Bark beetles and wildfire: Influence of overlapping disturbances on wood and light in a sub-boreal headwater system

by

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Abstract

Forest disturbances provide an important link between terrestrial and freshwater ecosystems. In this study I ask 1) how the recruitment of wood to streams varies depending on whether trees were dead or alive prior to a wildfire; and 2) what is the quantitative contribution of fallen wood spanning small streams to stream light. I found that wood recruitment is affected by overlapping, short-interval disturbances of insect outbreak followed by wildfire since being killed prior to fire makes a tree twice as likely to topple immediately post-fire. Additionally, the toppled wood lying above-stream provided a detectable buffer to incoming light in a post-fire landscape. The effects of disturbance history on stream communities and microclimate via wood warrants further study to improve our understanding of how landscape scale terrestrial processes are drivers of localized and watershed-scale changes to aquatic primary productivity and thermal variability.

Keywords: Large wood; disturbance history; fire; PAR; bark beetles; stream light

To my dad;

You loved the forest and spoke German; I know that much. I promise your affinity for outside lives on. I will carry my early memories of our morel hunts together forever. Still have to work on the German though.

To my wife and son;

This is for you and to all our adventures together.

Acknowledgements

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Chapter 1.

General introduction

Wood is an important biological pathway between land and water. Streamflow is altered by the presence of wood, creating ponds along channel margins, and deep pools, and riffles above and below submerged wood (Gurnell et al. 1995; Davidson 2015). Gravel deposited from altered streamflow is in turn used as spawning habitat by fish (Nelson et al. 2015; Swanson 2003). The surface of submerged wood accumulates macronutrients, particularly nitrogen, a limiting element in most freshwater environments and integral to primary production (Nelson et al. 2015; Lazar et al. 2014). Many fish species rely on the complexity of roots and branches provided by wood as refugia throughout all life stages (Nagayama & Nakamura 2010). Submerged wood itself serves as a stable substrate and is colonized by periphyton, a complex matrix of algae, fungi, and bacteria (Eminson & Moss 1980). Specialized invertebrate scrapers and grazers feed on periphyton (Gurnell et al. 1995) and the nymphs of these insects are in turn consumed by drift-feeding fish species (Johnson et al. 2005; Angermeier & Karr 1984; Gurnell et al. 1995). Systems devoid of submerged wood, or subjected to wood removal, have reduced biomass of freshwater fishes and altered macroinvertebrate assemblages (Fausch & Northcote 1992; Enefalk & Bergman 2016; Roni & Quinn 2001) as a result. The influence of wood is particularly high in headwaters as these smaller streams contribute the runoff, nutrients, and sediment to larger downstream reaches (Vannote et al. 1980). Therefore, understanding the factors influencing the delivery of wood to streams and how wood affects stream ecology in these areas is essential to managing overall watershed health (Fausch et al. 2002; Giannico & Hinch 2003).

Terrestrial disturbance events deliver pulses of wood to streams from the mass death and inevitable topple of riparian trees. Wildfires damage phloem tissues and roots and consume tree canopies, eliminating the capacity for photosynthesis or uptake and transport nutrients and water (Kauffman & Martin 1989), and while episodic population eruptions of tree-killing bark beetles and their fungal associates constrict nutrient uptake (Raffa et al. 2008). Wildfire and insect outbreaks are both part of the historical disturbance regime in the coniferous forests of western North America (Agee 1993;

Raffa et al. 2008), the role of fire as a substantial supplier of wood to streams draining these areas has been more thoroughly supported through field studies (Benda & Sias 2003; Jones & Daniels 2008; Zelt & Wohl 2004) than in comparison to beetle attack (Hassan et al. 2008; Jackson & Wohl 2015; King et al. 2013; Rinella et al. 2009). This is despite some watersheds reaching 100% mortality from outbreaks of bark beetles (Raffa et al. 2008; Dhar et al. 2016; Jackson & Wohl 2015). Regardless of whether killed by fires or beetles, fungal communities colonize the dead trees and, in the case of the conifers of western North America, the trees tend to fall roughly a decade after death (Martinez et al. 2011; Cluck & Smith. 2007; Mielke 1950; Lewis & Thompson 2009) from the structural weakening caused by fungal rot. In upland forests, toppling of dead trees occurs sooner when fires burn through the area (Bagne et al. 2008; Horton & Mannan 1988) as the fires consume the dead tree's rotted bases, thereby altering the amount of post-fire toppling when multiple disturbances occur in close (< 10 year) succession. Any trees falling into narrow headwater corridors will remain suspended above, or bridging, the stream surface for decades before breaking up and entering the water (Bahuguna et al. 2010; Robinson et al. 2005).

Disturbance events also shape aquatic ecological communities by regulating the amount of stream shade. The level of solar radiation reaching streams is the chief predictor of primary production (Kilroy et al. 2013; Kelly et al. 2003; Wagner et al. 2015; Denicola et al. 1992) and temperature (Brown 1969; Moore et al. 2005). The influence of sunlight is especially pronounced in the shallow headwaters in the coniferous forests of western North America; waters crucial for anadromous fish like salmonids (Isaak et al. 2010; Beakes et al. 2014; Warren et al. 2016). By defoliating riparian corridors, disturbance events remove the sources of stream shade and substantially increase the level of solar radiation reaching the stream, thereby driving stream periphyton communities and water temperature profiles (Bladon et al. 2016; Beakes et al. 2014; Klose et al. 2015). Stream solar loading is highest in the immediate (< 5 year) post-disturbance event period (Klose et al. 2015), before the canopy and understorey vegetation fully shade the stream over. Therefore, sources of shade, including any wood resting just above the stream surface, during the immediate post-disturbance period are understood as thermal buffers for elevated stream temperatures (Dunham et al. 2007; Jackson et al. 2001), but also have the potential to influence stream periphyton communities given the link between shade and photosynthesis.

Given the demonstrated importance of wood in aquatic ecosystems, key knowledge gaps remain concerning its path from land and function immediately afterwards. The link between eruptions in bark beetle populations and stream ecology remains unclear (Rhoades et al. 2013), but could manifest when fire burns through these landscapes affected by beetle outbreak if: 1) bark beetle outbreaks enhance the abundance of wood transferred to streams in the immediate (<5 year) post-fire period and 2) a quantitative relationship exists between those wood pieces and the light environment of the stream, associated with photosynthesis.

In this thesis I characterized the population of wood within headwater streams and the surrounding forests two years after fire in a landscape that has experienced widespread bark beetle outbreak in the decades prior. My research explores the effects of disturbance history on stream ecosystems by addressing two questions: 1) does the overlap of beetle outbreak and wildfire alter the amount and temporal transfer of wood into streams (**Chapter 2)**? And what is the extent to which the transferred wood affects stream light post-fire (**Chapter 3)**? I investigated these questions by collecting field data from recently disturbed headwaters in the sub-boreal, mixed conifer forests of central interior British Columbia, Canada.

Chapter 2.

Bark beetles enhance the amount of wood supplied by fire to streams.

2.1. Introduction

Riparian forest disturbance processes are central to the recruitment of wood into inland waters. Stand-replacing forest disturbances kill most if not all existing trees in an area, leaving an abundance of deadwood, standing snags and fallen coarse wood, in their wake (Oliver & Larson 1996). In western North American forests, stand-replacing fires in riparian areas (Agee 1993; Pettit & Naiman 2007) provide a major source of wood to adjacent streams (Jones & Daniels 2008; Zelt & Wohl 2004). Episodic population explosions of tree-killing, bark beetles are also part of the historical disturbance regime of many conifer forests in western North America. Entire stands can be killed as beetles and their fungal associates overwhelm tree defenses and constrict nutrient uptake (Raffa et al. 2008). The extent of deadwood left in the wake of bark beetles has been of interest to those investigating subsequent fire behavior, nutrient cycling, and forest successional processes (Hansen et al. 2015; Mikkelson et al. 2013). In the context of stream ecology, eruptions in bark beetle populations and subsequent wildfires occurring within a short interval of time in such fire-prone landscapes could influence the rate of wood recruitment to streams by affecting timing of tree fall. Understanding recruitment of wood in headwater areas is essential to managing overall watershed health (Fausch et al. 2002) as these smaller streams contribute the runoff, nutrients, and sediment to larger downstream reaches (Vannote et al. 1980).

All standing snags ultimately fall, snapping either along the stem or at the roots, often from fungal decay or exposure to strong winds. Fungal decay in snags is deepest near soil as this area retains a higher level of moisture (Cluck & Smith. 2007; Gara et al. 1985). Decayed wood is preferentially consumed by fire as the temperature at which rotten wood ignites is lower and its physical structure is more conducive to air circulation and combustion (Cornwell et al. 2009; Susott 1982; Donato et al. 2016). Stem breakage results if fires consume the base of dead trees, years after the onset of fungal decay (Bagne et al. 2008; Horton & Mannan 1988). A falling riparian snag is destined as either

terrestrial coarse wood (Figure 2.1A) or aquatic streamwood (Figure 2.1B). Streamwood can land either in the water (in-stream) or, as is common in narrow headwaters, rest above the water in a bridge position (bridgewood).
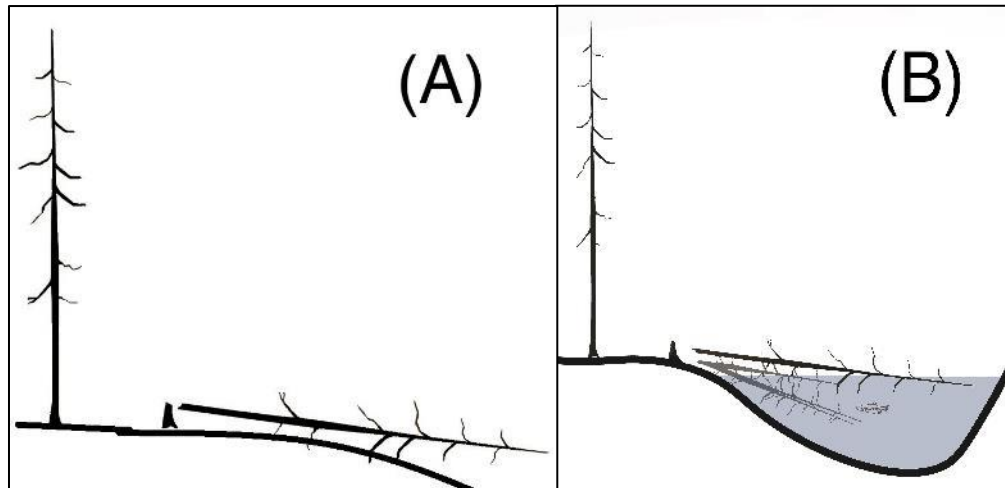
Figure 2.1   The toppling of snags recruits downed wood that can (A) fall to the forest floor as coarse wood, or (B) fall to the aquatic environment as streamwood which can be located in the water (in-stream) or bridging above the water (bridgewood).

A potential for an increased recruitment rate of streamwood via bark beetle epidemics in riparian forests has been recognized in the past. However, field data has yet to support whether, and how, insect outbreaks can influence the transfer of wood from forests to inland waters. In previous investigations, beetle-killed trees were almost completely absent from the riparian forests studied (Hassan et al. 2008; Jackson & Wohl 2015) or data were collected immediately following outbreak before the beetle-killed trees actually began to fall (King et al. 2013; Hassan et al. 2008).

Wildfire contributes important heterogeneity to the forest disturbance mosaic, and there has been growing interest in the implications of fire burning through forests containing abundant snags, either from insect kill or previous fires. Fire-killed conifer snags typically remain standing for roughly a decade in western North America (Martinez et al. 2011; Cluck & Smith. 2007) which translates to high inputs of streamwood after this period (Zelt & Wohl 2004). However if fire burns through forests that contain large volumes of existing snags, i.e., from recent insect outbreak, the amount of post-fire toppling can be altered by these multiple disturbances in close succession. In dry mixed conifer forests, recent results suggest that greater recruitment of terrestrial coarse wood

occurred in areas where wildfire burned forests killed by severe beetle outbreaks 3–8 years prior, in comparison to fires burning through unaffected forests e.g., alive at time of fire (Stevens-Rumann et al. 2015). Higher coarse wood recruitment arose in stands affected by two fires occurring six years apart in comparison to one fire occurrence (Bagne et al. 2008). Ultimately, tree fall, or toppling, of snags has been shown to be triggered by structural weakening from fire preferentially consuming a decayed portion of the tree's stem, yielding a rapid increase in ground-level coarse wood on the landscape and drastic reductions in snag populations within mixed conifer forests (Bagne et al. 2008; Horton & Mannan 1988).

The sub-boreal forests of the central interior of British Columbia (BC) provide a key opportunity to explore the effects of overlapping beetle outbreak and wildfire on streamwood recruitment. The amount of wood available for recruitment into a stream is proportionate to the scale of tree mortality in the surrounding forest (Wohl 2015). In BC alone an estimated 18 million ha of lodgepole pine (*Pinus contorta* var. *latifolia)* and 156,000 ha of interior spruce (*Picea glauca x englemannii*) forests have been impacted by the mountain pine beetle (MPB, *Dendroctonus ponderosae*) and the spruce beetle (SB, *D. rufipennis*) over the past 20 years (MFLNRORD, 2012). This area is so extensive that most recent wildfires in the region are burning through beetle-impacted forests, as will future wildfires (Edwards et al. 2015). My field study aimed to i) characterize the population of wood within headwater streams that are surrounded by riparian forests affected by beetle kill followed by wildfire, and ii) assess whether being dead at the time of fire increases a tree's probability of toppling and being recruited into these streams. Based on our knowledge of rot-combustion properties, I expected that after fire, insect killed (pre-fire killed) snags would be more likely to immediately topple and be recruited to adjacent streams on a post-fire landscape than would those trees that were alive at the time of fire.

2.2. Methods

2.2.1. Study area

The study was conducted in three headwater streams within the low elevation sub-boreal forests of Entiako Provincial Park and Protected Area. This remote wilderness is located in the upper Nechako River basin, in central Interior BC, Canada

(Figure 2.2). The region lies in the rain shadow of the Coast Mountains and experiences a dry, continental climate, with generally cool, short and dry summers, and long, cold and dry winters. Mean annual precipitation ranges from 441 mm to 464 mm across the study area (Banner et al. 1993). The plateau landscape that characterizes the park and protected area ranges between 850 and 1300 meters (Cichowski et al. 2001). The streams sampled are within the dry cool subzone of the Sub-Boreal Spruce (SBSdk) and the moist cold subzone of the Sub-Boreal Pine-Spruce (SBPSmc) biogeoclimatic zones (Pojar et al. 1987); Figure 2.2). Mature lodgepole pine forests dominate the landscape within the Park, ranging from 83% of forest cover in the SBPSmc to 88% in the SBSdk (Cichowski et al. 2001). Spruce stands (3-7% total forest cover) dominate along riparian corridors, although lodgepole pine is frequently present.

The sampled streams flow directly into Tetachuck and Entiako Lakes, which support populations of salmonids. The lakes are part of a system feeding the Nechako Reservoir that was created in the early 1950's from the construction of the Kenney Dam on the Nechako River. Prior to impoundment, these lakes sustained a large run of sockeye salmon (*Oncorhynchus nerka*) because they lead eventually to the Fraser River. Currently, a population of kokanee (landlocked sockeye) exists in the system. Streams feeding the lake system once contained anadromous rainbow trout (*Oncorhynchus mykiss)*, but now only support river-resident populations. Mountain whitefish (*Prosopium williamsoni*) and rainbow trout use these streams for spawning (British Columbia Ministry of Environment 2006). Both species were observed during this study.
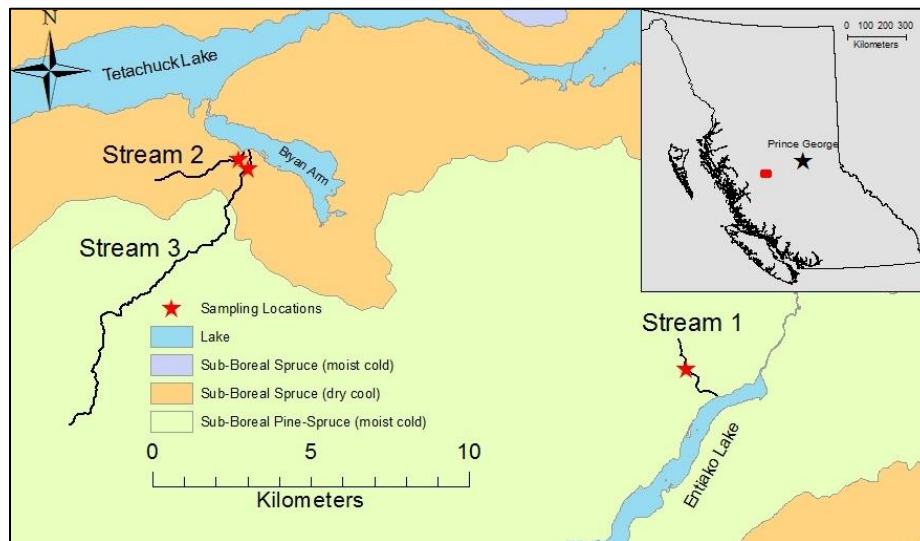
Figure 2.2   Map of the study sites within Entiako Provincial Park and Protected Area in central interior British Columbia, Canada. The red box on map inset represents the study area. The locations of streamwood and riparian forest measurements are denoted with red stars.

Multiple landscape-scale disturbance events have recently occurred across the study landscape. The area was the epicenter of a regional outbreak of MPB, resulting in widespread tree mortality that peaked in 2003/2004 (British Columbia Ministry of Environment 2006). The MPB outbreak has subsided in the region, but SB-caused mortality, within the spruce stands of northern BC, are on the rise, mostly in the Prince George Natural Resource District (BC Ministry of Forests Lands Natural Resource Operations and Rural Development n.d.). Although SB infestation remains small-scale in the study area due to the patchiness of spruce across the landscape, it is localized along riparian corridors. Together, these two bark beetles have resulted in high levels of tree mortality across the study landscape over the last decade. On average, large stand-replacing fires occur every 100-175 years within the area (Wong et al. 2003). From July to October 2014, 133,100 ha of forest within Entiako Provincial Park and Protected Area burned during the lightning-caused Chelaslie River fire. Minimal to no fire suppression ensued as the park is managed as wilderness. Although stand replacing fire effects dominate the landscape, a mosaic of fire severity resulted from the fire burning through forests composed of live and dead trees; a result of the recent bark beetle outbreaks, and other mortality factors.

8

Site selection

Sample locations were chosen using digital and field-based approaches. Potential study sample sites were selected using a Geographic Information System (ArcGIS 10.0; Environmental Systems Research Inst., Redlands, Ca, USA) and existing geospatial layers. Selection was finalized in the field based on accessibility and riparian forest presence.

Criteria for geospatial selection were conifer-dominated riparian areas along second-order streams that burned at high severity, i.e. as stand replacing fire. I deliberately focused on these particular stream channels for several reasons. First, the coniferous forests supplying them with wood would have been subjected to multiple disturbance events (insect outbreak and wildfire). A 400 m resolution model of bark beetle outbreak progression (Walton 2013) provided stand-level estimates of MPB-caused tree mortality. These data layers allowed me to select stands estimated as experiencing ≥50% cumulative mortality by MPB at the mapping resolution. Next, second-order streams within the Park provide crucial spawning habitat for local rainbow trout and mountain whitefish (British Columbia Ministry of Environment 2006) and this potential for fish habitat helped place my study into a biologically relevant context. Finally, stretches of riparian forests burned at high severity are much more likely to recruit trees to their respective streams overall (Zelt & Wohl 2004). Classification of fire severity based on the difference in normalized burn ratio (dNBR) allowed us to locate these stretches. The dNBR measures ecological change after a fire at 30 m resolution based on the loss of green vegetation and subsequent regeneration using remotely sensed Landsat images from before and after fire (Key & Benson 2006). Site selection was restricted to areas that experienced moderate/high to high severity (dNBR >440, Key and Benson, 2006). The pool of potential sample locations was further narrowed through analysis of recent orthographic photographs taken of the Park (BC MFLNRORD 2012) and only sites within a day's hike from two remote base camps were considered.

Figure 2.3   **Photos showing study streams with accumulations of in-stream and bridgewood. From left to right; Van Tine Creek (Stream 1), unnamed tributary of Tetachuck Lake (Stream 2), second unnamed tributary of Tetachuck Lake (Stream 3).**

Site selection was finalized using field reconnaissance to target stream reaches that were formerly forested. The final selection of streams was composed of approximately 370 m of Van Tine Creek (Stream 1) that drains into Entiako Lake, and 170 m (Stream 2), and 350 m of (Stream 3), both unnamed tributaries, on the south side of Tetachuk Lake, draining into Bryan Arm (Figure 2.3). Seventeen, 10-30 m study reaches were collected in total, seven in Stream 1, five in Stream 2, and five in Stream 3. Length of study reaches was 10× average bankfull channel width, resulting in 10 m reaches for Stream 1 and 2, and 30 m at Stream 3. I selected the location for reaches based on the presence of riparian trees on both stream banks; many stretches of stream lacked streamside forest. Understorey vegetation at the time of sampling was dominated by balsam willow (*Salix pyrifolia*) and fireweed (*Epilobium angustifolium*). These same stream plots were concurrently used to collect data for stream solar exposure measurements (Chapter 3). Reach spacing along sampled streams was based on the extent of forest cover on both stream banks, resulting in 50 m spacing for Stream 1 and 3, and 30 m for Stream 2. Sampling occurred during summer low-flow conditions in July-August 2016, two years post-fire and roughly 10 years post-MPB outbreak.

2.2.2. Field Measurements

To address my research objectives I quantified the relationship between disturbance history and streamwood recruitment at two spatial scales: the scale of

individual trees and the population (Figure 2.4). At the individual scale, I estimated the probability of stream recruitment for trees from the riparian zone as a function of several characteristics, including time of death (pre-fire vs. post-fire), in order to assess whether being dead at the time of fire increases a tree's probability of a) toppling and b) toppling in a direction that resulted in being recruited into these streams (Figure 2.4A). At a population scale, I measured the total amount of streamwood within each reach using streamwood surveys (Figure 2.4B). As reaches were nested within streams, the population then became the amount of wood sampled along each stream. Stream-wise recruitment could then be summarized according to time and cause of death. This characterized the populations of wood in headwater streams surrounded by riparian forests affected by multiple disturbances. The population of wood which transitioned from a snag to streamwood was ultimately the focus of this study, thus volumes of wood recruited were not emphasized, though this is a common practice in streamwood studies.
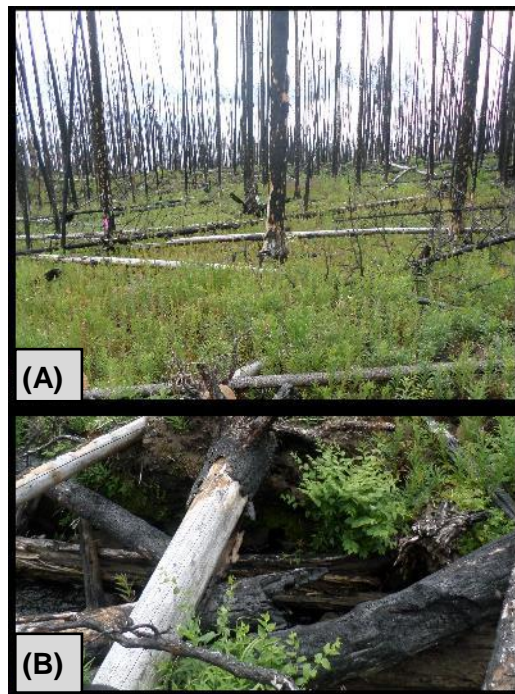
Figure 2.4   **Photo showing sample areas used to quantify the relationship between disturbance history and streamwood recruitment at two spatial scales: the scale of individual riparian trees (A) and the streamwood population (B).**

Population of recruited streamwood

Surveys were conducted to characterize the population of wood, both in-stream and bridgewood, recruited to study reaches. I used established metrics for streamwood to designate study reach boundaries and direct wood survey methodologies. Following standard wood survey protocol, reach length was 10× average bankfull channel width (Wohl et al. 2010) and resulted in study reaches of approximately 10 m for Stream 1 and 2, and 30 m for Stream 3. Beginning downstream, all downed wood pieces ≥10 cm in diameter and ≥1 m in length within the stream channel were recorded. The tree species of each wood piece was recorded by evaluating the bark, if present, and branch morphology (Jones and Daniels, 2008, Chen et al 2008). Unfortunately, evidence of bark beetle (SB, MPB) activity was recorded only at Stream 2 and Stream 3, which limited our inference into effects of bark beetle activity on streamwood.

The time of death of each wood piece was estimated, inspired and modified from methods used by Harvey et al. (2014) for terrestrial disturbance studies of wildfire and beetle outbreak. For each streamwood piece, pre-fire condition (pre-fire live, pre-fire dead) and recruitment timing (before fire versus fire) was recorded as either (1) killed and toppled to stream before the fire occurred (pre-fire dead, before fire), (2) killed before the fire (pre-fire dead) but recruited after fire (fire), (3) killed by the fire (pre-fire live) and toppled to stream after fire (fire), or (4) unable to be determined (unknown). For (1) lack of an identifiable stump, patterns of bole scorch and deep charring only on the top side of a piece, extensive decay, and absence of bark suggested a wood piece was likely already dead and downed, in or above the stream at the time of the fire. For (2), whole bole scorch, deep charring at the base, absence of bark, and nearby stumps unburnt at their break points suggested a wood piece was a riparian snag during fire occurrence, killed via another agent such as insects. Any presence of burned beetle galleries was further used to confirm pre-fire death. For (3) trees alive at the time of the fire but killed by fire in our study area possessed tightly attached bark. The presence of unburnt, broken bases and crowns full of needles and cones confirmed the piece was likely killed by fire and recruited during the 2 year period after the fire, but before sampling.

Controls on the toppling and recruitment of riparian trees

To determine whether being dead at the time of fire (disturbance history) increases a tree's probability of toppling and being recruited into streams I used a selection approach. This compares the population and characteristics of snags available for recruitment, i.e. all trees in the riparian area, to those that a) toppled, and b) toppled in a direction such that they were recruited as streamwood. Wood is generally recruited from within ~1 tree length away from the stream (Benda et al. 2003). As a result, riparian forest survey plots were 10 m wide by 10-30 m long, to match the stream transect. I surveyed the riparian forest on one side of the stream, chosen at random by coin toss; sampling both streambanks was not possible due to timing constraints. The riparian areas selected were uniformly flat and within areas of high burn severity, reducing the difference in outcome between the streambanks. Tree species was identified and diameter at breast height (DBH) was taken for each snag and coarse wood piece using a metric tape. The height of each snag as well its respective scorch height (maximum height of scorch on the tree) was determined using a rangefinder and the Pythagorean Theorem. When we were unable to obtain an accurate rangefinder reading to the top of the tree a clinometer was used. Coarse wood length was measured using a metric tape. Whether or not a toppled tree was recruited to the stream (either as in-stream or bridgewood) any evidence of bark beetle (SB, MPB) activity, the percentage of deep charring, and the scorch height on each piece was also recorded.

The time of death for each snag and coarse wood piece was estimated using the same methodology as described for streamwood pieces. As pre-fire coarse wood was nearly absent due to consumption by fire in the study area, for each snag and coarse wood piece, pre-fire condition (pre-fire live, pre-fire dead) was recorded as (1) killed before the fire (pre-fire dead), (2) killed by the fire (pre-fire live), or (3) unknown (unable to be determined). Site slope, aspect, and elevation were also measured and recorded using a clinometer, compass, and handheld GPS, respectively for each stream reach.

2.2.3. Analysis

Population of recruited streamwood

To characterize the populations of wood recruited I summarized the timing of recruitment, differences among species, and the timing of mortality within total

streamwood loadings across the study area as a whole, and compared these among the three study streams. Differences in odds of pre-fire vs fire recruitment between species across the study area was tested using Fisher's exact test for count data. The population of wood recruited pre-fire versus by fire among the three streams was evaluated using Pearson Chi-Square test, followed by post-hoc pairwise tests of independence using the 'fifer' package (Fife, 2017). The timing of mortality for trees recruited by the fire were compared among streams using the population of wood entering streams post-fire that was alive pre-fire versus dead pre-fire and Pearson Chi-Square test. Post hoc analysis used the 'fifer' package (Fife, 2017). The significance of all statistical tests was interpreted using a critical p-value of <= 0.05.

Controls on the toppling and recruitment of riparian trees

For the tree-scale selection analysis, the focus was to determine how toppling and recruitment to stream of an individual tree was affected by its condition pre-fire: live prior to fire versus dead prior to fire. For each riparian tree, I calculated the odds of a) topple and b) recruitment to the stream environment related to five tree level predictors: DBH, height, time of death, species, scorch height using a bivariate for each predictor. I used binomial generalized linear model (GLM) regression for statistical estimation. For a) all trees that had toppled at the time of study were coded as one and the remainder standing were coded as zero. For b) only the subset of trees that had toppled were considered, with those that toppled toward/into the stream coded as one and those that toppled away from the stream coded as zero. Predictors for fall direction (toward the stream coded as 1) were also tested. Final models were selected using lowest Akaike Information Criterion (AIC). The logistic regression coefficients, the change in the log odds of the outcome for each increase in predictor variables, were then converted to odds-ratios, i.e. the ratio of the odds that topple or recruitment will occur to the odds of not happening, using the exponential function. This then determined the influence of each variable on the outcome for both a) toppled and b) recruited. Tree level probability for toppling and recruitment could then be calculated using the extracted odds. Due to the sampling structure of individual trees nested within stream reaches, which were nested within streams, generalized mixed effect modeling was explored using the 'lme4' package (Bates et al, 2015) but found to not substantially improve model AIC. All analysis for this study was conducted using R Statistical Software (R Core Team, 2016).

To provide general context and support for the tree-level selection analysis, I first evaluated tree characteristics with toppling and recruitment rates using the populations of riparian trees. For these analyses, populations of toppling wood were defined at the stream scale to overlap with those of recruited streamwood. Differences in tree size (DBH), height, and fire severity (scorch height) among streams were tested using one-way analysis of variance (ANOVA) with stream as a factor using raw data. Tukey's honestly-significant difference test followed to assess significant differences between stream populations when significance was observed. I tested for differences in these populations of trees which were pre-fire snags, toppled, and recruited among streams using Pearson Chi-Square tests. Timing of mortality was quantified by the population of standing riparian trees killed pre-fire versus post-fire. Topple rate was quantified as the population of trees standing versus downed. Streamwood recruitment was quantified as the population of riparian trees that toppled into the stream environment versus those that toppled and became terrestrial coarse wood. Pairwise post hoc analysis between the streams followed these tests using the 'fifer' package (Fife, 2017). I tested whether the frequency of trees toppling and becoming streamwood was independent of time of death (pre-fire, post-fire) within each stream segment and across the study area as a whole using Chi-Square with Yates' continuity correction test. In cases of small counts (Stream 2) Fisher's exact test was used. The significance of all statistical tests was interpreted using a critical p-value of ≤ 0.05.

2.3. Results

Population of recruited streamwood

The recruitment timing (pre-fire or fire), pre-fire condition (pre-fire live or pre-fire dead), and species (pine versus spruce) of 201 streamwood pieces were determined, across 17 reaches spanning three streams (seven in Stream 1, five in Stream 2, and five in Stream 3. I found 61.8% (n=126) of streamwood fell post-fire indicating that the population had increased from pre-fire levels (n=77, Figure 2.5). Fifty-eight percent (n=74) of the 126 riparian trees which were transformed into streamwood by the fire were snags (pre-fire dead) at the time of fire rather than live (n=52) trees (Figure 2.6). Within the pre-fire dead, snag population, the ratio of spruce to pine deposited into streams across the study area was exactly 1:1 (n=37 of each species) as opposed to the vast majority of the 52 pre-fire live trees being spruce (n=51 spruce). Spruce

streamwood was more common (n=117) in the streams overall than lodgepole pine (n=87), but most did not enter the stream until transferred there by the fire (n =88) or streambank erosion (n=1). In comparison, more pines sampled (n=49) were recruited before the fire's occurrence as opposed to afterward (n=38). Due to the dominance of spruce streamwood was more common (n=117) in the streams overall than lodgepole pine (n=87), but most did not enter the stream until transferred there by the fire (n =88) or streambank erosion (n=1). In comparison, more pines sampled (n=49) were recruited before the fire's occurrence as opposed to afterward (n=38).

Streamwood composition differed among the three streams. Wood within Stream 3 was 96% pine (n = 84) whereas Stream 1 was 96% Spruce (n = 82), and Stream 2 100% Spruce (n = 34). Stream 3 also had more wood already present when the fire occurred (before fire) than did Streams 1 and 2 (X^2 = 32.2, df = 2, p<0.05, n = 52; Figure 2.4). The ratio of pre-fire dead to pre-fire live wood pieces recruited by the fire differed significant between all three streams (X^2 = 38.9, df = 2, p<0.05; Figure 2.5). Pre-fire MPB galleries were detected on 14% (n=14) of streamwood pieces within Stream 2, and 93% (n=80) of streamwood pieces along Stream 3, indicating spruce trees were attacked by MPB during the outbreak. Evidence of bark beetle activity was not assessed at Stream 1.
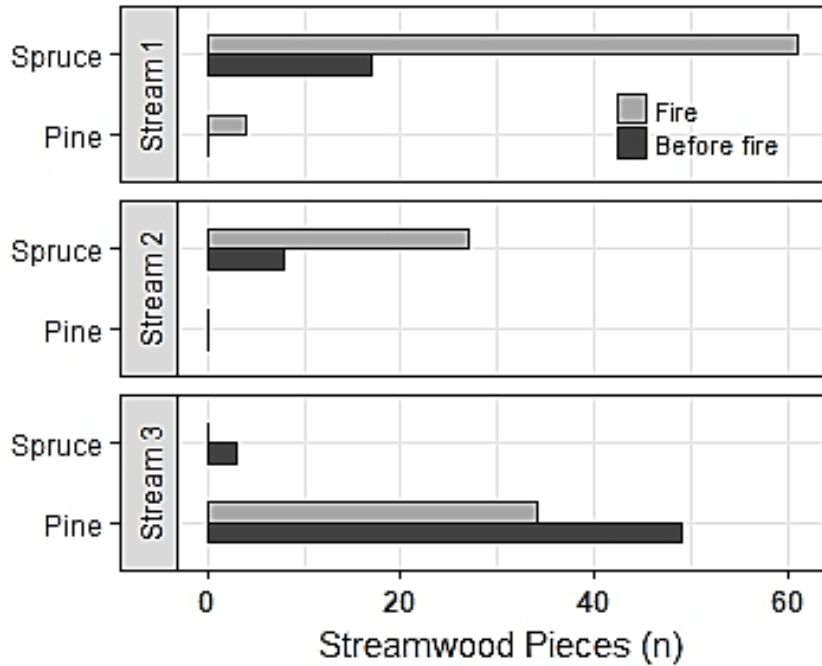
Figure 2.5 **Heterogeneity in wood species composition and recruitment timing between headwater streams burned by a wildfire in central interior British Columbia, Canada.** *Before fire* **indicates wood pieces that were in the stream prior to fire;** *Fire* **indicates the wood entered the stream after the area burned. The timing of wood recruitment in Stream 3 was significantly different from Streams 1 and 2. All streams were sampled two years post-fire.**
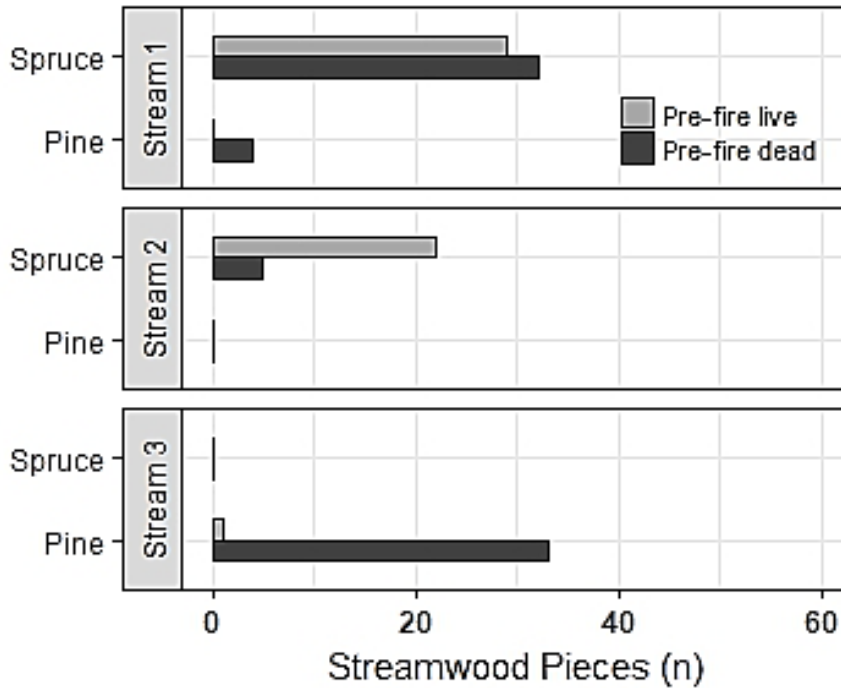
Figure 2.6 **Spatial comparison of standing pre-fire dead to pre-fire live wood piece populations recruited as a result of a wildfire between sub-boreal streams in central interior British Columbia, Canada.** *Pre-fire dead* **indicates snags in the riparian zone prior to fire whereas** *Pre-fire live* **represents trees alive before the fire occurred.**

Controls on the toppling and recruitment of riparian trees

I sampled 304 trees which had been standing, dead or alive, at the time of the fire (Table 2.1) in riparian forests adjacent to study stream reaches. Species composition in these forests was lodgepole pine (54%) and spruce (46%), however species distribution varied among streams. Riparian trees along Stream 1 were larger (25.9 cm, $p = <0.05$) and taller (18.3 m, $p = <0.05$) on average than in the other areas sampled (Table 2.1). Eleven percent (n =6) of trees sampled at Stream 2 and 67% (n =116) of trees at Stream 3 had evidence of pre-fire MPB activity, indicating non-pine hosts were attacked as well as pine. Trees along Stream 2 experienced significantly higher fire severity ($F = 21.4$, $df = 2$, $p>0.05$) than the other areas.

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Table 2.1. Summary of variability in riparian forests characteristics between headwater streams draining a sub-boreal pine-spruce ecosystem of central interior British Columbia, Canada. Streams lie within the dry cool subzone of the Sub-Boreal Spruce (SBSdk) and the moist cold subzone of the Sub-Boreal Pine-Spruce (SBPSmc) biogeoclimatic zones and were sampled two years post-fire.

Sample area	BEC zone	Total trees	Percent pine/spruce	Trees killed pre-fire (n)	Trees toppled (n)	Trees recruited (n)	Recruited (%)	Mean DBH (cm)	Mean Height (m)	Mean scorch height (m)
Stream 1	SBSdk	75	3/97	25	58	19	32.7	25.9±8.8**	18.5±6.3**	9.7±8.5
Stream 2	SBPSmc	57	0/100	17	36	11	30.5	20.9±8.1	14.5±5.9	13.7±6.4**
Stream 3	SBPSmc	171	96/4	120	76	29	38.1	19.2±6.9	14.9±5.6	7.1±5.8

Note: **$p < 0.05$

The majority of standing trees that fell in the two years after the Chelaslie fire were already dead during fire occurrence, but spatial heterogeneity in pre-fire status (dead versus live) and post-fire position existed among the riparian forests of my study streams (Figure 2.7). Overall, 53% (n=162) of the 303 trees for which time of death was determined died before the fire occurred and 56% (n=169) were fire-toppled. Sixty-four percent (n =109) of all 169 trees falling post-fire were pre-fire snags. Accordingly, when considering the entire population of trees, fire induced toppling was enhanced among pre-fire snags relative to live trees (X^2 = 17.7, df = 1, p <0.05). At the stream level, although the abundance of pre-fire snags was highest along Stream 3 (X^2 = 44.2, p <0.05, df =2, Figure 2.7; 70% mortality), the area dominated by lodgepole pine, the proportion of trees toppled post-fire was lowest (X^2 = 25.2, p <0.05, df =2; 43%). Despite this, whether a pine fell post-fire was still dependent on its pre-fire status i.e., being dead (X^2 = 44.8, df = 1, p <0.001). Conversely, pre-fire mortality within the spruce-dominated stands of Streams 1 and 2 was 34% and 31%, respectively, with 77% and 63% of the riparian tree population toppling in these forests. Similar to pine stands, whether spruce trees fell post-fire depended on their pre-fire status (X^2 = 5.3, df = 1, p <0.05), indicating that overall pre-fire death significantly enhances post-fire toppling.
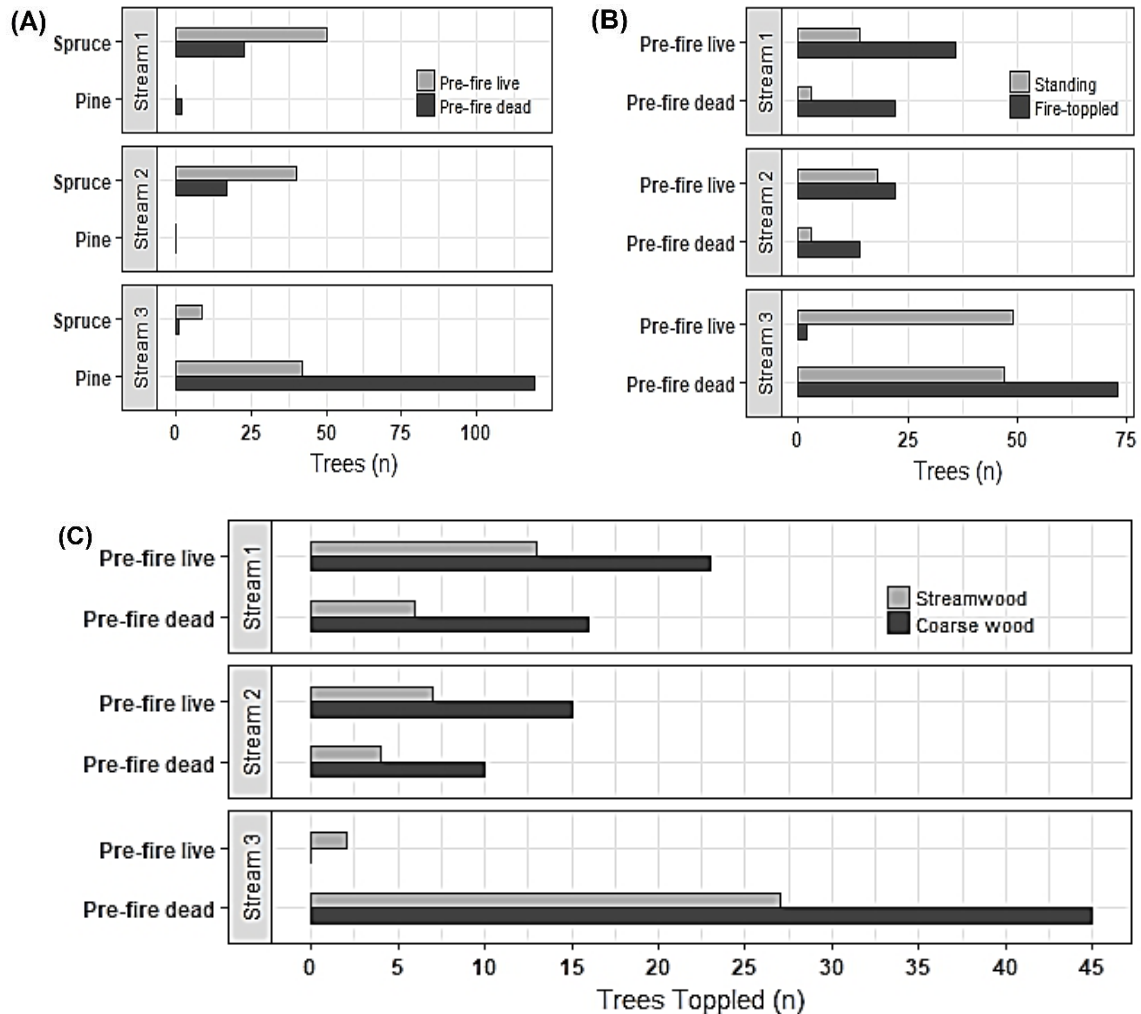
Figure 2.7   Spatial comparision of (A) the population of standing pre-fire dead to pre-fire live trees, (B) tree position, and (C) fate of toppled trees between three riparian forests in a sub-boreal pine-spruce ecosystem of central interior British Columbia, Canada. A) *Pre-fire dead* indicates snags in the riparian zone prior to fire whereas *Pre-fire live* represents trees alive before the fire occurred. B) *Standing* indicates trees still standing wheres *Fire-toppled* were downed. C) Toppled riparian trees can either fall to the forest floor as *Coarse wood* or to the aquatic environment as S*treamwood*.

The proportion of trees toppling into streams (Figure 2.8B) did not differ between the pine and spruce dominated streams. Recruitment was similar (X^2 = 1.0, df = 2, p = 0.6) regardless of differences in the abundance of pre-fire snags and the proportion of trees toppled post-fire (Figure 2.7), indicating recruitment from riparian forests was not significantly affected by pre-fire status (X^2 = 0.02, df = 1, p = 0.88) across the study area. Recruitment was also not related to pre-fire tree status within either spruce dominated

streams (n=97, X^2 = 0.31, df = 1, p = 0.57) or pine dominated streams (n=74, Fisher's p=0.15, one-sided). An average of 34.8% of the trees falling within a stand became streamwood (Table 2.1) indicating, at least at a riparian forest population level, the amount of streamwood is related to amount of toppling overall. Therefore, suggesting processes increasing the rate of toppling will also increase the amount of streamwood.
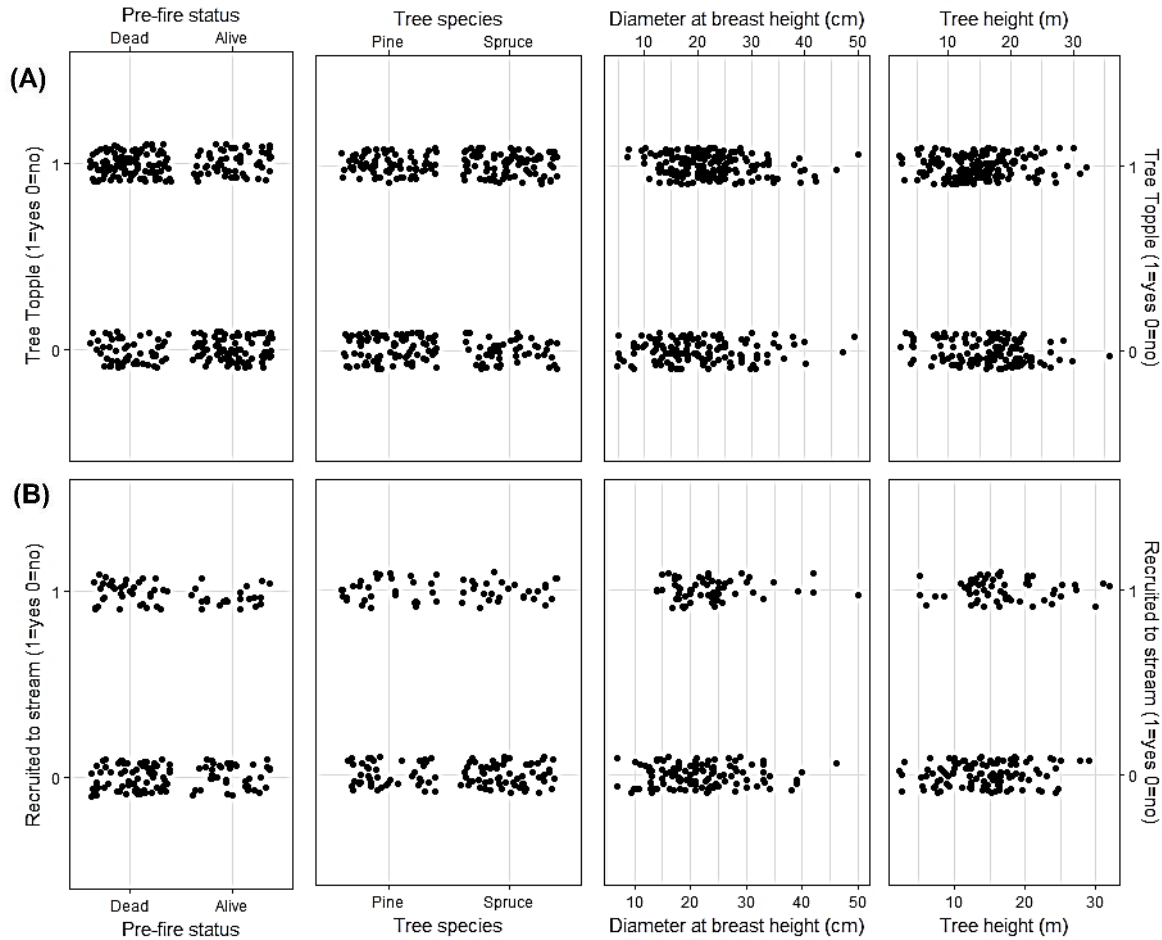
Figure 2.8.   **Scatterplot of predictors for the binary A) toppling of riparian trees and B) fate (*recruited* or not) of toppled trees in a sub-boreal pine-spruce ecosystem of central interior British Columbia, Canada.**

Bivariate regression models revealed disturbance history, i.e., being dead prior to fire, significantly enhanced tree topple, while tree height altered recruitment, two years post-fire for the individual sample units within a population. The ratio of the odds, i.e. the difference in the chances of an event occurring versus not, for post-fire toppling became 2.05 times higher if a tree was dead pre-fire instead of alive (Figure 2.9A). Individual spruce trees were twice as likely to fall post-fire as pines (Figure 2.9A, Table 2.2) with a 68% chance of falling, and that increased to 87% if they were killed pre-fire. Although the

inclusion of tree height in the model increased the odds (odds ratio= 3.16) of a snag toppling post-fire (1.149, SE 0.346, p> 0.001, df =300), it did not substantially change model AIC. Thus, removing tree height provided the simplest model possible. The odds of a tree toppling specifically into a stream environment post-fire increased by a factor of 1.07 (log odds of recruitment versus non-recruitment) increases by 0.07 SE 0.03, p=0.02, df = 163, for every meter increase in its height (Figure 2.9B). This indicates taller trees could simply be more likely to reach the stream channel after toppling because of the distance between the base of the tree and the stream channel.
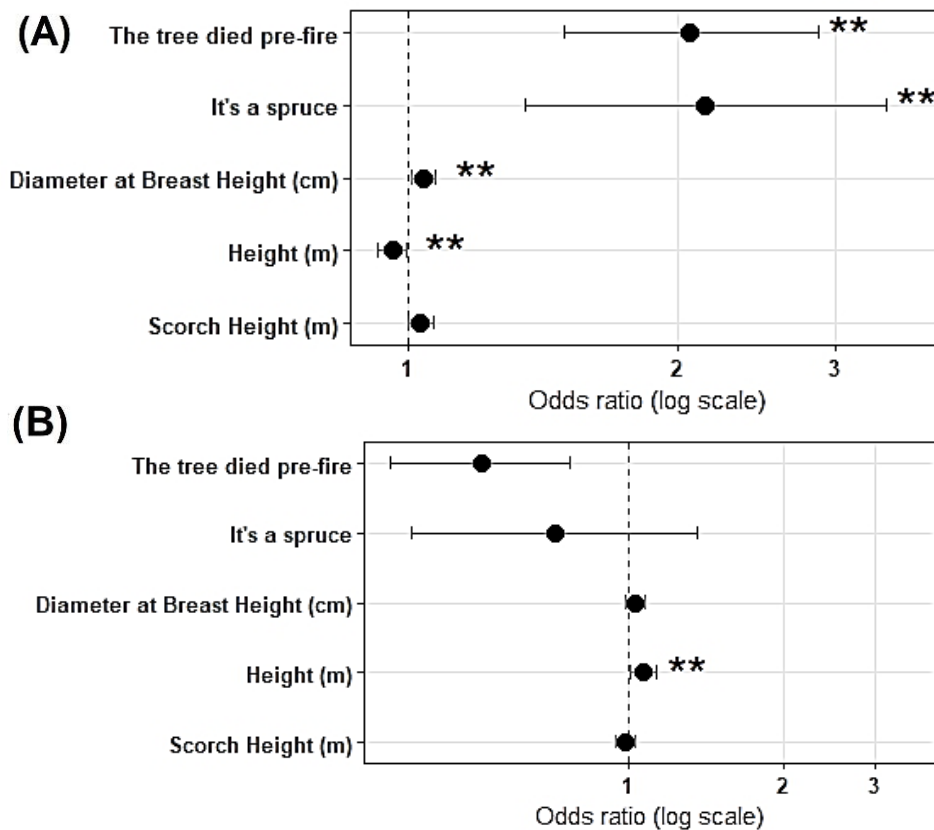
Figure 2.9   **Comparison of physical traits influencing the likelihood a standing tree A) topples and B) topples into a stream within two years after the occurrence of a wildfire in a sub-boreal riparian forest in central interior British Columbia, Canada. Dashed line at 1 represents equal odds for an event occuring (toppling, toppling into a stream) versus not between every factor level. ** indicates p<0.05**

Table 2.2 **Summary of bivariate generalized linear regression analyses for variables predicting the toppling of trees and the recruitment of streamwood in a sub-boreal pine-spruce riparian ecosystem of central interior British Columbia, Canada. (N = 303). Values in parentheses below model coefficients denote one standard error.**

	~ tree topple				~ streamwood recruitment			
Predictor	Model Coefficient	Observations	Log Likelihood	Akaike Inf. Crit.	Model Coefficient	Observations	Log Likelihood	Akaike Inf. Crit.
Pre-fire tree death	0.721*** (0.167)	303	-198.572	Δ 16.86	0.105 (0.336)	168	-108.845	Δ 1.90
Tree species	0.761*** (0.237)	303	-202.742	Δ 8.52	-0.348 (0.325)	168	-108.318	Δ 0.85
Tree DBH	0.039** (0.015)	303	-204.580	Δ 4.84	0.033 (0.022)	168	-107.713	Δ 0.35
Tree height	-0.042** (0.020)	303	-205.642	Δ 2.72	0.068** (0.028)	168	-105.917	Δ 3.95
Burn severity (height of bole scorch)	0.030* (0.017)	303	-206.359	Δ 1.28	-0.010 (0.024)	168	-108.812	Δ 1.83

Note: *p<0.1; **p<0.05; ***p<0.01

2.4. Discussion

Wildfire preferentially topples dead trees in sub-boreal riparian corridors, indicating that fire burning through beetle-killed forests results in increased streamwood recruitment than fire through live forest stands. Both pine and spruce trees were more likely to fall following wildfire if they were dead pre-fire, illustrating the general influence of bark beetles and wildfire as disturbance agents affecting post-fire coarse wood and streamwood structure. Overall, the death of a riparian tree before the occurrence of a wildfire doubled the odds of it toppling in the immediate (< 2 years) post-fire period, and the odds of toppling during this timeframe as a result of pre-fire death was higher in spruce dominated forests than pine. Over half (64%) of all the trees falling post-fire were pre-fire snags and a more than twofold increase in streamwood consequently resulted due to the fire. Accordingly, fires burning through mature conifer forests with abundant snags will rapidly deposit wood, both as in-stream and bridgewood, to adjacent aquatic systems and therefore shape post-fire stream communities through a beetle-fire-streamwood connection.

The duration of time between an outbreak of mountain pine beetles and wildfire in the study area controlled the wood species recruited by fire. Most fire-recruited wood was spruce as even time had passed (~10 years) since the peak of the beetle outbreak that the majority of beetle-killed pines had already toppled on the surrounding landscape before wildfire occurrence. This coincides with results from other bioregions in western North America where fall rates for lodgepole pine peak 8-11 years after death, with the majority (>90%) of snags down after 14 years from the structural weakening caused by fungal rot (Gara et al. 1985; Lewis & Thompson 2009). Consequently, spruce trees were roughly four times more likely to be recruited specifically by the fire than pines due to the interval between disturbance events. Although the importance of time since outbreak has been stressed in previous work to ascertain whether beetle-outbreaks increase streamwood populations (King et al. 2013; Hassan et al. 2008), these studies arrived too early rather than too late; most beetle-killed trees still standing versus most had fallen prior to the fire as in my study.

Support for the hypothesis that after fire, insect killed (pre-fire killed) snags would be more likely to immediately topple and be recruited to adjacent streams on a post-fire landscape than would those trees that were alive at the time of fire was found. In this

study pre-fire death by beetle, or other factors, enhanced the fire-toppling of trees and, in effect, the supply of streamwood. The absence of a pre-fire tree death signal in streamwood recruitment was likely due to stream valley topography. Previous field data and modeling in coniferous riparian stands in western North America found tree fall directionality (e.g. streamwood recruitment) was determined by hillslope steepness, with 1.5 to 2.4 times more wood toppled in stream reaches with steep hillslopes than to reaches with moderate side slopes or flat banks (Sobota et al. 2006). Stream banks across the study area were flat, and, although azimuths of logs were not taken, a more randomized pattern of topple direction resulted. This was despite general prevailing winds perpendicular to stream orientation. Fire-induced toppling overall was enhanced among pre-fire snags. In short, by doubling the odds of topple, pre-fire mortality circuitously doubled the odds of recruitment due to the random directionality of tree fall in the stream channels. Although spruce trees dominated the riparian forests, they are susceptible to attack in pine-dominated landscapes during mountain pine beetle outbreaks (Safranyik et al. 2010). In this study, roughly a third of the spruce was killed pre-fire, with 14% of the spruce streamwood pieces and 11% of the spruce trees sampled showing signs of pre-fire MPB attack (e.g., burned J-galleries). Because roughly a third (34.8%) of what topples post-fire in the riparian-stream forest interface is recruited to aquatic ecosystems as streamwood, bark beetle outbreaks ultimately increase the amount of wood deposited in streams by fires by enhancing the toppling of trees through increasing the magnitude of pre-fire riparian tree death. This effect was readily detected in tree species whom are shallow-rooted and susceptible to toppling such as interior spruce (BC Ministry of Forests and Range 2008) where roughly a third of the population was killed by beetles, or other factors, pre-fire.

Although evidence for how the overlap of beetle outbreak and wildfire alter the amount and temporal transfer of wood into streams was found, there are several ways this study could have been improved. Because taller individuals were the trees to be preferentially transferred into headwaters, it suggests wind could be key in conveying wood to steams as in other riparian stands of western Canada (Bahuguna et al. 2012; Johnston et al. 2011; Stathers et al. 1994). Thus, severity and timing of post-disturbance windthrow events could have similarly strong effect in Canada's sub-boreal central interior. Unfortunately, although certain topographic and meteorological variables were recorded in this study prevailing wind direction was not one of them, which coupled with

azimuths of fallen logs, would have greatly improved the study. Similar to other streamwood studies in MPB-infested landscapes (Jackson & Wohl 2015; Hassan et al. 2008; King et al. 2013), pine was sparsely found in the riparian zones, and the definitively beetle-killed trees in this area had already fallen by the time the fire occurred (Figure 2.4), potentially reducing sample size. Also, random one-sided sampling during this study resulted in cases where the streambank that supplied the sampled stream reach with its wood was missed, reducing sample size for recruited wood further. However, although increased sample size would have strengthened this study the remote location made more extensive sampling unfeasible.

As global temperatures increase, the likelihood that tree-killing events such as beetle outbreaks and fire, in combination with drought, will overlap in time and space also increases (Raffa et al. 2008; Westerling et al. 2011). The findings of my study suggest multiple disturbances (insect outbreak, wildfire) interact synergistically in altering streamwood pools, as well as terrestrial coarse wood. Wood shapes aquatic ecology and geomorphology of streams (Gurnell et al. 1995; Dolloff & Warren 2003; Montgomery et al. 2003). As such, the rapid transfer of wood into streams over entire landscapes after insect outbreak and fires could would elicit widespread alteration of streamflow, gravel deposition, and habitat availability for both aquatic invertebrates and fish. Given the annual area infested by spruce beetle outbreaks is rapidly rising alongside fire risk in western North America (Andrus et al. 2016), understanding the effect of their overlap on stream communities is of growing importance.

Chapter 3.

The influence of channel bridging, fire-toppled wood on stream light is comparable to a riparian understorey in sub-boreal post-wildfire environments

3.1. Introduction

Riparian forest processes are fundamental drivers of aquatic primary productivity and thermal variability for entire watersheds. Forests alongside streams intercept incoming solar radiation, in addition to providing nutrients and materials (leaf litter, wood) to nearby waters that contribute to habitat for stream-dwelling organisms (Kelly et al. 2003; Martin & Benda 2001; Warren et al. 2016). The amount of photosynthetically active radiation (400–700 nm wavelength) reaching the stream strongly determines stream primary production rates and algal standing stocks (Wagner et al. 2015; Warren et al. 2013; Eminson & Moss 1980). Increases in stream solar exposure heighten aquatic primary production whereas complete shading transitions aquatic food webs away from a base of photosynthetic algae to one built on invertebrate scrapers and grazers (Peckarsky et al. 2015). Solar radiation is also the primary determinant of water temperature, especially in the shallow headwaters used by anadromous fish like salmonids (Brown, 1969; Johnson, 2004; Moore et al., 2005). Water temperature affects the abundance and species composition of stream invertebrates and fish by controlling the concentration of dissolved oxygen, pH, and the metabolic rate of stream biota (Isaak et al. 2010). Even small increases in water temperature can cause a shift in overall species composition to favor those with higher temperature tolerances and change development rates in juvenile salmonids (Beakes et al. 2014). Food webs within subsequently larger downstream regions are in turn manipulated by processes in headwaters because these streams provide their energy and nutrients (Vannote et al., 1980). Because of the links between incoming solar radiation, photosynthesis, and temperature in streams, understanding local drivers of variability in streambed light in forested headwater streams is important for estimating localized and watershed-scale effects of forest processes.

Landscape-scale disturbance events, such as wildfire, change stream light availability and thus alter stream ecology. At high severities, these events cause mass mortality of riparian trees and for fire, consume the riparian understory leaving behind standing dead snags and stream banks devoid of vegetation until post-fire successional processes begin (Pettit & Naiman 2007). Without a full riparian canopy or understorey to intercept light, solar ultraviolet radiation reaching the stream benthos markedly increases. The standing dead trees, left in the wake of a wildfire or an insect outbreak, still regulate stream light (Leach & Moore 2010; Rex et al. 2012). The flux of sunlight reaching the stream is highest in the immediate post-disturbance event period (Klose et al. 2015), before the canopy and understorey vegetation fully returns. During the same period primary productivity is enhanced and stream temperatures increase rapidly, as high as 10 °C above pre-fire levels (Cooper et al. 2014; Isaak et al. 2010). Stream invertebrate and fish communities are then significantly altered as a result of these fire-induced changes to stream light (Bixby et al. 2015; Koetsier et al. 2007). As the riparian vegetation and canopy develop over time, levels of stream light then gradually decrease. Therefore, shade provided immediately post-fire by recovering streamside deciduous understorey vegetation acts as a thermal buffer for elevated stream temperatures (Dunham et al. 2007). The stream surface shade provided by a deciduous understorey has also been found to reduce incoming shortwave and longwave radiation in recently (< 5 years) clear-cut headwater riparian forests to pre-harvest levels (Klos & Link 2018).

The amount of wood recruited into streams is proportionate to the scale of tree mortality in the surrounding forest and the rate at which it is introduced. Mass tree mortality as a result of a wildfire or an insect outbreak equates to high inputs of wood to both streams and forest floors (Wei 2005; Pedlar et al. 2002; Bragg 2000; Harmon et al. 1986). Wildfires are part of the historical disturbance regime in temperate biomes (Agee 1993) and fire-killed riparian trees are a primary source of wood for inland waters (Wohl 2015). Recent bark beetle outbreaks have affected an unprecedented number of trees in western North America, with some watersheds reaching 100% mortality (Raffa et al. 2008; Dhar et al. 2016). One of the key outcomes from severe mortality events is the pulse of terrestrial downed wood, spurring probes into the subsequent effects on fire behaviour and suppression operations, nutrient cycling, and plant community development (Andrus et al. 2016; Page et al. 2013; Cigan et al. 2015; Edwards et al. 2015; Stevens-Rumann et al. 2015). However, the falling of beetle-killed trees and

subsequent accumulation of downed wood is not necessarily restricted to terrestrial environments as many forests supplying streams with wood have been impacted by insect outbreaks (Rinella et al. 2009; Dwire et al. 2015; Allen et al. 2006). Therefore, riparian forests experiencing overlapping disturbance events (insect outbreak, wildfire) will transfer a high quantity of wood to streams corridors quickly (Chapter 2).

Fallen, burnt wood shapes aquatic ecology by acting as a nutrient, and possibly shade, source. Burnt wood deposited within the stream alters invertebrate assemblages, likely from enhanced nutrient availability compared to unburned wood (Vaz et al. 2014). However, trees falling into narrow headwaters often remain suspended above the channel (Bahuguna et al. 2010). Wildfires occurring in riparian zones deliver pulses of wood, which are deposited during and after fire events into stream corridors, but often remain suspended above, or bridging, the stream surface for decades (Robinson et al. 2005), and are hereafter referred to as bridgewood. Fire-driven bridgewood could influence stream solar radiation levels in the immediate post-fire period by intercepting incoming sunlight, similar to a recovering understorey. Thus far, the effect of bridgewood on stream ecology remains understudied, having been depicted as functional only after it ceases to bridge the stream channel by breaking up and entering the water (Burrows et al. 2012; Jones & Daniels 2008). However, increases in stream temperature immediately following forest harvest operations have been shown to be moderated by accumulations of above-stream logging slash (unmarketable material including branches and treetops) that were deposited (Jackson et al. 2001). It has been proposed these fine, woody materials behaved as a thermal buffer by blocking incoming solar radiation to the streambed (Jackson et al. 2001; Haggerty et al. 2004), and stream invertebrate assemblages were subsequently altered in response to these above-stream woody accumulations. Accordingly, it seems logical to consider that fire-recruited bridgewood could act in the same way. Although Rex et al. (2012) suggested the substantial amount of channel bridging windthrown trees in their mixed conifer riparian ecosystem provided shade to the stream surface following forest harvest operations, the amount of shade this bridging wood specifically contributed was not quantified. Subsequently, we are unaware of any attempt to quantify the extent to which bridgewood influences stream solar loading much less any investigation into specifically the effect of fire-recruited bridgewood in the immediate (< 5 year) post-wildfire period.

My field study aimed to estimate the effect of fire-recruited bridgewood on stream surface light levels in the second year after fire. Based on our knowledge of bridgewood accumulated post-disturbance (Chapter 2) I predicted that bridgewood generated from a stand replacing wildfire has a strong influence on stream light and may be quantitatively comparable to residual riparian snags (standing wood) and deciduous understorey vegetation (streamside foliage) at intercepting stream light in the immediate post-fire period.

3.2. Methods

3.2.1. Study area

The study was conducted in two headwater streams within the sub-boreal forests of Entiako Provincial Park and Protected Area, located in the upper Nechako River basin, in central Interior BC, Canada (Figure 3.1). Mature lodgepole pine (*Pinus contorta* var. *latifolia)* forests dominate the landscape within the Park (Cichowski et al. 2001). Spruce (*Picea glauca x englemannii*) stands (3-7% total forest cover) dominate along riparian corridors, although lodgepole pine is frequently present. The area was the epicenter of a regional outbreak of MPB, resulting in widespread tree mortality that peaked in 2003/2004. From July to October 2014, 133,100 ha of forest within Entiako Provincial Park and Protected Area burned during the lightning-caused Chelaslie River fire. Minimal to no fire suppression ensued as the park is managed as wilderness and a mosaic of fire severity resulted. A full description of the Study Area can be found in Chapter 2.
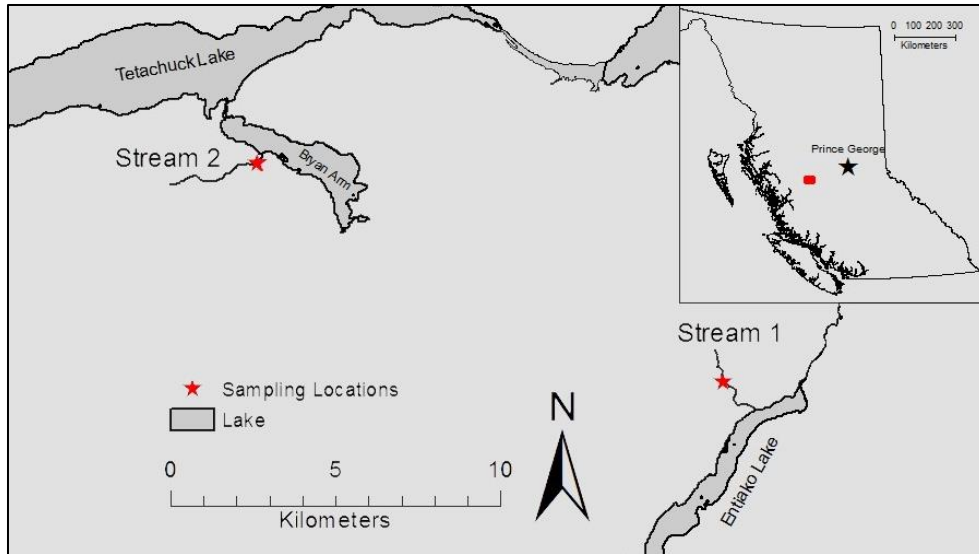
Figure 3.1. **Map of the study sites within Entiako Provincial Park and Protected Area in central interior British Columbia, Canada. The red box on map inset represents the study area. The locations of stream shade and light measurements are denoted with red stars.**

The sampled streams consisted of 370 m of Van Tine Creek (Stream 1) and 170 m of an unnamed tributary (Stream 2) on the south side of Tetachuk Lake (Figure 3.2). Seven, 10 m study reaches were sampled, consisting of four reaches in Stream 1 and three reaches in Stream 2. The location for reaches was based on suitability for this study, specifically on the presence of riparian trees, high severity fire effects, and an accumulation of downed wood. Many stretches of stream lacked streamside forest so I preferentially located study reaches with forest and bridged wood. Spacing between sampled reaches along study streams was 50 m and 30 m for Stream 1 and 2, respectively. Reach spacing was based on the extent of forest cover on both stream banks as these same stream plots were concurrently used to collect wood recruitment data (Chapter 2). Interior spruce dominated the forest cover of both streams with an early seral streamside understorey dominated by balsam willow (*Salix pyrifolia*) and fireweed (*Epilobium angustifolium*). Sampling occurred during summer low-flow conditions in July 2016, two years post-fire.

Figure 3.2. Photos showing study streams and typical accumulations of bridgewood suspended above the channel. From left to right; Van Tine Creek (Stream 1), unnamed tributary of Tetachuck Lake (Stream 2), and an example of an overhead view looking up from stream surface.

3.2.2. Field Measurements

To address my research objective I quantified the stream surface cover provided by each shade source. The relationship between the degree of stream surface shading solely contributed by bridgewood, deciduous understorey vegetation (streamside foliage), residual riparian snags (standing wood), and incoming stream light could then be compared. Previous studies investigating stream shade have combined all sources of shade to the stream either as one cover value or only differentiated between canopy and understorey vegetation. This study undertook partitioning cover values according to shade source in order to determine whether bridgewood can function as a shading mechanism that is as effective as residual standing live or dead trees or a recovering understorey in the second year after a stand-replacing wildfire. I also quantified the total amount of wood suspended above the channel within each stream reach using wood surveys and stream light transmissions were then used with these coverage quantities to further highlight the shading capacity of bridgewood in the immediate post-fire period.

Effectiveness of bridgewood shading relative to other sources

Sources of stream shade from standing wood, streamside foliage, and bridgewood were quantified using a spherical angular canopy densiometer (ACD). This spherical densiometer consists of a convex reflective lens with a pre-defined grid on

which one estimates overhead cover. Densiometers are a common method to estimate light availability in stream ecosystem studies as they provide a quick, inexpensive way to estimate overhead cover (Riley & Dodds 2012). I used the ACD to estimate shade during mid-summer, with samples taken between 10 am and 2 pm when solar radiation reaching the stream's surface is highest (Teti & Pike 2005). Shade levels were measured at the water surface in the center of the stream channel as this is where the highest amount of solar radiation reaches the stream (Warren et al. 2013). Point locations for readings were established systematically every 0.5 meters along a 10 m study reach. The percentage of each cell within the densiometer grid that was occupied by standing wood, streamside foliage, and bridgewood was recorded at each point location (Figure 3.3). Percent shade from each stream cover type in each of the grid squares was estimated to the nearest 10%. The same individual (Kurt Frei) conducted all of the estimates over the study period in order to address operator variability.

I measured light levels at the stream surface using a photosynthetically active radiation (PAR) sensor (Decagon Devices, Pullman, WA, USA). These data were used to establish a relationship between stream shade and stream solar exposure at both the scale of the reach and point. The sensor measures the Photosynthetic Photon Flux (PPF), in the range of 400–700 nm that is necessary for primary producers. PPF is measured in µmol m^{-2} s^{-1} from a field of view of 180 degrees. In order to capture PAR midstream, I installed the PAR sensor onto acrylic glass and wooden dowels (Figure 3.3). The length (1.5 m) of the dowels allowed the unit to span the channel without falling in and recordings to be made from behind streamside vegetation. A leveling plate was included to maintain the sensor at a horizontal (180°) and ensure the accuracy of readings. The unit was placed on the water surface at the same 0.5 m frequency along a study reach used for stream shade readings.

The PAR sensor was connected to a handheld data logger (Decagon Devices, Pullman, Washington). Readings were taken per minute over three minutes (n=3), and the average PPF measurement recorded. I limited stream light data collection to between 10 am and 2 pm, in order to capture maximum stream solar radiation. Raw recordings of PAR are inherently highly variable, but more so under changing cloud cover. Thus, I restricted readings to the clearest sky conditions possible to reduce the amount of variability in PAR recordings.
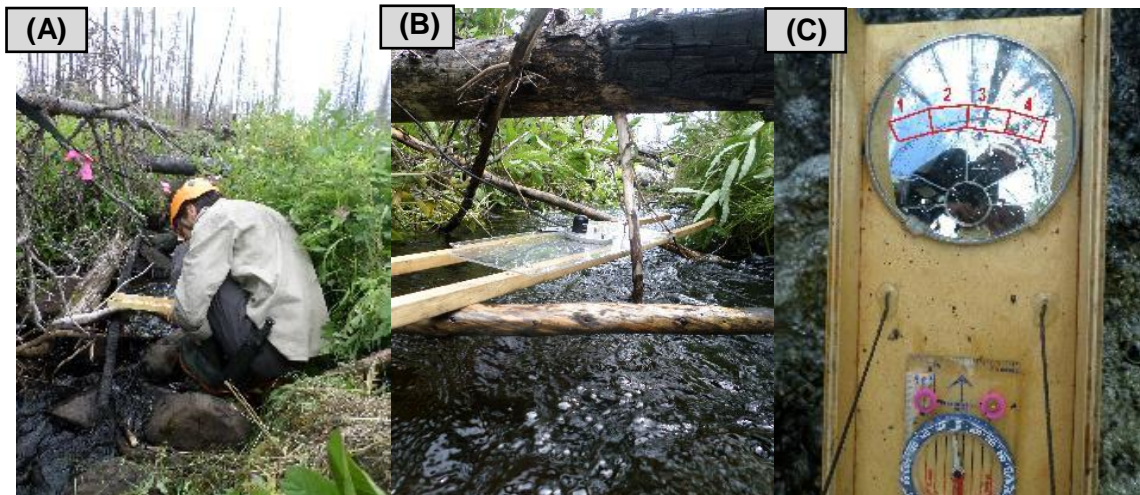
Figure 3.3. **Photos showing use of A) an angular canopy densiometer (ACD) and B) a photosynthetically active radiation (PAR) sensor for this study. The four top cells of the ACD represent solar path between 10 a.m. and 2 p.m. Percent of above-stream cover was C) partitioned respective to each shade source (bridgewood, streamside foliage, or standing wood) within each cell.**

Quantity of bridgewood shading along streams

Wood surveys were conducted at each reach to gain a quantitative estimate of the bridgewood cover intercepting solar radiation to the stream. Following standard streamwood survey protocol, reach length was 10-times the average bankfull channel width (Wohl 2010) and resulted in study reaches of approximately 10 m in length. Beginning at the downstream end, the length and diameter at mid-point of downed wood pieces spanning the channel in a bridging position (bridgewood) were measured using metric tapes. Measurements were constrained to pieces ≥10 cm in diameter and ≥1 m in length lying above the stream surface. The volume for each piece of wood was later calculated using the equation for the volume of a cylinder (Lienkaemper & Swanson 1987). Stream light transmissions were then used with these coverage quantities to further illustrate the shading capacity of bridgewood.

3.2.3. Analysis

To address inherently high variation in light intensity in the PAR values, raw stream light measurements (n=210) were converted to a percentage transmitted of reach-scale available light. High variability in light within and among reaches was likely

due to differing times of day and shifting cloud conditions during the sample period. As the available (fully unshaded) incoming light was not directly measured in the field, it had to be estimated. Values of reach-specific fully unshaded light were established by first plotting the point-wise percentages of an initial estimated total light transmission value against the pointwise total shade (combined bridgewood, standing wood, and streamside foliage) values. The initial value for total available light was then adjusted until full (100%) light transmission corresponded to shade cover values of zero. Observations indicating physical impossibilities, full transmission yet corresponding to full shade (100%), were omitted. Three reaches (one in Stream 1, two in Stream 2) were subsequently excluded as these locations wholly contained unusable observations; likely caused by variable cloud cover and the spatial offset between rays of incoming light and the cover directly overhead the sample points. The screening process resulted in a final sample of 144 stream light measurements across seven (n=7) reaches. To make consistent comparisons among reaches and correlation with the shading capacity of bridgewood, light transmission data were then base10 log-transformed for all analysis. However, light transmission is reported in percent for easier visual interpretation.

Effectiveness of bridgewood shading relative to other sources

To illustrate a comparison of shading in the post-fire riparian environment, pointwise shade values were filtered to separate the three shade sources (bridgewood, standing wood, and streamside foliage) from each other prior to analysis. To isolate the shading capacity of each type of stream cover densiometer shade recordings (points) where more than one cover type was present (n=120) were excluded. Generalized linear models using the filtered shade and light transmission data (n=90) assessed whether bridgewood is as effective at shading streams as the other shade sources. One model was built for each of the stream shade factors (bridgewood, standing wood, and streamside foliage). Sample size for each model predictor ranged from 17 to 47 for standing wood and bridgewood, respectively. Finally, a bivariate GLM was built using all densiometer shade recordings, including where more than one cover type was present, to ascertain whether the shade provided by each source was additive or interactive in altering stream light.

Differences in shade source densiometer values were assessed between both reaches and streams to provide further context and support of analysis and to offer a

general comparison with the distribution of bridgewood quantity. Each point location (n=210) had four densiometer cells, each cell broken up into the percentage covered by standing wood, streamside foliage, bridgewood. Average cover for each shade source was taken across the four cells at each point location. Differences in the percentage of cover contributed by bridgewood, standing wood, and streamside foliage between the streams was tested using a Levene's Test for Homogeneity of Variance after Shapiro-Wilk normality test, and followed by a Mann-Whitney-Wilcoxon test. Differences between the reaches were tested using one-way ANOVA with reach as a factor using point averages. Tukey's honestly-significant difference test followed to assess significant differences between reaches when significance was observed.

Quantity of bridgewood shading along streams

The effectiveness of bridgewood accumulations at intercepting solar radiation was evaluated using generalized linear model (GLM) regression. The regression was run using reach-specific means (n=7, log transformed percentage of light transmitted and wood quantity).

The spatial dynamics of bridgewood accumulation and stream light was assessed to provide further context for correlation between the two. Wood volumes were averaged per reach and divided by the channel area to quantify the wood coverage over each reach in mean cubic meters of wood per square meter of stream (m^3/m^2). Differences in wood coverage between streams was tested using F test to compare two variances after a Shapiro-Wilk normality test, and followed by a two-sample T test. Differences in light were tested using a Levene's Test for Homogeneity of Variance after a Shapiro-Wilk normality test, and followed by a Mann-Whitney-Wilcoxon test. Although reaches were nested (Hurlbert 1984) within streams, the amount of wood covering (m^3/m^2) and the amount of light transmitted (log %) between the reaches was also tested as this was the scale of data used for subsequent regression analysis. Differences between reaches were tested using one-way analysis of variance (ANOVA) with reach as a factor using raw data. Tukey's honestly-significant difference test followed to assess significant differences between reaches when significance was observed. The significance of all statistical tests was interpreted using a critical p-value of <= 0.05. All analysis was conducted using R Statistical Software (R Core Team, 2016).

3.3. Results

Effectiveness of bridgewood shading relative to other sources

A significant negative relationship existed between increasing cover from bridgewood and the transmission of sunlight to the stream surface. Densiometer estimates of the percentage of bridgewood cover accounted for 40% of the variability in stream light (Table 3.1). Generalized linear regression using the screened, log-transformed stream light data also revealed streamside foliage as a significant regulator of light, with increasing cover equating to lower PAR. Bridgewood and streamside foliage elicited similar responses in stream light as every once percent increase in either cover type caused a one percent decrease in stream light at the stream surface (Table 3.1). However, streamside foliage cover explained slightly less (R^2=0.38) of the variation in PAR reaching the stream surface than bridgewood. In contrast, percent cover from standing wood did not contribute significantly to explaining variability in stream PAR (Table 3.1). Generalized linear regression using the unscreened (all points where more than one shade source was present at measurement location included) shade and light data exhibited additive rather than interactive shading between shade sources in the study system (Figure 3.4), as the slope of the relation matched single shade source models (Table 3.1).

Table 3.1. Generalized linear regression model summary for variables predicting the percentage of available mid-summer photosynthetically active radiation (PAR) transmitted to headwater streams two years after a wildfire in central interior British Columbia, Canada. Relationships significant at the 0.05 level are in bold.

Model Predictor	Coefficient (SE)	Observations	Adjusted R2	Residual Std. Error	F Statistic	Log Likelihood	Akaike Inf. Crit.
Shade from bridgewood	**-0.01***** (0.002)	44	0.40	0.39 (df = 42)	30.01*** (df = 1; 42)	-20.44	Δ 21.72
Shade from foliage	**-0.01***** (0.003)	25	0.38	0.38 (df = 23)	15.70*** (df = 1; 23)	-10.97	Δ 11.01
Shade from standing wood	-0.003 (0.003)	17	-0.01	0.20 (df = 15)	0.91 (df = 1; 15)	3.52	Δ 0.99
Shade from all sources	**-0.01***** (0.001)	140	0.41	0.38 (df = 138)	96.40*** (df = 1; 138)	-62.94	Δ 72.17

*p<0.1; **p<0.05; ***p<0.01
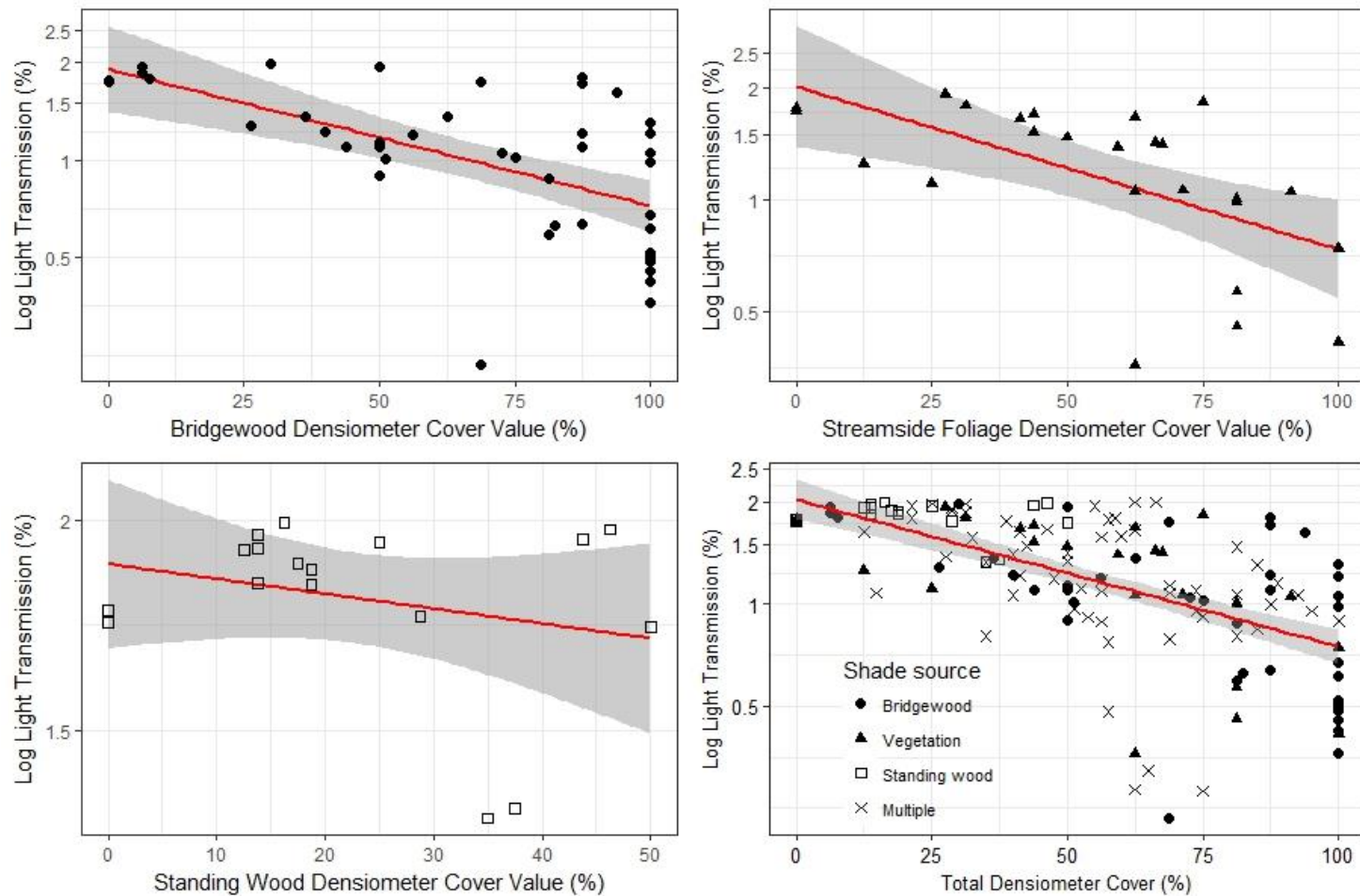
Figure 3.4. The amount of light reaching the stream decreases as shading increases. Linear regression analysis on screened data depicts the additive effect of shade sources on the percentage of photosynthetically active radiation (PAR) transmitted to the stream surface in a small, sub-boreal headwater system two years post-wildfire in central interior British Columbia, Canada. Shading indicates 95%confidence interval.

Quantity of bridgewood shading along streams

A significant negative relationship existed between bridgewood quantity and light transmission to the stream surface (Figure 3.5), further illustrating the shading capacity of bridgewood. The generalized linear regression analysis revealed the mean cubic meters of wood per square meter of stream accounted for 55% (Adjusted R^2=0.55) of the variability in stream light transmitted to the stream reaches (-4.2, SE 1.45, t-value -2.9, $p<0.05$).
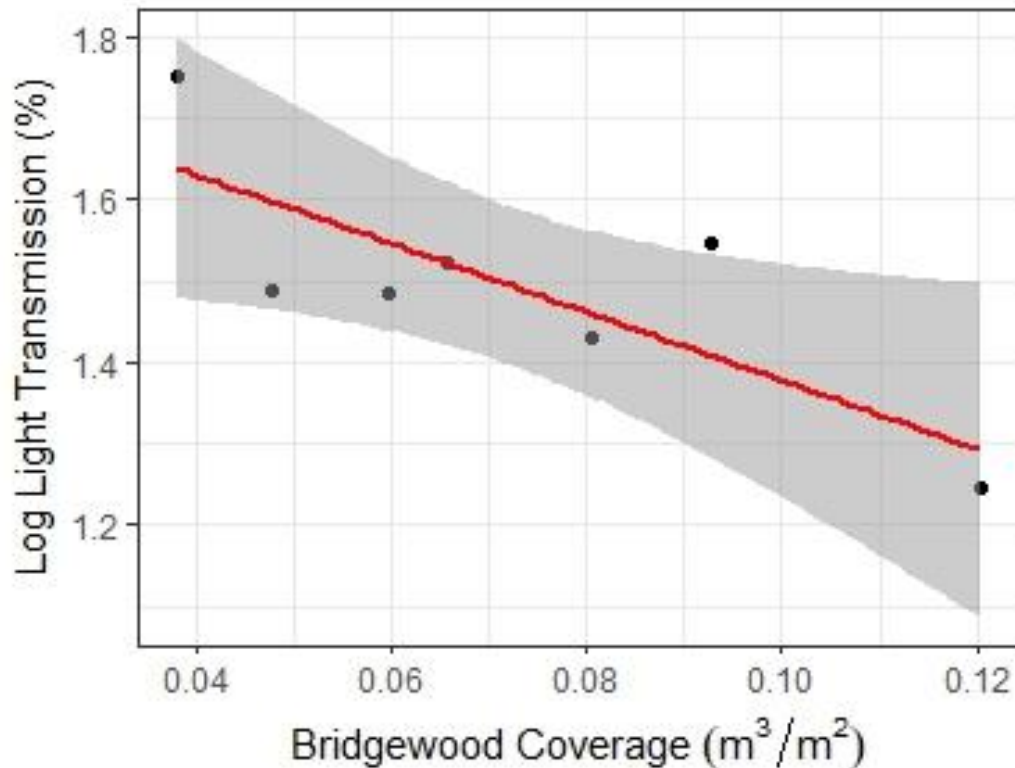
Figure 3.5. **Light reaching the stream surface decreases with increasing quantity of bridgewood above the stream. Bivariate generalized linear regression analysis depicts the measured effect of mean cubic meters of bridgewood per square meter of stream on the percentage of photosynthetically active radiation (PAR) transmitted to the stream surface in a small, sub-boreal headwater system two years post-wildfire in central interior British Columbia, Canada. Shading indicates 95%confidence interval.**

The assessment of spatial heterogeneity in light and quantity of wood between the reaches revealed mixed results (Table 3.2). Overall, light transmission was significantly higher (W = 3223, p-value <= 0.05) within Stream 1 (36.7% ± 3.3) than at Stream 2 (27.23% ± 3.9). However, the accumulation of bridgewood over Stream 1 (0.07 m^3/m^2) did not differ (t = -0.43, df = 5, p > 0.05, 95% CI [-0.67, 0.05]) from that over Stream 2 (0.08 m^3/m^2). There was also no significant difference in the quantity of bridgewood covering the stream surface (F value = 0.52, df =1, p> 0.05) at the reach-scale. However, there was a significant difference between the reaches in light transmission (F value = 4.24, df = 6, p <0.05), indicating the importance of other sources of shade, beyond bridgewood, influencing light transmission. The stream surface within Reach 4 received significantly more light than Reach 1 (28.02%, 95% CI [0.57, 55.47], p <0.05), Reach 3 (29.44%, 95% CI [2.31, 56.57], p<0.05), and Reach 7 (38.63%, 95% CI [11.50, 65.76], p<0.05, Table 3.2).

Table 3.2 **Summary of variability in bridgewood accumulation and light transmitted to headwater streams draining a sub-boreal pine-spruce ecosystem of central interior British Columbia, Canada. Reaches with the same letter are not significantly different in mean light transmission. Streams were sampled two years post-fire and did not significantly differ in wood accumulation.**

	Reach	Channel area (m^2)	Bridgewood volume (m^3)	Bridgewood Coverage (m^3/m^2)	Mean light transmission (%)	Tukey Groups*
Stream 1	1	13.43	0.80±0.18	0.06	28.26±6.66	B
	2	15.60	1.45±0.82	0.09	35.07±5.49	AB
	3	12.60	1.01±0.27	0.08	26.84±5.66	B
	4	15.10	0.57±0.15	0.04	56.29±7.08	A
Stream 2	5	10.80	0.71±0.34	0.07	33.28±6.49	AB
	6	9.13	0.43±0.27	0.05	30.16±9.29	AB
	7	10.00	1.20±0.74	0.12	17.65±3.75	B

*Note: Groups according to probability of means differences and alpha level (0.05).

Spatial heterogeneity existed in sources of stream shade as shading was dominated by either bridgewood or streamside vegetation. Overall, stream shade was primarily (33.44% ± 2.94) provided by bridgewood rather than streamside deciduous foliage (20.05% ± 2.34) and residual standing wood (5.60% ± 0.83). Significantly more wood (W = 3142, p<0.05) provided cover for Stream 1 (36.6% ± 3.9) than Stream 2 (24.8% ± 4.3, Figure 3.6). In contrast, significantly more (W = 1459.5, p<0.05) stream

shade was derived from streamside foliage within Stream 2 (31.9% ± 4.1) than Stream 1 (10.9% ± 2.3). The amount of shade contributed by standing wood did not differ between the streams (W = 2786, p = 0.35) but did between reaches (F value = 13.74, df = 6, p <0.05). Significantly more stream surface was shaded by standing wood within Reach 3 (17.02% ± 3.66) and 4 (12.70% ± 2.06) than all the other stream reaches (Table 3.3), and these areas did not significantly differ from each other (-4.33, 95% CI [-11.95, 3.3], p<0.05). Similar patches in the amount of cover offered by bridgewood and streamside foliage within Stream 1 and 2, respectively also existed (Table 3.3).

Table 3.3 Summary of variability in the amount of post-wildfire, stream shade within two headwater streams a sub-boreal pine-spruce ecosystem of central interior British Columbia, Canada. Estimates of shade, by source, were derived using an angular canopy densiometer (ACD) at the stream surface. Reaches with the same letter are not significantly different in percentage of cover by source. Both streams were sampled during mid-summer, two years post-fire.

	Reach	Mean bridgewood densiometer cover (%)	Tukey Groups* (bridgewood)	Mean streamside foliage densiometer cover (%)	Tukey Groups* (streamside foliage)	Mean standing wood densiometer cover (%)	Tukey Groups* (standing wood)
Stream 1	1	53.24±7.30	A	12.83±5.35	BC	0.00	B
	2	16.79±5.07	BC	27.02±5.44	B	0.00	B
	3	45.24±8.46	AB	2.80±1.40	C	17.02±3.66	A
	4	30.39±8.11	ABC	0.00	C	12.70±2.06	A
Stream 2	5	27.26±6.94	ABC	15.29±4.13	BC	4.23±1.41	B
	6	33.81±8.75	ABC	27.38±7.71	B	2.92±1.28	B
	7	13.27±6.39	C	53.12±6.29	A	3.04±0.92	B

*Groups according to probability of means differences and alpha level (0.05).
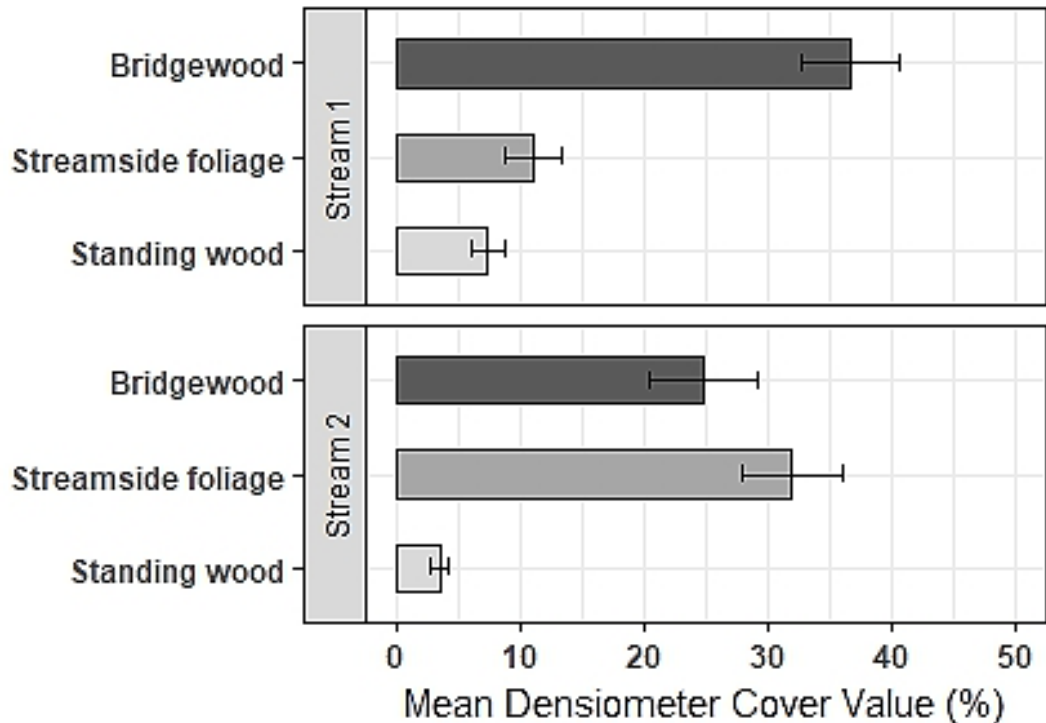
Figure 3.6.   **Spatial heterogeneity in the amount of post-wildfire shade by respective shade source, between two headwater streams in central interior British Columbia, Canada. Shade values were estimated by partitioning shade cover from each source within each cell of an angular canopy densiometer (ACD). Error bars denote one standard error from the mean.**

3.4. Discussion

Channel bridging, fire-recruited trees significantly reduce incoming solar radiation to the stream surface in the post-fire period. A specific capacity of bridgewood accumulations in decreasing stream solar radiation was detected using both percent overhead cover and overall wood quantity data. At a fine scale these wood pieces can be quantitatively comparable to deciduous understorey vegetation, a recognized key regulator of solar radiation following stand-replacing disturbance events, in reducing the amount of photosynthetically active radiation (400–700 nm wavelength) reaching the stream. Both shade sources elicited an equivalent reduction in the percentage of incoming stream light reaching the stream for each unit increase in shade at the scale of an individual location within a stream. Stream surface light transmission also declined

significantly with an increasing quantity of bridgewood for a given area of the stream channel, with over half of the variability in light explained by the reach-scale amount of wood lying above the stream surface. Solar radiation is the key factor determining temperature and biota in aquatic ecosystems (Beschta 1997; Kelly et al. 2003; Warren et al. 2016). Accordingly, accumulations of bridgewood have the potential to influence primary productivity, stream temperature, microclimate, and thus stream communities in the immediate post-fire period through their shading capacity.

Patches of bridgewood can translate to local and patchy decreases or absence in primary production. My study found evidence bridgewood has an effect on PAR, the spectrum of sunlight which regulates periphyton standing stocks (Wagner et al. 2015; Warren et al. 2013; Eminson & Moss 1980). Therefore areas of formerly forested stream where more wood (by number of falling trees) is recruited and bridges stream reaches could conceivably contain less periphyton in the immediate post-fire period due to the shading capacity of the wood pieces. The importance of burnt legacy wood for localized primary production in post-fire landscapes has been documented in terrestrial ecosystems (Marañón-Jiménez et al. 2013; Goldin & Hutchinson 2015) and deserves similar consideration in forested streams.

Wildfire-driven bridgewood could also potentially ameliorate or intensify the effects of canopy removal on stream microclimate in the post-fire period. Given the estimated shading capacity of wood in this study, that solar radiation is the primary determinant of water temperature, and that even small increases in water temperature can cause a shift in overall species composition, bridgewood could feasibly alter the abundance and distribution of thermally sensitive species and the composition of aquatic invertebrate communities due to the wood pieces overall intercepting solar radiation. The ameliorating effect of wood lying above the stream surface on stream temperature, therefore stream communities, following forest canopy removal has been suggested (Haggerty et al. 2004; Rex et al. 2012). However, blackened wood in burned areas possesses a lower albedo relative to unburned wood (Burles & Boon 2011). Thus, alternatively fire-recruited bridgewood could potentially absorb more radiative energy from incoming shortwave radiation and result in greater longwave radiation emitted to the stream surface, thus exacerbating post-fire stream heating. As such, whether fire-toppled wood mitigates or exaggerates the effects of wildfire on stream temperature merits further research.

Although evidence for the extent to which bridgewood affects incoming solar radiation was found, there are several ways this study could have been improved. The methodology used involved deploying a highly accurate PAR sensor, however the readings were taken as one-time, spot measurements rather than a deployment of longer-term data loggers. This no doubt substantially increased the inherent variability of incident PAR. Likewise, these spot measurements were taken solely at the stream surface below the stream banks, without a direct measurement of fully unshaded PAR outside the channel. As fully unshaded PAR was not directly measured it was estimated, thereby potentially altering model accuracy. Pairing instream measurements with those taken immediately beside the stream would have strengthened the study design by capturing total possible incoming PAR. Although the use of an ACD in this study aimed to encapsulate the offset of light attenuation, directly comparing an ACD cover value with a PAR meter recording has to my knowledge never been attempted, and could entail inherent limitations. The efficacy of correlating cover values derived from an ACD with PAR meter recordings warrants further study as the effect of spatial offset, between the location of incoming sunlight associated with a light recording and the location of shade directly related to the densiometer measurement location, likely caused some full transmission values to correspond with full shade; values omitted during data screening and thereby reducing sample size.

Future patterns of stream light availability are linked to fire activity as riparian forests are at an increasing risk of not only defoliation by wildfires, but insect attack with rising global temperatures (Running 2006; Westerling et al. 2011; Raffa et al. 2008). Although non-target trees covered the streams in this study, evidence was found these trees were affected by the overlap of insect outbreak and wildfire (Chapter 2) and a quantitative relationship exists between these wood pieces and a proxy for stream photosynthesis (sunlight). It is clear that changes to aquatic primary production and temperature profiles result from the complete removal of riparian vegetation in the riparian zone. As slight changes in water temperature can shift stream communities, thermal buffers or amplifiers to streams have the capacity to alter community composition. Ameliorating or intensifying effects of residual, burnt bridgewood accumulations could be an important for thermally sensitive species such as salmonids who seek thermal refugia following wildfires when the flux of sunlight reaching streams is highest (Isaak et al. 2010). Although stream temperatures are a result of the intricate

exchanges between solar radiation and local hydrology (Beschta 1997), findings from my study indicate that bridgewood detectably intercepts the increased solar energy following a disturbance in the riparian zone. In a similar northern sub-boreal interior watershed, Rex et al (2012) suggested accumulations of bridgewood, in combination with deciduous riparian understory vegetation, were responsible in reducing air tempertures 0.5 m above the stream by intercepting incoming solar radiation. Fire-driven bridgewood yet can conceivably have an effect, similar to what has been documented for standing wood (Leach & Moore 2010), on above-stream microclimates in wildfire-disturbed watersheds. Because the shading provided by bridgewood is not dependent on foliage, its shading capacity could be especially pronounced in the window of time before the recovery of deciduous understory after a wildfire, but also seasonally i.e. before full-leaf-out in the growing season. This would make bridgewood shading different from streamside foliage and a fully developed riparian canopy. because the shading does not depend on having leaves Overall, whether the presence of these understudied materials can alter stream communities and microclimate warrants further study and will improve our understanding of how landscape scale terrestrial processes are drivers of localized and watershed-scale aquatic primary productivity and thermal variability.

Chapter 4.   General Discussion

Pre-fire tree death enhanced post-fire tree topple, consequently reducing stream light in the northern sub-boreal forests sampled during this study. Multiple disturbances (insect outbreak, wildfire) interacted synergistically in altering downed wood pools as trees killed by beetles, or other factors, before the occurrence of a wildfire were twice as likely to be toppled by the fire. Because roughly a third of the tree stems that toppled in the riparian-stream interface were recruited to the narrow streams as bridgewood, enhanced tree topple equated to enhanced bridgewood accumulation. In spruce dominated riparian zones, the accumulated bridgewood significantly decreased incoming solar radiation to the stream surface in the immediate post-fire period; a timeframe when the amount of sunlight reaching small streams is highest. Therefore, pre-fire mortality, at least within spruce stands, indirectly reduced post-fire stream light by increasing tree topple in the riparian zone.

Wood is a biological pathway between land and water and, in a landscape affected by a sequence of bark beetles and wildfire, the abundance of wood within streams in the immediate post-fire period was found to be enhanced and a quantitative relationship existed between those wood pieces and a proxy for stream photosynthesis (sunlight). Although the exact cause of pre-fire mortality within spruce dominated forests remains unclear, evidence of pre-fire attack by MPB was found, suggesting many spruce were killed collaterally during the landscape-scale MPB outbreak which occurred pre-fire. Regardless of cause of mortality, the more spruce trees which were killed pre-fire, the more bridgewood resulted from enhanced fire-toppling. The solar intercepting effects of residual, burnt bridgewood accumulations could be important for thermally sensitive species such as salmonids, especially in the study area where it has been reported summer water temperatures in many streams already reach levels too high for salmonids (British Columbia Ministry of Environment 2006). However, because the amount of wood that enters the water is dependent upon channel width (Hassan et al. 2005; Johnston et al. 2011) it is worth noting these implications lie solely within headwater streams where bridgewood is possible due to the small channel width relative to trees height. Wider (> 3m) streams additionally have a greater stream surface area exposed to sunlight, providing further constraints on the extent of these results.

A biological link between eruptions in bark beetle populations and stream ecology has remained elusive (Costigan et al. 2015; Rhoades et al. 2013; Rinella et al. 2009; King et al. 2013), yet my study provides evidence of a link through a beetle-fire-streamwood pathway in headwater streams. Increasing future global temperatures brings not only increased possibility that watershed-scale events such as beetle outbreaks, fire, and drought will overlap in time and space (Raffa et al. 2008; Andrus et al. 2016) but also increased solar loading on stream ecosystems (Bixby et al. 2015). For that reason, an increasing extent and severity of bark beetle mortality prior to a wildfire within stream corridors has the potential to affect stream ecology, through enhanced bridgewood delivery and the shade it provides. This carries the implication that bark beetle outbreaks can vicariously shape stream algal communities and microclimates because of the amount of wood they enable subsequent wildfires to provide to small forested streams. Whether the presence of these understudied materials can alter stream communities and microclimate warrants further study and will improve our understanding of how landscape scale terrestrial processes are drivers of localized and watershed-scale aquatic primary productivity and thermal variability.

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