01$, adj. $R^2 = 0.89$; Fig. 4.6). Additionally, the categorical variable disturbance condition was significant in explaining variations in GPP ($p < 0.05$, adj. $R^2 = 0.71$). The total number of wood pieces and the total volume of wood were highly significant in explaining variations in modeled rates of k at both spatial and temporal scales. The positive relationship between the daily aeration values and total number, or frequency, of large wood within the channel was marginally significant ($p < 0.1$, adj. $R^2 = 0.55$; Fig. 4.7 A) while the relationship between aeration values and the total volume of wood within the channel area was highly significant ($p < 0.01$, adj. $R^2 = 0.82$; Fig. 7 B). There

was a significant positive relationship between aeration and both the total number of wood pieces ($p < 0.1$, adj. $R^2 = 0.46$; Fig. 8 A) and volume of wood ($p < 0.05$, adj. $R^2 = 0.60$; Fig. 8 B), but these relationships were not as strong as those found at the daily scale. This suggests that the frequency and volume of wood are better predictors of daily aeration rates rather than rates per spatial unit of stream.

Discussion

Ecosystem metabolism in mountain systems

Our midsummer estimates of GPP, ER, and NEP are consistent with values found in other mountain streams (Table 4.2) and fall within the lower limits of values found in other ecoregions (Bernot et al. 2010). The low rates of GPP found in this study are indicative of low light environments characteristic of forested headwater streams and probably the relatively low nutrient concentrations that characterize mountain streams, while low values for ER are consistent with the low abundance and high recalcitrance of allochthonous organic material associated with coniferous systems (Hagen et al. 2010). Similarities in GPP/ER, which capture the relationship between autochthonous and allochthonous carbon sources, suggest that the heterotrophic reaches rely on a similar proportion of allochthonous material to drive the respiratory component of metabolic activity. The one exception to this is Horse Creek which was the only stream found to be characterized by autotrophy. The heterotrophic nature of these systems is consistent with the River Continuum Concept and empirical observations in forested headwater streams where allochthonous inputs exceed autochthonous production (Vannote et al. 1980). The results of this study capture metabolic conditions associated with the lower discharge conditions characteristic of the summer flow regime following snow melt.

Disturbance and Metabolism

Ecosystem metabolism can be an effective metric for assessing and monitoring stream health because of its ability to capture subtle differences in system perturbations (Young and Collier 2009). However, the results presented here show only modest effects related to the legacy of tie-driving and suggest that there are temporal differences in recovery response times for difference abiotic drivers. Tie-driven streams have shallow, plane-bed channels coupled with thinner woody riparian communities compared to non-driven systems (Ruffing et al., in press)

which led to our prediction that these altered conditions would translate to altered metabolic characteristics due to differences in light and organic matter storage. Explaining the differences in metabolic responses between disturbance conditions provides an opportunity to parse out the different ways a disturbance of both the riparian and channel portions of a stream can impact the components of ecosystem metabolism.

Differences in GPP were partially explained by canopy cover as well as tie-driving despite the lack of significant linear relationships with other altered physical variables associated with light availability (e.g. W:D, depth, and basal area). Riparian community composition was similar between sites, but basal areas differed significantly between disturbance conditions and ranged from 32.9 to 82.6 m² ha⁻¹ in Horse and Beaver Creek, respectively, yet the results presented here indicate that there was not a direct correlation between basal area and canopy cover. The lack of significance in bankfull channel geometry suggests tie-driven reaches are not influenced by bank shading (Ruffing et al., in press). While there is strong evidence that differences in light availability impact rates of GPP (Roberts et al. 2007; Bernot et al. 2010), few studies link nuanced metrics of riparian and channel characteristics with variations in GPP. Previous investigations have shown that increases in basal area, or the area within a stand that is occupied by trees, decreases the amount of solar radiation that penetrates through the canopy (Warren et al. 2013) and channel depth and W:D ratios influence the amount solar radiation received by the benthic zone by determining the thickness of water column and degree of bank shading (Julian et al. 2011). However, altered rates of GPP have been associated with increases in woody riparian vegetation in other systems, although these studies take place in grassland settings where the role of woody riparian vegetation is characterized as open or full canopy and do not capture intermediate conditions (Riley and Dodds 2012; Burrell et al. 2014). Given the nature of the tie-driving, riparian mechanisms controlling light availability may not have fully recovered in the decades since the practice originally occurred.

There were no significant differences in ER between disturbance conditions and riparian and channel variables failed to explain significantly explain observed differences between sites. Despite the lack of significant differences there is evidence (Minshall et al. 1992; Entekin et al. 2008) and a strong theoretical foundation (Vannote et al. 1980) to support our original hypotheses that the amount of allochthonous material coupled with the channel's ability to retain that material would be important variables influencing ER. Non-driven streams were associated

with greater roughness values although midseason standing stocks of coarse and fine particulate organic matter were not significantly different. It is also possible that ER is influenced by components of hyporheic activity which we assumed would be similar across sites. Temperature variations were consistent between upstream and downstream stations within each study reach which suggests that there were no major contributions from the hyporheic zone between stations. However, we did not account for differences in the concentration of O₂ in groundwater relative to stream water. Previous investigations have shown that even minimal inputs of low O₂ water from hyporheic exchange can increase estimates of ER (Hall and Tank 2005), although the overall contributions of hyporheic exchange to whole-stream estimates are notoriously difficult to study (McCutchan et al. 2002). Compared to structural drivers controlling GPP, mechanisms influencing ER are linked to conditions much deeper within the structure of the channel. Stream temperature and hyporheic exchange reflect geologic controls on both lateral and longitudinal subsurface flowpaths that are more resistant to disturbance, however once they are altered, may be characterized by a longer recovery period.

Aeration, or the rate of gas exchange between the water and atmosphere, dictates how quickly dissolved gasses in the water column can come to equilibrium with the atmosphere. This physical process is indirectly related to the measurement of metabolism because it captures the limit of O₂ away from saturation. The relationship between channel properties such as mean depth, velocity, reach slope and discharge have long been recognized and are incorporated in empirical aeration modeling equations (Cox 2003). Aeration is often thought to be an expression of the effects of bedforms on flow turbulence; however, the significance of wood over bedform roughness found in this study suggests this relationship might be more complex than previously thought. Tie-driven streams have significantly lower roughness values, as characterized by substrate classes and bedforms, in both the longitudinal and cross-sectional directions (Ruffing et al., in press). While roughness generally relates to turbulence within the water column, the results of this study suggest that this metric may not be indicative of gas-exchange rates at the water's surface. Wood in headwater streams is less likely to be fully submerged due to the limited channel capacity (Wohl and Goode 2008) and only 11% of all wood sampled in the study reaches was fully incorporated within the channel (Ruffing et al., in press). Our comparison of aeration over spatial and temporal scales suggests that in-channel wood is not only slowing water down, but increasing gas exchange. Like the surficial drivers of GPP, overall channel roughness

reflects surficial controls in regards to overall ecosystem structure. Aeration rates would respond to relatively fast recovery times associated with wood recruitment compared to geologic controls governing grain size and channel form.

The implications of alteration of aeration rates by large wood are broader than just our ability to measure metabolism. For example, streams worldwide are a substantial source of nitrous oxide to the atmosphere (Beaulieu et al. 2011) and aeration rates, in part, determine if this gas emits to the atmosphere prior to reduction to N₂ gas by microbes in the streams. Aeration also influences methane transfer rates, and in cases where there may be high biological oxygen demand (e.g. septic inputs into mountain streams) may influence the probability that a stream become hypoxic or anoxic. Large instream wood has previously received attention from the management community given the significant channel responses to wood removal or additions and its prevalence as a restoration technique (Piegay et al. 2005; Chin et al. 2008; Lassetre and Kondolf 2012), but to our knowledge the relationship between wood and aeration has not been previously recognized.

Legacy Disturbance, Ecosystem Metabolism, and Management

The selection of reference reaches is a common management strategy employed to guide management decisions and monitor stream health (Bernhardt and Palmer 2007). Historic wood removal activities have been recognized in other regions and are associated with altered contemporary wood loads, as well as impacts on geomorphic heterogeneity as captured by increased sediment transport, channel widening, and the simplification of habitat units throughout stream reaches (Magilligan et al. 2008; Czarnomski et al. 2008; Mellina and Hinch 2009). Such drastic changes to the stream environment represent potential mechanisms for cascading effects to stream metabolism through the alteration of light, organic matter storage, and flow variability. Evaluating legacy disturbances provides a unique opportunity to evaluate the dynamics between ecosystem structure and function as well as explore trajectories of ecosystem recovery. However, our study suggests that disturbance legacies may confound the reference selection process.

Both GPP and ER are highly variable (Young and Huryn 1996, 1999; Mulholland et al. 2001, 2006). However, it has been speculated that with properly chosen reference reaches, reasonable parameters of ecosystem metabolism can be derived (Young et al. 2008). Legacy disturbances

complicate reference reach selection not only through identification but also in terms of expected ecosystem function. For example, the streams chosen in this investigation were chosen to control for a range of differences such as geology, catchment land use, and stream size to isolate differences associated with the legacy of tie-driving. When the results presented here are compared to the reference range methods identified by Young et al. (2008), estimates of GPP, ER, and P/R at all sites except for Horse Creek fall within the upper 75th and lower 25th percentiles categorized as “healthy” (Table 4.6). The low absolute value for ER and high P/R values for Horse Creek place it in the “poor” range for both categories (lower 5th percentile and 95th percentile, respectively; Young et al. 2008). Similarly, when compared directly with reference reaches, Horse Creek is identified as “severely impaired” in respect to GPP and ER while Trail Creek is identified as having a mild effect on ecosystem functioning in respect to ER (Young et al. 2008). Horse Creek has the lowest wood loads and lowest riparian basal area of all of the study sites and these physical constraints likely influence potential ranges of both GPP and ER. While the legacy of tie-driving is still evident in the structure of the disturbed streams in this study, designations such as “severely impaired” may be overstated and effectively uncouple the functional components of metabolism from the physical structure of the stream. Capturing variability in GPP, ER, and NEP through time following a disturbance is a considerable undertaking but understanding shifts in metabolic state following disturbances will likely characterize some of the many challenges for future water resource management.

Given the widespread nature of tie-driving within the region, the most common stream conditions are relatively shallow with low roughness values and is devoid of wood, despite mature riparian forest stands and high streams gradients. If the results of this work are any indication, then it is likely that many of these streams have relatively high rates of GPP compared to other un- impacted forested mountain headwaters. However, due to the nature of the disturbance history, this stream type is not necessarily a realistic model for management goals or restoration targets. If metabolism is to be used as an effective metric for assessing stream health, stronger relationships between controlling environmental variables and metabolic responses are needed to guide reference reach selection.

Conclusion

Tie-driving has created a pervasive and long-lasting disturbance to stream channel morphology, wood loading, and GPP in the mountain headwater streams of the Rocky Mountain Front Range. Overall, the tie-driven streams in the Medicine Bow National Forest display relatively high rates of GPP compared to non-driven reference reaches although rates of ER and NEP were similar between the two conditions. Altered wood loads impact aeration but no measurable effect was seen on GPP or ER. Despite the extensive literature examining trends in ecosystem metabolism and the role of abiotic drivers, this study is one of the first, to our knowledge, that addresses the metabolic response following an extensive historic disturbance that has dramatically altered channel geomorphology, wood loads, and riparian condition.

References

- Acuña, V., C. Vilches, and A. Giorgi. 2011. As productive and slow as a stream can be—the metabolism of a Pampean stream. *Journal of the North American Benthological Society* 30 (1): 71-83.
- Beaulieu, J. J., J. L. Tank, S. K. Hamilton, W. M. Wollheim, R. O. Hall, P. J. Mulholland, B. J. Peterson, L. R. Ashkenas, L. W. Cooper, and C. N. Dahm. 2011. Nitrous oxide emission from denitrification in stream and river networks. *Proceedings of the National Academy of Sciences* 108:214.
- Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. C. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G.M. Kondolf, P.S. Lake, R. Lave, J.L. Meyer, T.K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. *Science* 308: 636-637.
- Bernot MJ, Sobota DJ, Hall RO, Mulholland PJ, Dodds WK, Webster JR, Tank JL, Ashkenas LR, Cooper LW, Dahm CN. 2010. Inter-regional comparison of land-use effects on stream metabolism. *Freshwater Biology* 55: 1874-1890.
- Betts, E.F. and J.B. Jones. 2009. Impact of Wildfire on Stream Nutrient Chemistry and Ecosystem Metabolism in Boreal Forest Catchments of Interior Alaska. *Arctic Antarctic and Alpine Research* 41(4):407-417.
- Bilby, R.E. and G.E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 61(5):1107-1113.
- Bilby, R. E., and J. W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clearcut, and second-growth forests in southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 48:2499-2508.
- Bisson P.A., R.E. Bilby, M.D. Bryant, C.A. Dolloff, G.B. Grette, R.A. House, M.L. Murphy, K.V. Koski and J.R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present and future. In: *Streamside Management: Forestry and Fishery Interactions*. (Eds E.O. Salo & T.W. Cundy), pp. 143–190. Proceedings of the Symposium, February 12–14, 1986, Seattle, Washington, College of Forest Resources, Contribution 57. University of Washington, Washington.

- Bott, T.L. 2006. "Primary productivity and community respiration." in *Methods in stream ecology*, edited by F. R. Hauer and G. A. Lamberti, 663–690. San Diego: Elsevier.
- Brooks, A. P., & Brierley, G. J., 2002. Mediated equilibrium: the influence of riparian vegetation and wood on the long-term evolution and behaviour of a near-pristine river. *Earth Surface Processes and Landforms*, 27(4), 343-367.
- Bunn, S.E., Abal, E.G., Smith, M.J., Choy, S.C, Fellows, C.S., Harch, B.D., Kennard, M.J., and Sheldon, F. 2010. Integration of science and monitoring of river ecosystem health to guide investments in catchment protection and rehabilitation. *Freshwater Biology* 55:223-240.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. *Soc. Method. Res.* 33, 261–304.
- Burrell, T.K., O'Brien, J.M., Graham, S.E., Simon, K.S., Harding, J.S., McIntosh, A.R. 2014. Riparian shading mitigates stream eutrophication in agricultural catchments. *Freshwater Science* 33(1):73-84.
- Chin, A., M.D. Daniels, M.A. Urban, H.Piegay, K.J. Gregory, W. Bigler, K. Boyer, A. Butt, J. Grable, S.V. Gregory, M. LaFrenz, L.R. Laurencio, and E. Wohl. 2008. Perceptions of Wood in Rivers and Challenges for Stream Restoration in the United States. *Environmental Management*. 41 (6), 893-903.
- Cox, B.A. 2003. A review of dissolved oxygen modelling techniques for lowland rivers. *Science of the Total Environment* 314:303-334.
- Czarnomski, N.M., D.M. Dreher, K.U. Snyder, J.A. Jones, and F.J. Swanson. 2008. Dynamics of wood in stream networks of the western Cascades Range, Oregon. *Canadian Journal of Forestry Research* 38,2236-2248, doi:10.1139/X08-068.
- Daniels, M.D. 2006. Distribution and dynamics of large woody debris and organic matter in a low-energy meandering stream. *Geomorphology*, 77(3-4): 286-298.
- Daniels, M.D. and B.L. Rhoads. 2004. Effect of LWD configuration on spatial patterns of three-dimensional flow in two low-energy meander bends at varying stages. *Water Resources Research*, 40 (11) W11302, doi:10.1029/2004WR003181.
- Dewson, Z.S., James, A.B.W., Death, R.G. 2007. Stream ecosystem functioning under reduced flow conditions. *Ecological Applications* 17(6):1797-1808.

- Dillon, G.K., Knight, D.H., Meyer, C. B. 2005. Historic range of variability for upland vegetation in the Medicine Bow National Forest, Wyoming. RMRS-GTR-139, Fort Collins, CO; USDA Forest Service, Rocky Mountain Research Station. 85 pages.
- Dodds WK. 2006. Eutrophication and trophic state in rivers and streams. *Limnology and Oceanography* 51: 671-680.
- Dodds, W.K., Gido, K., Whiles, M.R., Fritz, K.M., Matthews, W.J. 2004. Life on the edge: The ecology of great plains prairie streams. *Bioscience* 54(3):205-216.
- Dodds WK, Veach AM, Ruffing CM, Larson DM, Fischer JL, Costigan KH. 2013. Abiotic controls and temporal variability of river metabolism: multiyear analyses of Mississippi and Chattahoochee River data. *Freshwater Science* 32: 1073-1087.
- Elosegi, A., J. Diez, and M. Mutz. 2010. Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. *Hydrobiologia* 657:199-215.
- Entrekin, S.A., J.L. Tank, E.J. Rosi-Marshall, T.J. Hoellein, and G.A. Lamberti. 2008. Responses in organic matter accumulation and processing to an experimental wood addition in three headwater streams. *Freshwater Biology* 53(8): 1642-1657.
- Fellows, C.S., H.M. Valett, and C.N. Dahm. 2001. Whole-stream metabolism in two montane streams: Contribution of the hyporheic zone. *Limnology and Oceanography* 46 (3): 523-31.
- Fisher, S.G. 1997. Creativity, idea generation, and the functional morphology of streams. *Journal of the North American Benthological Society*. 16(2):305-318.
- Flores, L., Larranaga, A., Diez, J., Elosegi, A., 2011. Experimental wood addition in streams: effects on organic matter storage and breakdown. *Freshwater Biology*, 56(10), 2156-2167.
- Gippel, C.J. 1995. Environmental hydraulics of larger woody debris in streams and rivers. *Journal of Environmental Engineering*, 121(5): 388-395.
- Grimm, N.B., and S.G. Fisher. 1984. Exchange between interstitial and surface-water – implications for stream metabolism and nutrient cycling. *Hydrobiologia* 111 (3): 219-28.
- Gurnell, A.M., K.J. Gregory and G.E. Petts. 1995. The role of coarse woody debris in forest aquatic habitats: implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5: 143-166.

- Hagen, E.M., McTammany, M.E., Webster, J.R., Benfield, E.F., 2010. Shifts in allochthonous input and autochthonous production in streams along an agricultural land-use gradient. *Hydrobiologia* 655(1):61-77.
- Hall, R.O. and Tank, J.L. 2005. Correcting whole-stream estimates of metabolism for groundwater input. *Limnology and Oceanography – Methods* 3:222-229.
- Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S., Jones, E.B.D. 1998. Stream biodiversity: The ghost of land use past. *Proceedings of the National Academy of Sciences of the United States of America* 95(25):14843-14847.
- Hill, W.R. 1996. "Effects of light." in *Algal Ecology*, edited by R.J. Stevenson, M.L. Bothwell, and R.L. Lowe, 121-144. San Diego: Academic Press.
- Hoellein, T.J., Tank, J.L., Entekin, S.A., Rosi-Marshall, E.J., Stephen, M.L., Lamberti, G.A. 2012. Effects of benthic habitat restoration on nutrient uptake and ecosystem metabolism in three headwater streams. *River Research and Applications* 28(9):1451-1461.
- Holtgrieve, G.W., D.E. Schindler, T.A. Branch and Z.T. A'mar. 2010. Simultaneous quantification of aquatic ecosystem metabolism and reaeration using a Bayesian statistical model of oxygen dynamics. *Limnology and Oceanography* 55:1047-1063.
- Houser, J.N., P.J. Mulholland, and K.O. Maloney. 2005. Catchment disturbance and stream metabolism: Patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance. *Journal of the North American Benthological Society* 24 (3): 538-52.
- Jassby and Platt (1976) Jassby AD, Platt T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnology and Oceanography* 21: 540-547.
- Julian, J.P., Seegert, S.Z., Powers, S.M., Stanley, E.H., Doyle, M.W. 2011. Light as a first-order control on ecosystem structure in a temperate stream. *Ecohydrology* 4(3):422-432.
- Keller, E.A., Swanson, F.J., 1979. Effects of large organic material on channel form and fluvial processes. *Earth Surface Processes and Landforms* 4 (4), 361–380.
- Lake, P.S. 2000 Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19(4):573-592.

- Lassette, N.S. and G.M. Kondolf. 2012. Large woody debris in urban stream channels: Redefining the problem. *River Research and Applications* 28(9),1477-1487. DOI: 10.1002/rra.1538.
- Lienkaemper, G.W., Swanson, F.J., 1987. Dynamics of large woody debris in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* 17,150-156.
- Lisle, T.E. 1995. Effects of coarse woody debris and its removal on a channel affected by the 1980 eruption of Mount St. Helens, Washington. *Water Resources Research* 31(7): 1797-1808.
- Love, J. D. and A. C. Christiansen. 1985. *Geologic Map of Wyoming*. US Geological Survey.
- Magilligan, F.J., K.H. Nislow, G.B. Fisher, J. Wright, G. Mackey, and M. Laser. 2008. The geomorphic function and characteristics of large woody debris in low gradient rivers, coastal Maine, USA. *Geomorphology* 97:467-482.
- Maloney, K.O., J. W. Feminella, R. M. Mitchell, S. A. Miller, P. J. Mulholland, and J. N. Houser. 2008. Landuse legacies and small streams: Identifying relationships between historical land use and contemporary stream conditions. *Journal of the North American Benthological Society* 27 (2): 280-294.
- Marston, R. A., Girel, J., Pautou, G., Piegay, H., Bravard, J. P., & Arneson, C., 1995. Channel metamorphosis, floodplain disturbance, and vegetation development: Ain River, France. *Geomorphology*, 13(1), 121-131.
- McCutchan, J.H. and W.M. Lewis. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnology and Oceanography*. 47(3):742-752.
- McTammany, M.E., W.F. Benfield, J.R. Webster. 2007. Recovery of stream ecosystem metabolism from historical agriculture. *Journal of the North American Benthological Society* 26(3):532-545.
- Mellina, E. and S.G. Hinch. 2009. Influences of riparian logging and instream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. *Canadian Journal of Forestry Research* 39,1280-1301, doi:10.1139/X09-037.
- Meyer, J.L., Strayer, D.L., Wallace, J.B., Eggert, S.L., Helfman, G.S., Leonard, N.E. 2007. The contribution of headwater streams to biodiversity in river networks. *Journal of the North American Benthological Society* 43(1):86-103.

- Minshall G., R.Petersen, T.Bott, C. Cushing and K. Cummins. 1992. Stream ecosystem dynamics of the Salmon River, Idaho - An 8th-order system. *Journal of the North American Benthological Society*, 11:111-137. Montgomery, D.R., J.M. Buffington, R.D. Smith, K.M. Schmidt,
- Montgomery, D.R., T.M. Massong, and S.C.S. Hawley. 2003. Influence of debris flows and log jams on the location of pools and alluvial channel reaches, Oregon Coast Range. *Geological Society of America Bulletin* 115:78-88.
- Montgomery, D.R. and J.M. Buffington. 1997. Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* 109(5),596-611.
- Mulholland, P.J., C.S. Fellows, J.L. Tank, N.B. Grimm, and J.R. Webster, S.K. Hamilton, E. Marti, L. Ashkenas, W.B. Bowden, W.K. Dodds, W.H. McDowell, M.J. Paul, and B.J. Peterson. 2001. Inter-biome comparison of factors controlling stream metabolism. *Freshwater Biology* 46 (11): 1503-17.
- Muotka, T., and P. Laasonen. 2002. Ecosystem recovery in restored headwater streams: The role of enhanced leaf retention. *Journal of Applied Ecology* 39 (1): 145-156.
- Naegeli, M.W., and U. Uehlinger. 1997. Contribution of the hyporheic zone to ecosystem metabolism in a prealpine gravel-bed river. *Journal of the North American Benthological Society* 16 (4): 794-804.
- Odum, H.T. 1956. Primary productivity in flowing waters. *Limnology and Oceanography* 1:102-117.
- Palmer, M.A., H.L. Menninger, and E.S. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: A failure of theory or practice? *Freshwater Biology* 55: 205-222.
- Parkhill and Gulliver (1999) Parkhill KL, Gulliver JS. 1999. Modeling the effect of light on whole-stream respiration. *Ecological Modeling* 117: 333-342.
- Piegay, H., K. J. Gregory, V. Bondarev, A. Chin, N. Dahlstrom, A. Elozegi, S. V. Gregory, V. Joshi, M. Mutz, M. Rinaldi, B. Wyzga, and J. Zawiejska. 2005. Public perception as a barrier to introducing wood in rivers for restoration purposes. *Environmental Management* 36(5),665-674.
- PRISM Climate Group, Oregon State University, <http://prismmap.nacse.org/nn/index.phtml?lvartype=ppt&month=14&year0=1895&year1=2012>

- Resh, V.H., Brown, A.V., Covich, A.P. Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., Wissmar, R.C. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7(4):433-455.
- Riley AJ, Dodds WK. 2013. Whole-stream metabolism: strategies for measuring and modeling diel trends of dissolved oxygen. *Freshwater Science* 32: 56-69.
- Riley AJ, Dodds WK. 2012. The expansion of woody riparian vegetation, and subsequent stream restoration, influences the metabolism of prairie streams. *Freshwater Biology* 57(6):1138-1150.
- Roberts, B.J., Mulholland, P.J., Hill, W.R. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* 10(4):588-606.
- Ruffing, C., M. Daniels, and K. A. Dwire. Disturbance legacies of historic tie-drives persistently alter geomorphology and large wood characteristics in headwater streams, southeast Wyoming (in revision for *Geomorphology*).
- Sedell, R., F.N. Leone and W.S. Duval. 1991. Water transportation and storage of logs. *American Fisheries Society Special Publication* 19:325-368.
- Sinsabaugh, R.L. 1997. Large-scale trends for stream benthic respiration. *Journal of the North American Benthological Society* 16 (1): 119-22. Sudduth, E.B., B.A. Hassett, P.Cada, and E. S. Bernhardt. 2011. Testing the field of dreams hypothesis: Functional responses to urbanization and restoration in stream ecosystems *Ecological Applications* 21(6):1972-1988.
- Thompson, D. M. 1995. The effects of large organic debris on sediment processes and stream morphology in Vermont. *Geomorphology* 11(3): 235-44.
- Tullos, D.D., D.L. Penrose, G.D. Jennings, and W.G. Cope. 2009. Analysis of functional traits in reconfigured channels: Implications for the bioassessment and disturbance of river restoration. *Journal of the North American Benthological Society* 28(1): 80-92.
- Uehlinger, U., and M.W. Naegeli. 1998. Ecosystem metabolism, disturbance, and stability in a prealpine gravel bed river. *Journal of the North American Benthological Society* 17 (2): 165-78. Uehlinger, U., B. Kawecka, and C.T. Robinson. 2003. Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl). *Aquatic Sciences* 65:199-209.

- Uehlinger, U. 2000. Resistance and resilience of ecosystem metabolism in a flood-prone river system. *Freshwater Biology*. 45:319-332.
- Uehlinger, U., B. Kawecka, and C.T. Robinson. 2003. Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl). *Aquatic Sciences* 65:199-209.
- Valett, H.M., C.L. Crenshaw, and P.F. Wagner. 2002. Stream nutrient uptake, forest succession, and biogeochemical theory. *Ecology* 83:2888-2901.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37 (1): 130-137.
- Warren et al. 2013
- Wohl, E. 2006. Human impacts to mountain streams. *Geomorphology* 79(3-4):217-248.
- Wohl, E. and J.R. Goode. 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. *Water Resources Research* 44(W09429):1-14.
- Wohl, E. and D. Merritt. 2008. Reach-scale channel geometry of mountain streams. *Geomorphology* 93 (3-4): 168-85.
- Young, M.K., D. Haire, and M.A. Bozek. 1994. The effect and extent of railroad tie drives in streams of southeastern Wyoming. *Western Journal of Applied Forestry* 9(4): 125-130.
- Young, R.G. and Collier, K.J. 2009. Contrasting responses to catchment modification among a range of functional and structural indicators of river ecosystem health. *Freshwater Biology* 54(10):2155-2170.
- Young, R.G. and Huryn, A.D. 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. *Canadian Journal of Fisheries and Aquatic Sciences* 53(10):2199-2211.
- Young, R.G., and A.D. Huryn. 1999. Effects of land use on stream metabolism and organic matter turnover. *Ecological Applications* 9 (4): 1359-76.
- Young, R.G., C.D. Matthaei, and C.R. Townsend. 2008. Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. *Journal of the North American Benthological Society* 27(3):605-625.

Figure 4.1 Historic photographs and maps detailing the tie-driving process. (A) Railroad ties were cut and stored adjacent to streambanks before (B) being pushed into the channel immediately following peak flow. (C) Occasionally, ties would become congested within the channel causing a tie jam. (D) Ultimately, ties were floated to larger order rivers in order to be delivered to processing centers. (E) A map of tie-driving within the Medicine Bow National Forest depicts how pervasive this practice was within the study area, although not all streams were tie-driven along their entire length. Locations of study sites are denoted with circles and tie-driven reaches are identified with a T following the reach name. Photographs are courtesy of the American Heritage Center and the Grand Encampment Museum.



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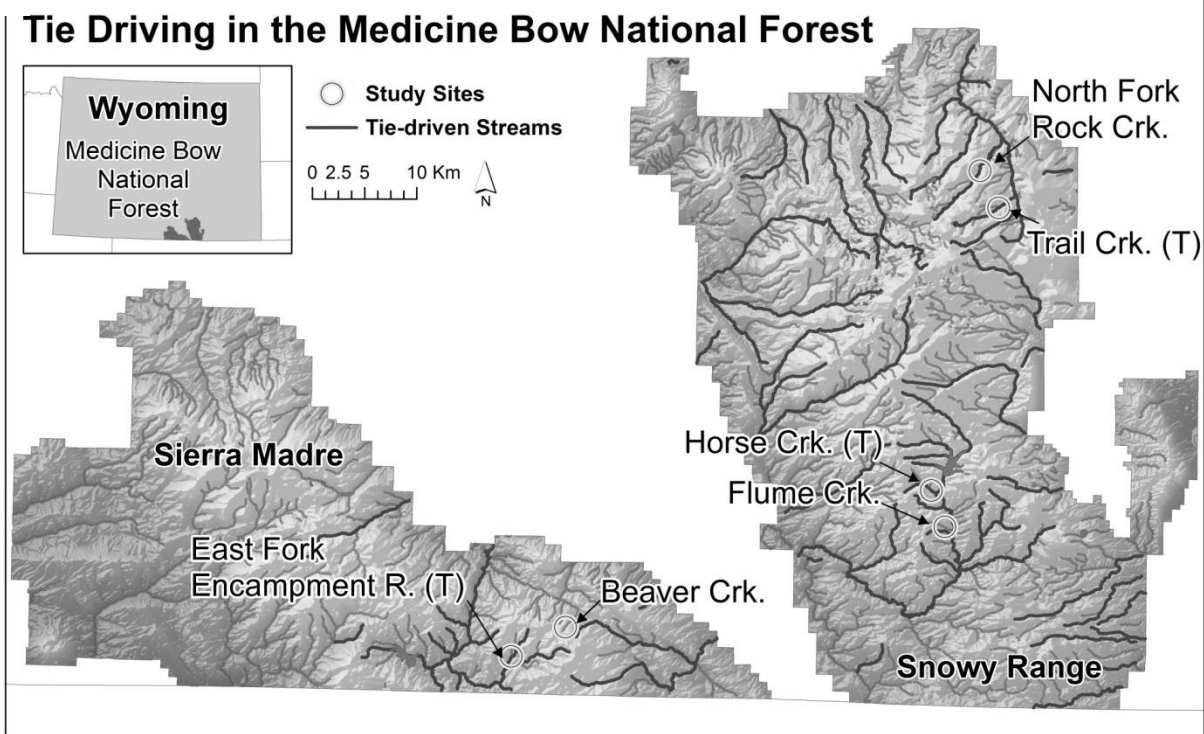


Figure 4.2 Representative photographs of each study site. Tie-driven sites are on top and their non-driven reach pair is below.

East Fork Encampment R.
(Tie-driven)



Horse Crk. (Tie-driven)



Trail Crk. (Tie-driven)



Beaver Crk. (Non-driven)



Flume Crk. (Non-driven)



North Fork Rock Crk.
(Non-driven)

Figure 4.3 Temperature ranges for up and downstream stations for each site. Reaches are ordered by pair and grey shading denotes the non-driven reach within each pair.

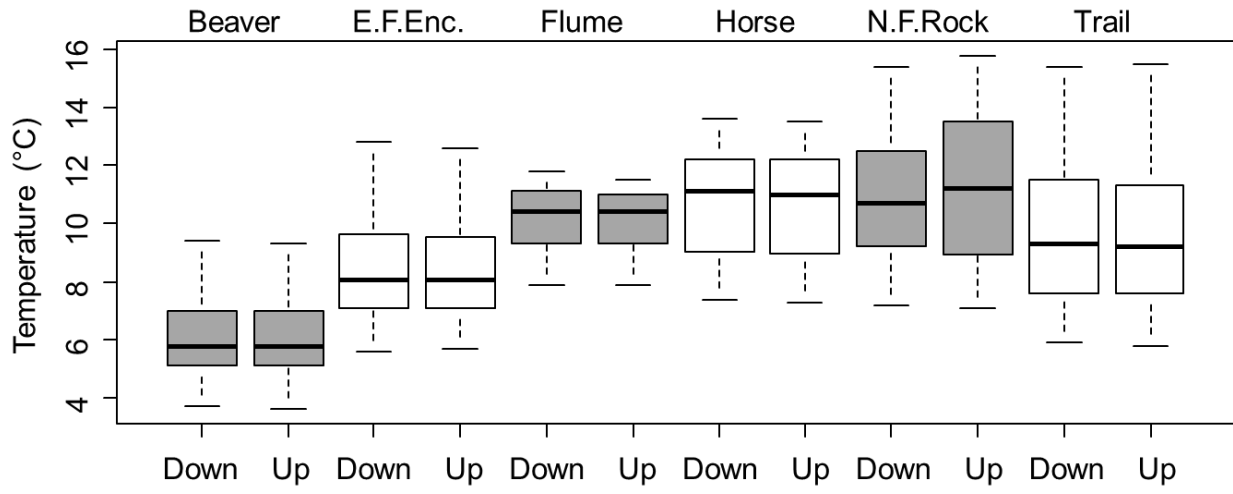


Figure 4.4 Diel temperature and O₂ swings for the logging period of each site. Light circles represent O₂, dark circles represent temperature, and grey background shading indicates night periods. Individual time steps represent each 15 minute sampling interval.

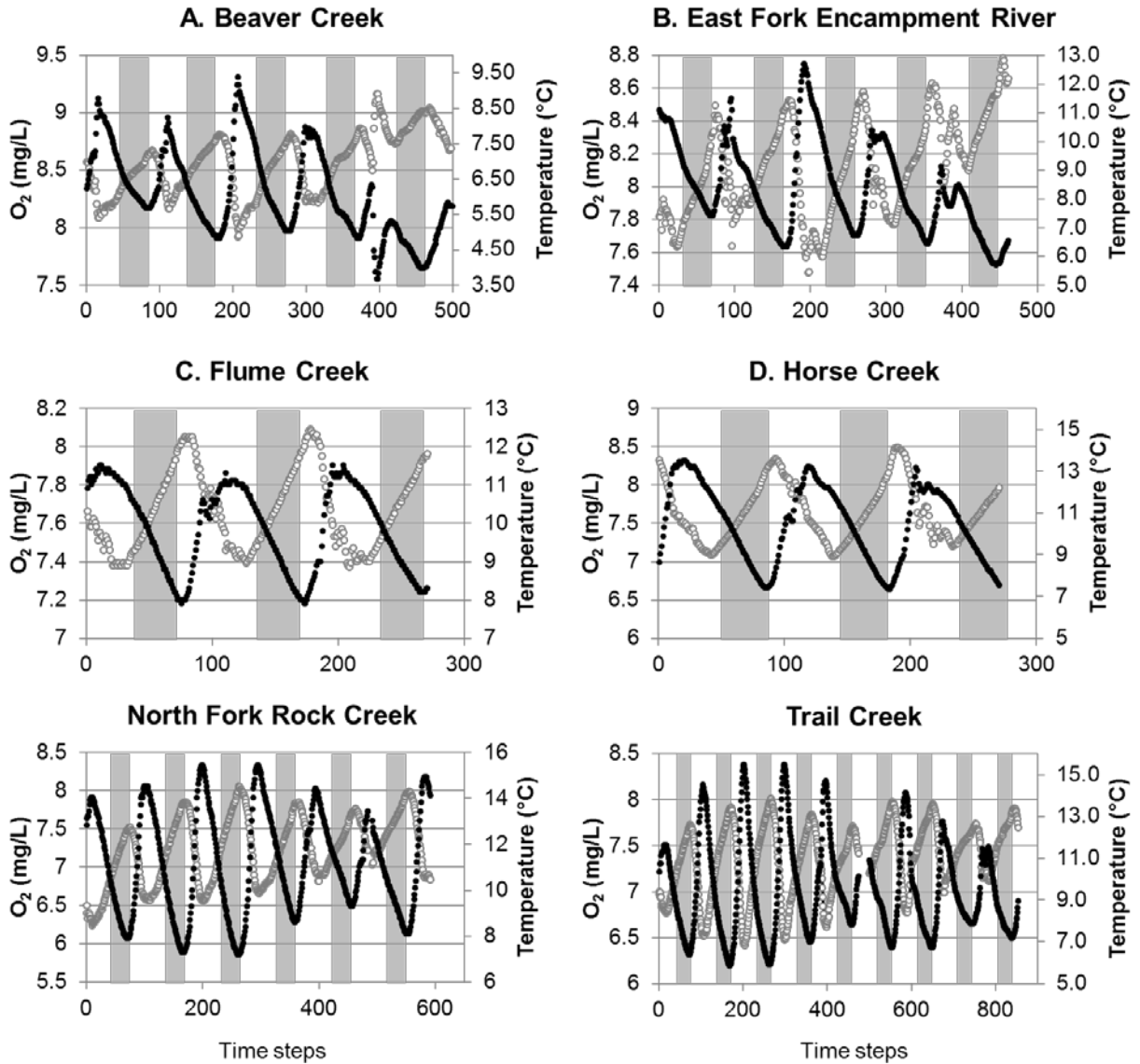


Figure 4.5 Average daily rates of (A) gross primary production (GPP), (B) ecosystem respiration (ER), and (C) net ecosystem production (NEP) between tie-driven and non-driven conditions

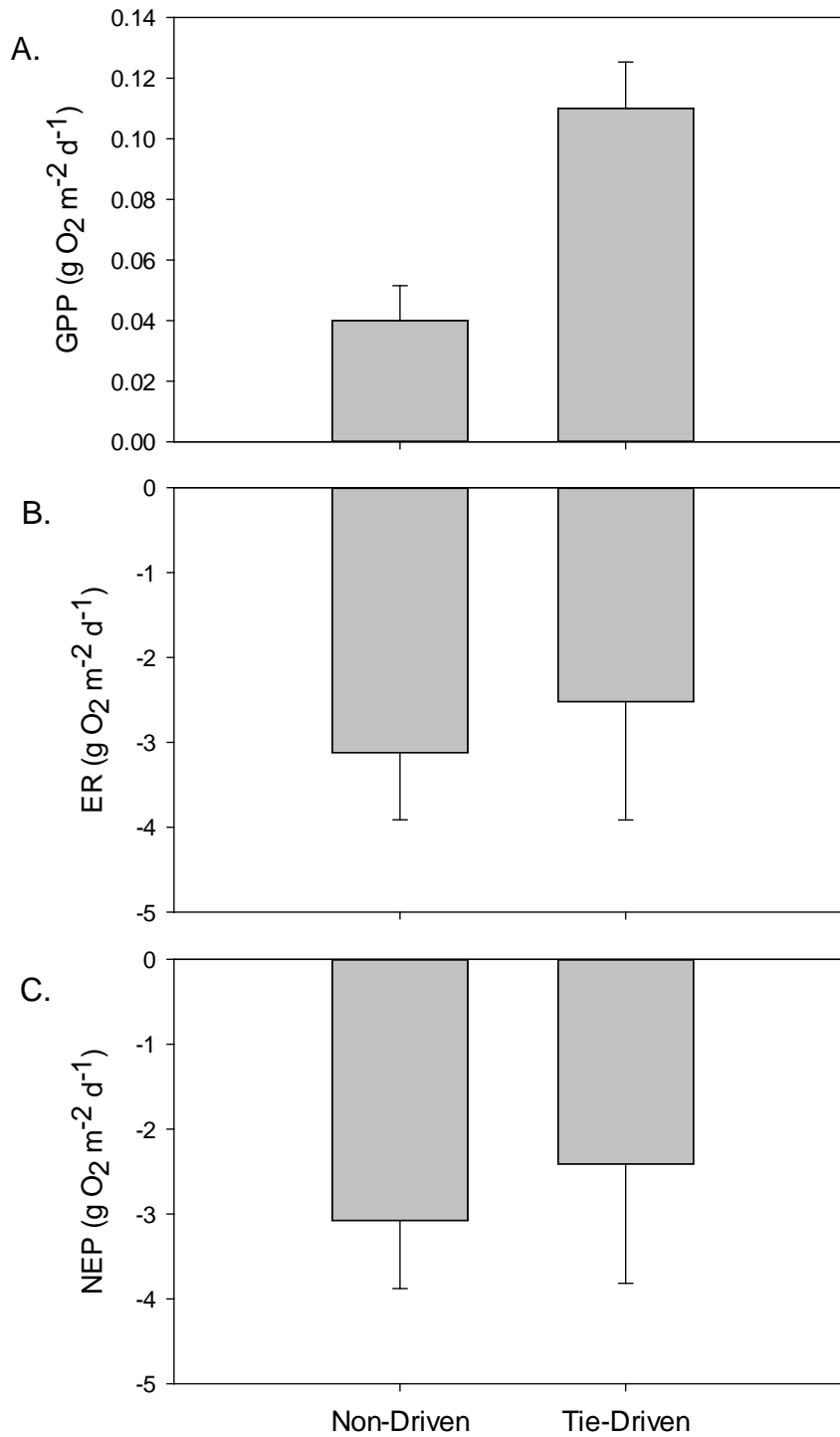


Figure 4.6 Linear relationships between daily rates of GPP ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and riparian canopy density (%). Triangles represent tie-driven reaches and circles represent non-driven reaches.

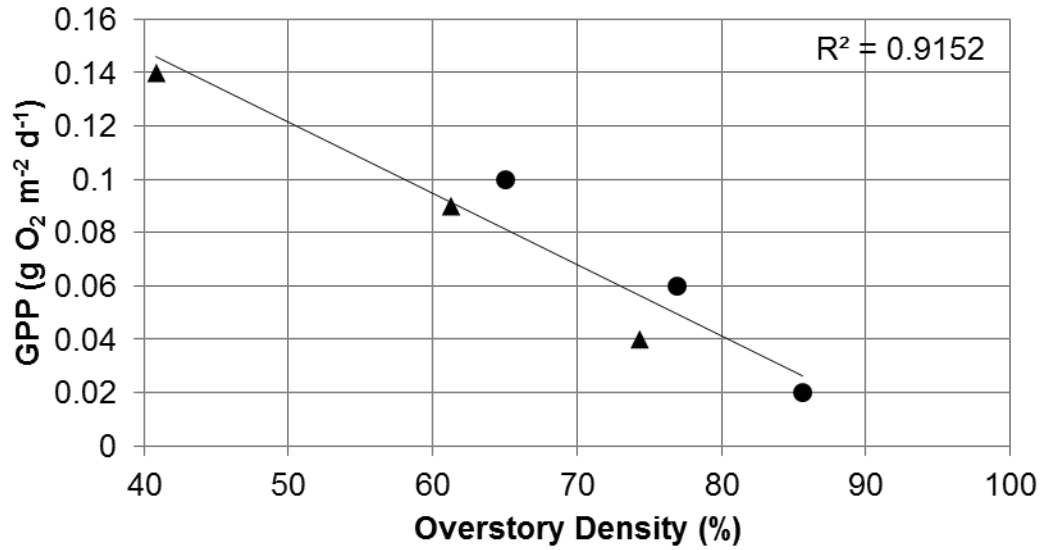


Figure 4.7 Linear relationships between (A) daily estimates of aeration ($k_{O_2} d^{-1}$) and total pieces of in-channel wood as well as (B) daily estimates of aeration ($k_{O_2} d^{-1}$) and total volume of wood within the bankfull channel. Triangles represent tie-driven reaches and circles represent non-driven reaches.

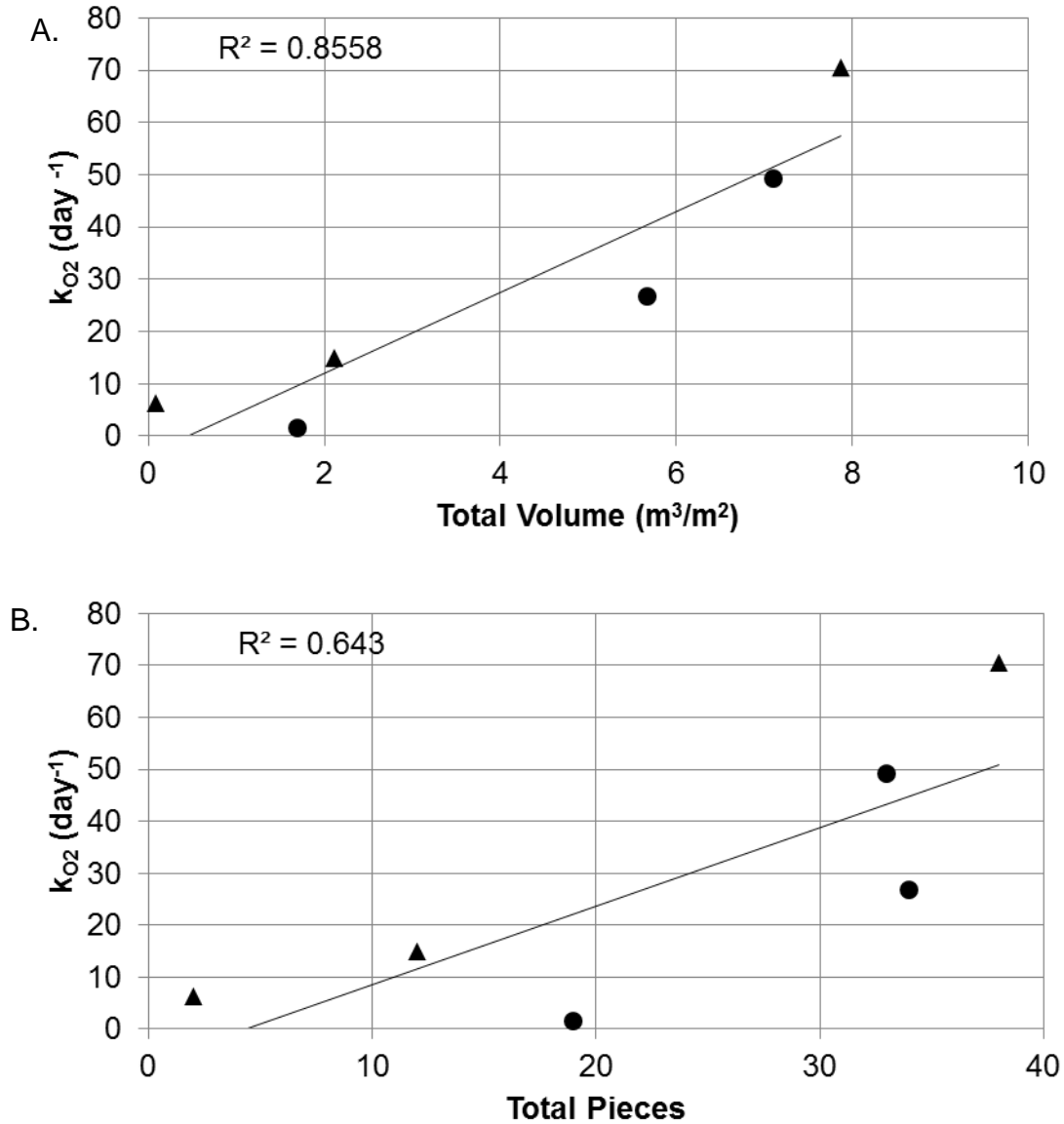


Figure 4.8 Linear relationships between (A) areal estimates of aeration ($k_{O_2} \text{ m}^{-2}$) and total pieces of in-channel wood as well as (B) areal estimates of aeration ($k_{O_2} \text{ m}^{-2}$) and total volume of wood within the bankfull channel. Triangles represent tie-driven reaches and circles represent non-driven reaches.

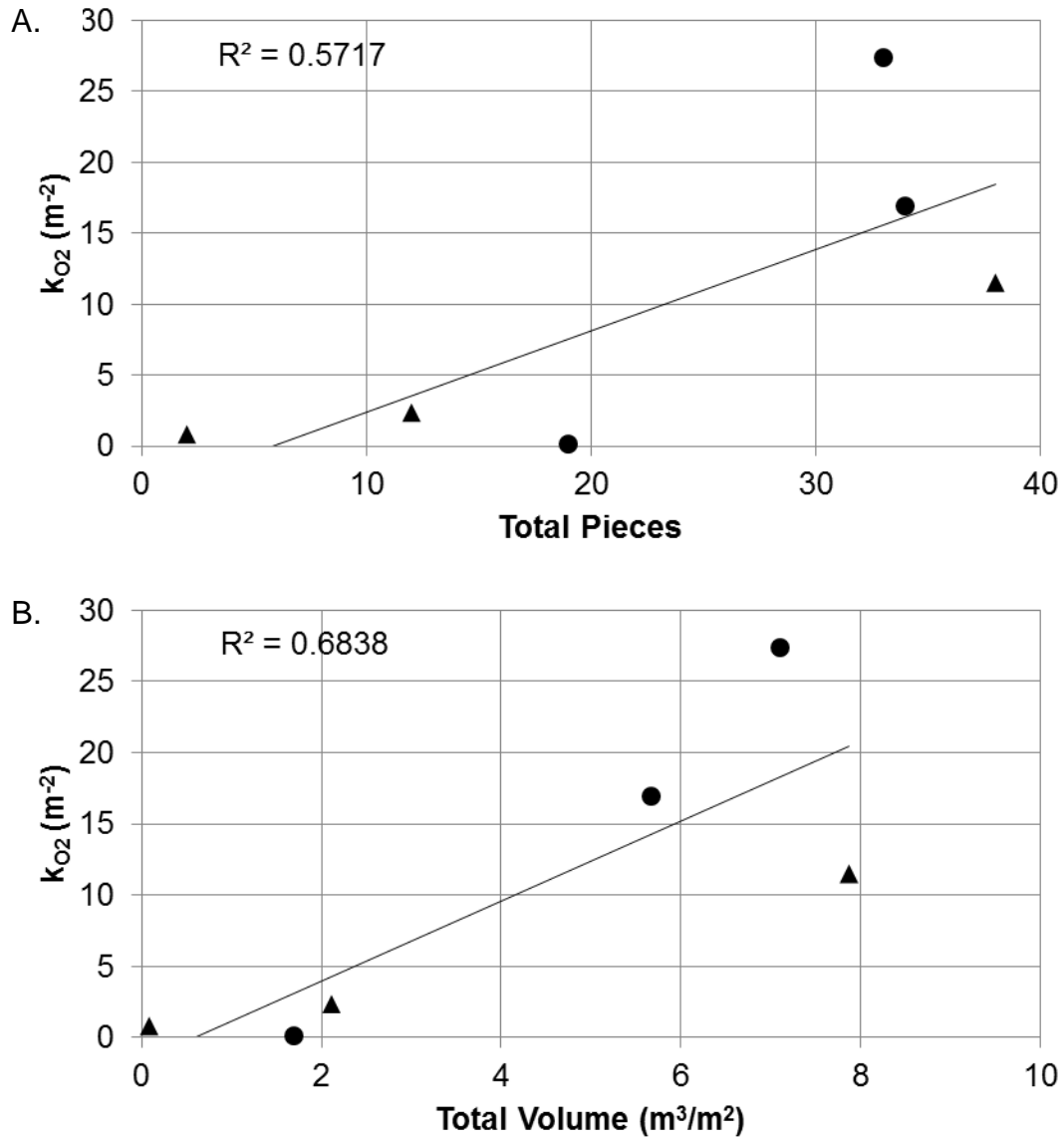


Table 4.1 Physical characteristics of sites.

Reach (Site Pair)	Drive	Length (m)	Mean Depth (m)	Wetted Width (m)	Slope (m/m)	Mean Velocity (m/min)	Q (m ³ /m)	Total Wood Pieces
Beaver Creek (A)	Non	91.4	0.33	2.57	0.06	9.14	7.77	38
East Fork Encampment River (A)	Tie	92.3	0.17	2.46	0.04	13.06	5.5	12
Flume Creek (B)	Non	88.5	0.34	1.55	0.02	4.66	2.45	19
Horse Creek (B)	Tie	90.25	0.26	2.08	0.02	6.64	3.07	2
North Fork Rock Creek (C)	Non	208	0.29	4.39	0.03	11.5	14.82	34
Trail Creek (C)	Tie	226	0.51	3.55	0.04	9.04	16.38	33

Table 4.2 Comparison of stream reach characteristics and mean daily values for aeration (k), gross primary production (GPP), and ecosystem respiration (ER) in mountain streams.

Source	Mountain Range	Stream	Q (L s ⁻¹)	Velocity (min ⁻¹)	Width (m)	Depth (m)	k _{O2} (d ⁻¹)	GPP (g O ₂ m ⁻² d ⁻¹)	ER (g O ₂ m ⁻² d ⁻¹)
Bott and Newbold 2013	Andes, Peru	Q. Tambopata	9.7	2.1	4.4	0.06	25.8	0.078	1.882
Hall and Tank 2003	Teton Range, Wyoming, USA	Ditch Creek	231	17	5.8	0.14	98	1.94	6.45
		Spread Creek	87	9.7	5.5	0.1	49.9	3.11	8.37
		Two Ocean Lake Outlet	144	16.7	4.1	0.13	44.1	1.63	8.77
		Pilgrim Creek Channel 1	46	12.1	4.1	0.06	66.6	0.24	0.97
		Pilgrim Creek Channel 2	12	6.8	2.5	0.04	108.1	0.13	1.59
		Lizard Creek	25	5.7	2.5	0.11	47.6	0.6	4.1
		Bailey Creek	118	12.7	5.4	0.1	69.7	1.04	2.02
		Glade Creek Tributary	149	19.7	3	0.15	126.3	1.08	13.3
		North Moran Bay Creek	9	4.6	0.8	0.14	135	0.35	5.76
		Moose-Wilson Road Creek	25	11.3	2.2	0.09	143.8	0.18	6.05
		Paintbrush Canyon Creek	4	3	1.3	0.06	58.7	0.31	1.87
		Bott et al. 1985	Cascade Mountains, Oregon, USA	Devils Club Creek	2	-	0.6	0.05	-

		Mack Creek	92	-	3.0	0.22	-	0.34	0.42
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Table 4.3 Description of control and response variables used in the regression analyses.

Response Variables		
	Variable	Description (units)
	GPP _{Daily}	Gross Primary Production (g O ₂ m ⁻² d ⁻¹)
	ER _{Daily}	Ecosystem Respiration (g O ₂ m ⁻² d ⁻¹)
	NEP _{Daily}	Net Ecosystem Production (g O ₂ m ⁻² d ⁻¹)
Control Variables		
Category	Variable (units)	Description
Site	Disturbance condition	Categorical (non-driven=1, tie-driven=2)
	Site pairs	Categorical (Pair A=1, B=2, C=3)
	Stream order	Categorical (first order=1, second order=2)
Geomorphic	Width to depth ratio	Continuous; Calculated from surveyed cross-sections
	Roughness	Continuous; standard deviation of bed elevation measurements obtained from surveyed cross-sections
	Area (m ²)	Continuous; Calculated for surveyed cross-sections
Wood	Total pieces	Number of pieces per study reach (#)
	Total volume	Total volume/channel area (m ³ /m ²)
Riparian	Canopy Density	Average canopy density taken from spherical densitometer readings (%)
	Basal area (m ² ha ⁻¹)	Continuous; calculated from riparian plot data and includes all trees sampled
	Basal area of dead trees (m ² ha ⁻¹)	Continuous; calculated from riparian plot data and includes only dead trees sampled
Organic Matter	Coarse particulate organic matter	Continuous; measured from organic matter sampling (g AFDM m ⁻²). This variable was only used in regressions testing ER _{Daily} and NEP _{Daily} .
	Fine particulate organic matter	Continuous; measured from organic matter sampling (g AFDM m ⁻²). This variable was only used in regressions testing ER _{Daily} and NEP _{Daily} .

Table 4.4 Modeled estimates for aeration (k), gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) in study reaches. Bold number represent averages for the entire period of data collections and are the values included in statistical analyses.

Reach (Site Pair)	Drive	Method	Length of record	k_{O_2} (m^{-2})	k_{O_2} (d^{-1})	ER (g $O_2 m^{-2}$ d^{-1})	GPP (g $O_2 m^{-2}$ d^{-1})	NEP (g $O_2 m^{-2}$ d^{-1})	P/R
Beaver Creek (A)	Non	2 station	8/4/2013 11:15 - 8/9/13 15:30	11.51	70.55	2.06	0.04	-2.01	0.02
East Fork Encampment River (A)	Tie	2 station	8/4/2013 14:30 - 8/9/13 9:45	2.36	14.96	2.63	0.09	-2.54	0.03
Flume Creek (B)	Non	2 station	7/30/2013 12:45 - 8/1/13 3:45	0.14	1.44	4.67	0.02	-4.65	0.00
Horse Creek (B)	Tie	2 station	day 1 - 7/30/13 11:15 - 7/31/13 11:15	0.82	6.3	0.05	0.09	0.04	1.74
		2 station	day 2 - 7/31/13 11:30 - 8/1/13 21:00	0.94	7.2	0.05	0.19	0.14	3.88
		Average		0.82	6.3	0.05	0.14	0.09	2.78
North Fork Rock Creek (C)	Non	1 Station - DS	DS 7/20/13 14:00 - 7/24/2013 24:00	16.93	26.70	3.24	0.09	-3.14	0.03
			DS 7/24/13 00:15 - 7/26/2013 24:00	16.43	25.92	2.35	0.05	-2.31	0.02
			DS 7/27/13 00:15 - 7/29/2013 13:45	16.93	26.70	2.29	0.04	-2.25	0.02
			Average	16.93	26.70	2.63	0.06	-2.57	0.02
Trail Creek (C)	Tie	2 station	7/20/2014 1:00:00 PM - 7/22 24:00	20.06	36	4.53	0.05	-4.48	0.01
		2 station	7/22/2014 12:00:00 AM - 7/25 11:30	30.49	54.72	5.44	0.14	-5.30	0.03
		2 station	7/25/2014 6:00:00 PM 7/29 10:30	32.09	57.6	4.66	0.11	-4.55	0.02
		Average		27.39	49.17	4.88	0.10	-4.78	0.02

Table 4.5 Linear regression models testing control variables and gross primary productivity (GPP), ecosystem respiration (ER), and net ecosystem productivity (NEP).

GPP			
	Control Variables in Model	<i>p</i> Value	Adj. R ²
Site	Drive	0.02	0.71
Geomorphic	no significant variables	n/a	n/a
Wood	TotPiece + TotVol	0.12	0.59
Riparian	no significant variables	n/a	n/a
ER			
	Control Variables in Model	<i>p</i> Value	Adj. R ²
Site	no significant variables	n/a	n/a
Geomorphic	no significant variables	n/a	n/a
Wood	no significant variables	n/a	n/a
Riparian	no significant variables	n/a	n/a
Organic Matter	no significant variables	n/a	n/a
NEP			
	Control Variables in Model	<i>p</i> Value	Adj. R ²
Site	no significant variables	n/a	n/a
Geomorphic	no significant variables	n/a	n/a
Wood	no significant variables	n/a	n/a
Riparian	no significant variables	n/a	n/a
Organic Matter	no significant variables	n/a	n/a

Table 4.6 Assessment of ecosystem function using the framework outlined by Young et al. 2008. The subscript t represents the test site (tie-driven streams) and r represents the reference site (non-driven streams).

Method	Stream	GPP		ER	
Reference (GPP _t /GPP _r) (ER _t /ER _r)	East Fork Encampment River	2.25	no evidence of impact	1.28	no evidence of impact
	Horse Creek	7.0	severely impaired	0.01	severely impaired
	Trail Creek	1.67	no evidence of impact	1.86	mild effect on ecosystem function
Actual Value GPP _t (g O ₂ m ⁻² d ⁻¹) ER _t (g O ₂ m ⁻² d ⁻¹)	East Fork Encampment River	0.09	no evidence of impact	2.63	no evidence of impact
	Horse Creek	0.14	no evidence of impact	0.05	severely impaired
	Trail Creek	0.10	no evidence of impact	4.88	no evidence of impact

Chapter 5 - Conclusions

This dissertation sought to integrate feedbacks between the geomorphic structure and processes of headwater stream environments with corresponding responses in ecosystem function within the context of a legacy disturbance regime. Tie-driving was an extensive timber floating activity that took place from 1860-1940 along stream channels in the Rocky Mountain region of the United States. The legacy of tie-driving is still present in area streams today, most notably in terms of altered stream conditions associated with the widespread removal of large instream wood. While a comprehensive understanding of the feedbacks between altered channel structure and ecosystem function is a vast undertaking, the three empirical studies presented here begin to capture geomorphic and riparian discontinuities related to tie-driving and integrate associated alterations with contemporary carbon storage and ecosystem metabolism. This research is a novel approach to bridging the disciplines of geomorphology and freshwater ecology through the use of disturbance legacies as a lens through which to study functional connections between the abiotic and biotic components of the stream environment. Additionally, this work is unique because it integrates biogeochemical contexts at a variety of scales within a geomorphic framework.

Chapter 2, *Disturbance legacies of historic tie-drives persistently alter geomorphology and large wood characteristics in headwater streams, southeast Wyoming*, addresses the geomorphic response and wood loading characteristics following tie-driving. The historic removal of in-stream wood loads has created lasting impacts that dictate geomorphic complexity in a variety of ways. Tie-driven reaches are wider, shallower, with higher width-to-depth ratios and lower roughness values compared to non-driven reaches. Tie-driven reaches also had lower wood loads. Of the wood that was present in tie-driven channels, the majority was arranged as ramps and no pieces were incorporated in the channel. This suggests that wood in tie-driven streams has been added to the channel relatively recently compared to non-driven streams. Riparian basal area, stream power, and reach slope were identified as primary mechanisms explaining wood recruitment and retention in study streams.

Chapter 3, *Carbon pools in stream-riparian corridors: legacy of disturbance along mountain streams of southeastern Wyoming*, investigates the impacts of tie-driving on carbon storage. Stream ecosystems are linked to the global carbon cycle through processes related to

storage, transport, and their importance in dictating biogeochemical conditions of stream ecosystems. Non-driven reaches had greater carbon storage compared to tie-driven reaches. Standing trees and coarse downed wood on the floodplain and in the channel were the largest components of carbon storage across sites. The legacies of tie-driving were evident in terms of the amount of carbon stored in large wood within the channel, coarse downed wood and fine downed wood on the floodplain. Carbon reflecting ecosystem components in the stream and riparian area were quantified in order to determine how tie-driving has influenced overall carbon storage. The results of this work indicate that contemporary channel storage capacity and riparian composition reflect disturbance legacies and result in differing carbon storage capacities.

Chapter 4, *Influence of stream channel disturbance legacies on ecosystem metabolism in headwater streams, southeast Wyoming*, demonstrates that metabolic characteristics and abiotic factors are sensitive to disturbance and can result in altered metabolic characteristics. While rates of net ecosystem productivity (NEP) and ecosystem respiration (ER) were not significantly different between disturbance conditions, gross primary productivity (GPP) was significantly greater in tie-driven reaches. Additionally, aeration rates (k) were more strongly correlated to wood loads at the temporal scale but not at spatial scales, suggesting in-stream wood is an important driver of gas exchange.

The research presented here addresses significant gaps in our current understanding of interactions between abiotic stream processes and associated impacts on biogeochemical properties of these systems. Disturbances, which are fundamental determinants of ecosystem structure, can leave lasting imprints not only on the form of stream ecosystems but on functional characteristics as well. First, altered geomorphic conditions persist long after the initial tie-driving activity and are evident at a variety of scales. Characteristics such as channel geometry, stream planform, and wood loading represent discrete components of ecosystem structure that are influenced by tie-driving and encompass different spatial and temporal scales that make them relevant to differing ecosystem processes (Fig. 5.1A). Additionally, alterations to the channel and riparian area related to tie-driving fundamentally alter carbon storage in a range of ecosystem components including tree biomass, downed wood on the floodplain, and large wood in the stream channel. Individual carbon storage compartments span wide spatial and temporal scales suggesting that recovery time will be unique for individual components (Fig. 5.1B). Third, changes to the physical stream template related to tie-driving have cascading impacts on

select components of instream metabolism. Alterations to riparian vegetation related to tie-driving correspond to increased rates of GPP although none of the abiotic drivers captured in this research explained variations in ER (Fig. 5.1C). This further supports the notion that abiotic drivers recover at different rates and spatial scales, which in turn adds complexity to the understanding of disturbance and system recovery.

The role of temporal and spatial scale as well as complexity is an inherent theme in previously published frameworks articulating the role of disturbance in shaping ecosystems. However, the nature of system recovery is often secondary to the initial impacts of the disturbance in such frameworks, likely due to constraints associated with studying the impacts of disturbance over extended periods of time. This leads to assumptions regarding presumed states of equilibrium that serve as target conditions symbolizing recovery (Fig.5.2A). This research suggests that recovery times are not necessarily equal across ecosystem components and that in some cases, ecosystem processes can recover before the physical structure of the ecosystem (Fig. 5.2B). Ecosystem metabolism, a relatively short-term biogeochemical process, no longer shows strong signs of the tie-driving legacy and thus would be considered close to recovery. Alternatively, carbon storage, a relatively long-term biogeochemical process, is still characterized by alterations related to tie-driving. Similarly, channel morphology and wood recruitment also reflect impacts associated with this legacy. Since carbon storage in this ecosystem is largely dictated by vegetation regrowth and mortality and stream channel recovery encompasses the combined domains of vegetation (i.e. wood loading) and geology (i.e. valley bottom characteristics), it follows that carbon storage would be expected to return to baseline conditions more quickly than changes to the channel, barring other disturbances. This effectively represents an uncoupling of the physical template of the ecosystem with biogeochemical processes in the recovery period following the initial disturbance. A refined view of recovery following disturbances has tremendous implications for the modern perspective guiding water resource management as well as the current understanding of freshwater ecosystems. Differentiating between temporal and spatial scales of recovery relevant to abiotic drivers and associated biogeochemical processing remains a significant challenge, relevant management concern, and fruitful future research direction.

References

Lake, P.S. 2000 Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19(4):573-592.

Figure 5.1 Conceptual diagram of spatiotemporal scale associated with tie-driving and its effects on (A) channel geomorphology, (B) carbon storage, and (C) ecosystem metabolism. The circles indicate ecosystem characteristics that have not yet recovered to a predisturbance state. The white box indicates scales that fall under the scope of this dissertation.

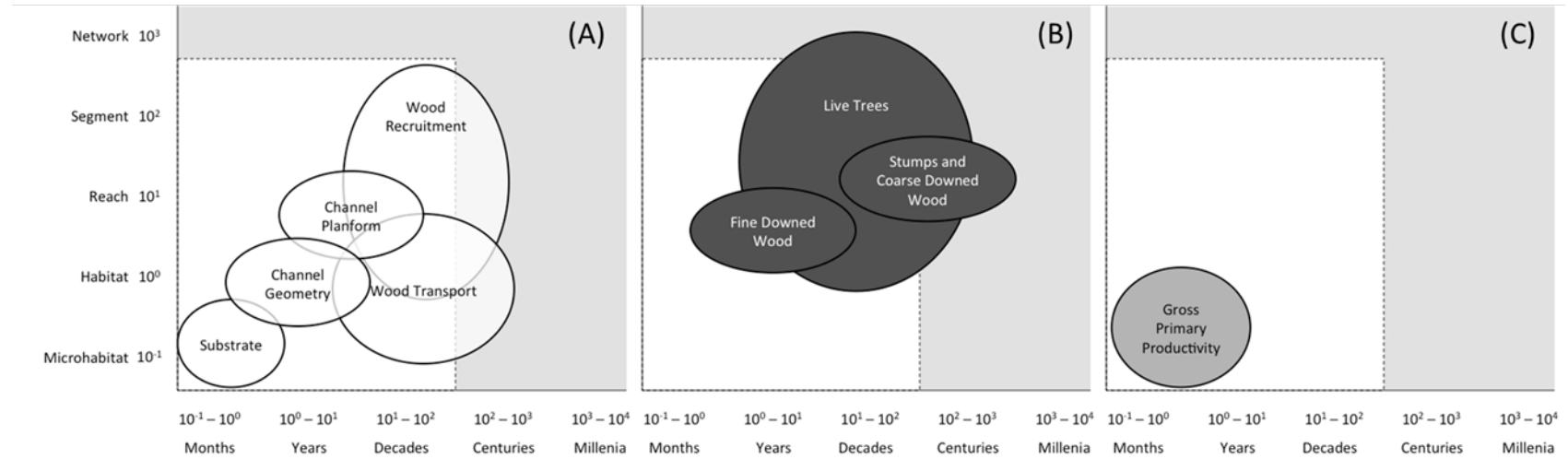


Figure 5.2 Conceptual diagram of a press disturbance and response adapted from Lake 2000. The black horizontal bar indicates the disturbance and the grey horizontal line indicates predisturbance conditions. Previously published frameworks (A) imply that responses to disturbance are coupled. The results of this dissertation suggest that recovery of ecosystem components becomes uncoupled and response trajectories are characterized by a lag in recovery (B).

