Vegetation responses following mountain pine beetle attack in lodgepole pine forests of west-central Alberta

by

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Abstract

Natural disturbances are an integral part of forest ecosystems and drive successional change. The boreal forest is adapted to stand-replacing fires, which have different ecological impacts than less severe disturbances, such as insect attacks. In recent years, mountain pine beetle (MPB), a bark beetle native to western North America, has undergone an unprecedented range expansion into lodgepole pine forests in west-central Alberta. MPB indirectly influences understory resources and vegetation, but does not necessarily provide suitable conditions for pine regeneration. Lodgepole pine typically requires open, disturbed areas to regenerate, where there are suitable regeneration seedbeds, limited competition, and sufficient heat to open serotinous or semi-serotinous cones. This study explores how vegetation in forests in Alberta will respond to MPB attacks.

To gauge how forests in Alberta will respond, we visited lodgepole pine-dominated, grey-attack stage, high severity MPB-killed stands throughout a variety of ecosites within west-central Alberta. We collected data to assess the potential for natural regeneration and used model selection to examine which factors best explained pine regeneration. We also conducted an experiment with an untreated control, medium and high severity simulated MPB-attack, and simulated salvage logging to assess responses of understory vegetation seven years after disturbance. We used univariate and multivariate analysis to examine differences in responses of understory vegetation among these treatments.

Less than half of the post-MPB sites assessed had any evidence of pine regeneration. Rich quality sites, broadleaf advance regeneration, and spruce basal area negatively impacted pine regeneration. These factors likely resulted in a shading of the forest floor and competition with seedlings for resources. Some pine seedlings were found in poorer quality sites, especially those with pre-existing pine advance regeneration. Cones in richer sites were more strongly serotinous and will likely create a forest floor seedbank, while cones in poorer sites had less strongly serotinous cones that may open with sufficient heat from solar radiation.

The simulated-MPB attack experiment showed that the severity of disturbance determined the magnitude of vegetation changes. Only simulated salvage logging resulted in immediate changes. Seven years post-treatment, vegetation richness and diversity increased along the gradient of treatment severity, while total cover had returned to pre-treatment levels. This was accompanied by a change in species composition; feathermosses were indicative of the untreated control, shade-tolerant species increased their relative abundance in the medium severity (~50%) simulated MPB treatment, both shade-tolerant and -intolerant species increased their relative abundance in the high severity (100% kill) simulated MPB treatment, and disturbance-adapted, shade-intolerant species (including lodgepole pine) were indicators of salvage logging.

High severity MPB-attack provided a better understory light environment for pine regeneration, but this effect was negated by competitive effects arising from the responses of understory vegetation and continued overstory shading by standing dead and residual live trees. Richer sites are less likely to experience pine regeneration, and higher severity MPB attacks result in more drastic changes in vegetation cover and composition that can result in pine seedlings being outcompeted. Thus, successional pathways may be altered in richer and in high mortality sites; these sites should be prioritized for lodgepole pine rehabilitation in Alberta. Poorer sites that experience some pine regeneration and sites with less severe attacks that have minimal understory impacts may remain on their current successional trajectories. These results can be used to inform management decisions regarding the need for the rehabilitation of lodgepole pine sites in Alberta.

Preface

Some of the data collection for this thesis was done so collaboratively with others at the University of Alberta. Some of the data included in Chapter 2 were collected in 2014; data collection was led by Lori Schroeder, with assistance from Christina Stinn, Bryanna Jeske, and Sean Robbins. The remainder of data included in Chapter 2 were collected in 2015 and 2016; data collection was led by myself, with assistance from Annika Clark (2015) and Kaitlyn Trepanier (2016). Some of the data included in Chapter 3 were collected by others: data collection in 2008 to 2010 was led by Anne McIntosh, canopy cover data in 2012 and 2013 were collected by Anne McIntosh and Ellen Macdonald, tree data collection in 2013 was led by Chris Williams, and finally, the vegetation, nutrient, and canopy cover data collection in 2014 was led by Lori Schroeder, with assistance from Christina Stinn, Bryanna Jeske, and Sean Robbins.

Some of the data found within Chapter 3, including everything up to and including 2010, was previously published. The publication details are as follows:

McIntosh, A.C.S., and Macdonald, S.E. 2013. Short-term resistance of ecosystem properties and processes to simulated mountain pine beetle attack in a novel region. Ecosphere **4**(6): 68. doi:10.1890/ES12-00344.1.

Dedication

I would like to dedicate this to my family, who have been a continual source of support.

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Chapter 1: General Introduction

Forest disturbances

Natural disturbances are an integral part of forest ecosystems and drive successional change. The severity of the disturbance plays an important role in how much the forest changes and in subsequent development (Buma et al. 2013). Forests are adapted to the type of natural disturbance regime they normally experience; disturbances can vary in size and intensity, from being a less intense stand-releasing/modifying disturbance to a more intense stand-replacing/initiating disturbance. Stand-replacing fires are the dominant disturbance regime throughout the boreal forest in North America (Johnson 1992), including in Alberta.

More severe disturbances result in very different forest conditions than do low severity disturbances. Fire and harvesting act as stand-replacing disturbances that have large impacts on resource availability, remove the overstory, and may increase vegetation heterogeneity (Pec et al. 2015). Less severe disturbances such as windthrow, insect outbreaks, and canopy dieback influence forest dynamics in older stands by removing dominant individuals, increasing resource availability; this in turn affects understory vegetation, likely increasing the number of species able to grow in that environment (Hart and Chen 2006). Insects act as a stand-releasing disturbance (Axelson et al. 2010) that kills the overstory but does not directly disturb the understory or forest floor (Burton 2008). Forest changes occur more slowly after low severity disturbances, such as bark beetle attacks, that do not promote immediate establishment of seedlings (Waring and Pitman 1985), compared to high severity disturbances that often result in more immediate changes. Nutrients return to the soil slower after insects than after fire, and residual vegetation is left behind to help shape the new forest stand (Stone and Wolfe 1996, Pec et al. 2015).

Mountain pine beetle

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Coleoptera: Scolytidae; MPB) is a destructive, coniferophagous bark beetle native to western North America. MPB ranges from northern Mexico to northwestern British Columbia (BC), and from the Pacific coast to South Dakota in the US (Carroll and Safranyik 2004) and the eastern edge of the Rockies in Canada

(Ono 2004). It has historically been limited to small and scattered outbreaks in western North American pine forests, reaching no further than the southern portion of the eastern slopes of the Rocky Mountains in Canada, near the Alberta-BC border (Ono 2004), and parts of southern Alberta (Nealis and Peter 2008). This bark beetle has co-evolved with conifer species in North America, including lodgepole pine (*Pinus contorta* Dougl. ex Loud.), which is widely distributed and is the most susceptible species. The range of MPB was previously constrained by natural barriers, including the northern Rocky Mountains (Raffa et al. 2008, Axelson et al. 2009, Hubbard et al. 2013, Cigan et al. 2015), where a change in continental climate previously prevented beetle expansion into Alberta. In moist coastal regions such as BC, where fire is not prevalent (Anhold et al. 1996), MPB has been an important component of the disturbance regime, acting as a thinning agent and having an important effect on forest structure (Wilson 2004).

Fungi, including three blue stain fungi that have a symbiotic relationship with the beetle, *Grosmannia clavigera*, *Leptographium longiclavatum*, and *Ophiostoma montium*, are transferred to trees during MPB attacks and these help to defeat the host defenses (Rice et al. 2008, Goodsman et al. 2012). The blue stain fungi are carried by MPB from tree to tree, and the spores from these fungi germinate quickly and penetrate cells in the trees' xylem and phloem; this not only disrupts transpiration and stops the trees defensive resin production, but also physically conditions the phloem for larvae, contributing to the beetles' diet (Carroll and Safranyik 2004, Hubbard et al. 2013). Adult beetles consume the phloem as they build egg galleries (Hubbard et al. 2013) and larvae consume the phloem circumferentially around the tree, girdling it, and overwinter in it before pupating in the spring and taking flight as adults mid-summer (Safranyik et al. 2002). While the tree remains green and healthy looking for the first year after MPB attack (green-attack), within 2-3 years pine needles turn red (red-attack), and by 4-5 years after attack, the foliage is lost (grey-attack).

During endemic MPB attacks the beetles target older, less resistant, low-vigour trees with thin phloem; this limits brood production and maintains low endemic population levels (Amman 1972, Taylor and Carroll 2004). These trees may be diseased, lightning-struck, or senescing (Klutsch et al. 2009). Although larger diameter trees have thicker phloem, which provides better habitat (Klutsch et al. 2009), larger trees are often more vigorous and able to produce more resin to protect themselves from insect attacks (Safranyik et al. 2002, Carroll and Safranyik 2004).

Drought and stress can weaken these larger diameter pine trees, making them more susceptible to MPB, allowing a proliferation of MPB (Safranyik et al. 2002). Under ideal conditions for the beetle, populations can grow to the point where they can easily mass attack vigorous, large diameter trees with thick phloem and adequate moisture content, exhausting the trees' defenses and killing them, perpetuating the cycle and resulting in an epidemic (Amman and Schmitz 1988, Anhold et al. 1996, Safranyik et al. 2002, Carroll and Safranyik 2004, Ono 2004, Taylor and Carroll 2004, Whitehead et al. 2007, Axelson et al. 2009). During epidemics, bark beetles go from selectively killing stressed or old, weak trees to overcoming tree defenses and killing healthy mature trees as well (Stone and Wolfe 1996, Carroll and Safranyik 2004, Axelson et al. 2009).

The main conditions required for MPB outbreaks are suitable temperatures that increase brood survival and large expanses of homogeneous susceptible stands, which allow for increased MPB dispersal (Amman and Schmitz 1988, Whitehead et al. 2004). Forest management activities that are designed to sustain a long term cut, including selective harvesting and effective fire suppression techniques (Nealis and Peter 2008), may influence susceptibility of forests to MPB; these activities have created large tracts of mature, even-aged pine forests in BC and Alberta, mostly between 80 to 120+ years old, which are less resistant to the blue stain fungi that the beetles carry and are ideal MPB habitat (Carroll and Safranyik 2004, Ono 2004, Raffa et al. 2008, Axelson et al. 2010, Hubbard et al. 2013). Winter air temperatures may help control beetle survival (Rhoades et al. 2013), but as mild winters have become more frequent and the landscape in western Canada is covered by susceptible pine stands, ideal MPB conditions have been met (Ono 2004, Taylor and Carroll 2004, Whitehead et al. 2004, Wilson 2004). After upper atmospheric winds blew MPB across the Rocky Mountains into Alberta in 2006 (Natural Resources Canada 2017), the suitable conditions described above allowed the beetles to survive and expand their distribution further east into west-central Alberta (Nealis and Peter 2008). MPB has also expanded further north within BC (Ono 2004). This has resulted in not only the largest known MPB outbreak in BC in recorded history (Axelson et al. 2009), but a continental-scale expansion in North America at new latitudes and elevations, including an unprecedented wave into Alberta (Nealis and Peter 2008), earning it the title of 'native invader' (Simberloff 2011). Millions of hectares (ha) of western North America's pine forests have been affected so far (Nealis and Peter 2008, Natural Resources Canada 2017). While research has been conducted on the impacts of MPB in its historical habitat, it is unknown how forests in Alberta will respond to this new disturbance.

Changing disturbance regimes

While lodgepole pine forests throughout the North American boreal forests are adapted to stand-replacing fires (Johnson 1992), MPB has also been an important part of BC's disturbance regime (Nealis and Peter 2008, Axelson et al. 2010), but this is not the case in Alberta. The impact of this new MPB disturbance in Alberta may have long term effects on the future of these forest stands. Unlike after fire, overstory responses to MPB are not immediate and the forest floor is not directly impacted (Collins et al. 2011); thus, suitable pine regeneration microsites (e.g. mineral soil) may not be available after MPB. Differing disturbance types can result in different understory communities (Rees and Juday 2002) due to legacy vegetation that was not impacted by MPB (Edburg et al. 2012) and changes in resource availability that allow new species to establish. Responses of understory communities can have long lasting effects on forest communities (Chapin et al. 2004); pine can be outcompeted, hindering germination and establishment, while shade-tolerant species may be able to flourish (Collins et al. 2011). Additionally, disturbances may interact with each other in boreal lodgepole pine forests; for example, insect attacks increase fuel loads, setting the stage for high intensity fires (Lotan et al. 1985). This can result in a compound disturbance that will result in different disturbance effects; for example a MPB attack followed by fire could result in post-fire stands with greater canopy openness or if the fire was of higher severity it could have consumed the seedbank (Edwards et al. 2015). MPB epidemics in Alberta might, therefore, alter the forest structure of stands as well as their future successional trajectory.

As winters become milder, beetle fecundity, and therefore population growth can increase while beetle winter mortality decreases (Morris et al. 2015). This is especially concerning since MPB is not only a new threat to lodgepole pine forests within Alberta, but has successfully expanded into jack pine (*Pinus banksiana* Lamb.) forests in eastern Alberta; this puts susceptible pine species throughout the entire Canadian boreal forest at risk from this new disturbance (Cullingham et al. 2011). Although the future of MPB within this new range east of the Rocky Mountains is unknown, milder winters resulting from climate change will likely allow MPB to remain in this new habitat (Safranyik et al. 2010), modifying the disturbance regime of lodgepole pine (and possibly other pine) forests throughout North American boreal forests (Nealis and Peter 2008). Forest insect disturbances are anticipated to increase in frequency and intensity as the climate warms (Dale et al. 2001), resulting in large ecological changes (Logan et al. 2003). To combat potential impacts from this expanding disturbance agent, salvage logging operations have been implemented in many MPB-attacked stands, but not all stands will receive this treatment (Astrup et al. 2008). Lodgepole pine are known to regenerate prolifically following stand-replacing disturbances such as fire and clearcutting, but it is unknown how canopy death resulting from MPB attack in Alberta will affect lodgepole pine regeneration in unmanaged stands, and therefore the future forest dynamics of these stands. Understanding what is happening on the ground post-MPB, both in terms of tree regeneration and understory vegetation, can help shed light on the future vegetation dynamics in these stands.

Lodgepole pine regeneration

Lodgepole pine is one of MPB's preferred host species. It is widely distributed throughout western North America, ranging from Alaska and the Yukon to southern California, and from the Pacific coast to areas east of the Rockies (Lotan and Critchfield 1990); lodgepole pine dominated forests cover an area of 5.2 million hectares (ha) in the USA and 19.8 million ha in Canada (Amman and Schmitz 1988, Lotan and Critchfield 1990). It can be found at elevations from sea level to 3500 meters (Amman and Schmitz 1988). This species has serotinous or semi-serotinous cones, which require heat to break the resin bonds and release seed. Millions of seeds per ha may be released simultaneously onto a prepared seedbed following a disturbance, the majority landing within 60m, resulting in the regeneration of pine as a dense monoculture (Lotan et al. 1985, Lotan and Critchfield 1990). These seeds can stay viable for a prolonged period of time in closed cones (Lotan et al. 1985, Lotan and Critchfield 1990, Gärtner et al. 2014) embedded or buried in the forest floor, while viability of seeds in arboreal closed cones decreases quickly after 15 years of age (Teste et al. 2011b).

Lodgepole pine typically needs disturbed areas to regenerate due to its shade-intolerance (Lotan and Critchfield 1990). Disturbed mineral soils in open areas with plenty of light provide excellent germination microsites (Vyse and Navratil 1985, Lotan and Critchfield 1990). Because

MPB attacks do not provide these conditions they are likely to impact forest regeneration with subsequent effects on stand age structures, species composition, canopy cover, and species abundance (Sibold et al. 2007). While it is often thought that a lack of stand-replacing disturbance results in pine being replaced by later successional species (Lotan and Critchfield 1990), in some parts of lodgepole pine's range it is not highly serotinous (Muir and Lotan 1985) and can regenerate under its own canopy resulting in self-perpetuating lodgepole pine stands (Despain 1983, Parker 1986); indeed, lodgepole pine has been observed to regenerate following MPB (Stuart et al. 1989, Sibold et al. 2007, Axelson et al. 2010). However, other studies have found that, following MPB attacks, lodgepole pine was replaced by shade-tolerant species that had existed in the stand as a suppressed sub canopy or advance regeneration (Roe and Amman 1970, Heath and Alfaro 1990, Axelson et al. 2009). Studies have shown that MPB killed stands experience pulses of establishment of shade-tolerant species or lodgepole pine, creating complex, multi-aged stands (Sibold et al. 2007, Axelson et al. 2009, 2010). This may also vary by attack severity and the nutrient and moisture regime of an area; xeric sites and high severity MPB outbreaks (>80% canopy mortality) have resulted in pine regeneration and establishment under its own canopy, while submesic sites or low severity outbreaks (<50% canopy mortality) have resulted in mixed stands or stands dominated by shade-tolerant species (Sibold et al. 2007, Clason et al. 2014).

There is variation in the degree of serotiny of lodgepole pine and this will have important implications for regeneration post-MPB. It is therefore important to better understand the serotiny in MPB-attacked lodgepole pine stands in Alberta, since this may indicate if natural regeneration is possible with sufficient ground disturbance after MPB-attack. In MPB-killed stands, some pine seeds remain in closed cones attached to dead trees in the canopy, while some seeds may be released from arboreal cones (Teste et al. 2011a). Additionally, some branches are typically broken shortly after tree death, resulting in closed cones falling to the ground, some of which may open on the ground, releasing seed, while other cones remain closed and become buried, creating a seed bank in the forest floor (Teste et al. 2011a). As the degree of serotiny can vary between and within populations, and the cones in the canopy are not exposed to high temperatures, cone responses from different stands in Alberta may vary, possibly resulting in limited opportunities for cones of highly serotinous populations to open and for regeneration to take place naturally. Once cones are buried in the forest floor, soil disturbance would expose cones and create a suitable seedbed for regeneration, and at the same time, increase soil surface temperatures so that cones open (Teste et al. 2011b). Some pine populations in MPB's native range may already be adapted to MPB and are able to regenerate after MPB attack (Stuart et al. 1989, Sibold et al. 2007, Axelson et al. 2010), likely due to lower serotiny; thus, it is possible that pine forests in Alberta could adapt to this new disturbance over time. However, lodgepole pine may not have a chance to regenerate on the landscape since seed viability may be lost before conditions are suitable for pine germination and establishment. As pine regeneration is extremely variable after MPB attack, it is important to discover what influences regeneration the most heavily in Alberta.

Understory vegetation responses to disturbances

Even if lodgepole pine is able to regenerate successfully in stands post-MPB, the seedlings might be outcompeted by later successional species and vegetation. Understanding the impacts of MPB on the understory in Alberta is important since understory vegetation communities not only contain the majority of plant diversity in North American boreal forests (Hart and Chen 2006), but they also have an important influence on tree regeneration by affecting availability of regeneration microsites and through the potential to outcompete pine seedlings. Changes to understory vegetation diversity, abundance, richness, and composition can therefore help shape stand dynamics following a disturbance, including ecosystem processes and overstory succession (Hart and Chen 2006, 2008, Edwards et al. 2015, Pec et al. 2015).

Although understory vegetation is not disturbed directly by MPB (Stone and Wolfe 1996), attacks may indirectly affect understory vegetation abundance, composition, and distribution because of increases in resources and a decrease in competition, which can vary with the severity of attack (Stone and Wolfe 1996, Barbier et al. 2008, Axelson et al. 2009, Pec et al. 2015). As trees are killed by MPB, gaps are created in the canopy (Stone and Wolfe 1996), and soil moisture and nutrients can increase due to fewer trees using these resources. Increased canopy openness can result in altered moisture conditions in the understory due to changes in canopy interception of precipitation, and will also lead to increased solar insolation reaching the forest floor (Axelson et al. 2009, Dhar and Hawkins 2011). Overstory removal/death also results in increased leaf litter and decreased soil temperatures (Griffin et al. 2011). Together, elevated soil moisture and solar insolation can lead to increases in decomposition and mineralization, in turn increasing soil nutrient availability (Hart and Chen 2006, Cigan et al. 2015). Needles falling from mature bark beetle-killed trees have been found to have elevated concentrations of nutrients compared to needles falling from mature uninfected trees (Morehouse et al. 2008, Griffin et al. 2011, Cigan et al. 2015); this might further increase soil nutrient availability post-MPB.

Post-disturbance forest changes can impact vegetation in a variety of ways. Shade intolerant species, such as grasses, may increase in abundance (Lotan et al. 1985), or a few native species may increase in abundance to dominate the understory, use up additional resources, and inhibit pine regeneration (Royo and Carson 2006). Richer sites tend to have more understory vegetation, which results in more competition in these sites for pine seedlings; these richer sites also tend to have more frequent and intense MPB attacks (Cole and Amman 1980), which means that the areas that are hit the hardest by MPB may be the ones with the least likely chance of regeneration. MPB-caused canopy death in Colorado resulted in changes to understory vegetation in grey attack stands (McCambridge et al. 1982). Stone and Wolfe (1996) also found changes to understory vegetation in grey attack stands in Utah, where increased light, space, moisture, and nutrient resources led to a release of existing/remaining vegetation, while also facilitating establishment of new vegetation. These vegetation responses in Utah peaked under moderate levels of mortality (Stone and Wolfe 1996). Studies by McIntosh and Macdonald (2013) and Klutsch et al. (2009) found that understory vegetation did not respond immediately, and exhibited an initial resistance to MPB attack. This apparent understory vegetation resistance may be temporary, and as stands transition into grey-attack stage, understory vegetation changes may become more apparent. Although studies have begun to emerge in Alberta concerning the response of understory vegetation to MPB attacks (McIntosh and Macdonald 2013, Pec et al. 2015), no long-term studies have yet been conducted as these stands transition into grey-attack stage.

How will lodgepole pine forests in Alberta respond to MPB?

The goal of this thesis is to gain insight as to vegetation responses in Alberta's lodgepole pine forests that have been exposed to MPB. Understanding how pine regeneration and understory vegetation will respond to MPB attacks is important not only for future forest productivity and biodiversity, but also overall ecological values. Not only are MPB attacks now more widespread and severe in BC, MPB's native range, but MPB has expanded into Alberta where the disturbance regime is now shifting from including primarily stand-replacing fire events to include MPB, which impacts the forest quite differently. Much of the research on responses of forests to MPB outbreaks done in Canada has been conducted on the western side of the Rocky Mountains, and so it is unknown how Alberta forests will respond since the climate, hydrology, and forest composition of lodgepole pine forests east of the Rockies is different than those to the west. The information contained in this thesis can help determine which MPB-killed pine stands in Alberta are most at risk of being replaced by other tree species, or of showing very poor tree regeneration, and can give us an idea of how much we can expect the understory to change after different attack intensities. This can help us determine the most likely successional trajectories of these stands, and can help guide prioritization for rehabilitation, if needed.

In the second chapter, I determine whether pine will regenerate naturally after high severity MPB-attacks in Alberta and what influences this regeneration (or lack thereof). I expected to find regeneration in areas with sufficient light to open cones and poorer sites with less competing vegetation, while I expected little to no regeneration in areas with high cover of moss. I collected data that fit into the following categories: ground influence, tree/canopy influence, advance regeneration, site influence, and cone openness. The data were collected in MPB-attacked stands representing a variety of ecosites within west-central Alberta. I used model selection to determine which factors within the above-mentioned categories best explained variation in pine regeneration among these stands.

In the third chapter, I examine differences in responses of forest understory vegetation and resources between stands in west-central Alberta that were subjected to varying severities of simulated MPB attack and salvage logging, to determine the potential forest changes that may occur under these different scenarios. I expected to find increases in resources along the gradient of increasing disturbance, accompanied by changes to understory vegetation. Stands were monitored one year prior to treatment, through seven years post-treatment. Overstory, above-ground (vegetation, ground cover, etc.), and below-ground (soil moisture and nutrient) data were collected in three different severity treatments and an untreated control, and I used univariate and multivariate analysis to examine changes occurring in the understory.

Literature Cited

Amman, G.D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. J. Econ. Entomol. **65**(1): 138.

Amman, G.D., and Schmitz, R.F. 1988. Mountain pine beetle: Lodgepole pine interactions and strategies for reducing tree losses. Ambio **17**(1): 62–68. doi:10.2307/4313420.

Anhold, J.A., Jenkins, M.J., and Long, J.N. 1996. Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. West. J. Appl. For. **11**(2): 50–53. doi:10.1093/wjaf/11.2.50.

Astrup, R., Coates, K.D., and Hall, E. 2008. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. For. Ecol. Manage. **256**(10): 1743–1750. doi:10.1016/j.foreco.2008.07.025.

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. For. Ecol. Manage. **257**(9): 1874–1882. doi:10.1016/j.foreco.2009.01.047.

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2010. Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. For. Chron. **86**(1): 87–99. doi:10.5558/tfc86087-1.

Barbier, S., Gosselin, F., and Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved-A critical review for temperate and boreal forests. For. Ecol. Manage. **254**(1): 1–15. doi:10.1016/j.foreco.2007.09.038.

Buma, B., Brown, C.D., Donato, D.C., Fontaine, J.B., and Johnstone, J.F. 2013. The impacts of changing disturbance regimes on serotinous plant populations and communities. Bioscience **63**(11): 866–876. doi:10.1525/bio.2013.63.11.5.

Burton, P.J. 2008. The mountain pine beetle as an agent of forest disturbance. BC J. Ecosyst. Manag. **9**(3): 9–13. Available from http://jem.forrex.org/index.php/jem/article/viewArticle/402.

Carroll, A.L., and Safranyik, L. 2004. The bionomics of the mountain pine beetle in lodgepole pine forests: establishing a context. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 21–32.

Chapin, F.S., Callaghan, T.V, Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G., and Zimov, S.A. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? Ambio **33**(6): 361–365. doi:10.1579/0044-7447-33.6.361.

Cigan, P.W., Karst, J., Cahill, J.F., Sywenky, A.N., Pec, G.J., and Erbilgin, N. 2015. Influence of bark beetle outbreaks on nutrient cycling in native pine stands in western Canada. Plant Soil **390**: 29–47. doi:10.1007/s11104-014-2378-0.

Clason, A.J., Macdonald, S.E., and Haeussler, S. 2014. Forest response to cumulative disturbance and stress: Two decades of change in whitebark pine ecosystems of west-central British Columbia. Écoscience **21**(2): 174–185. doi:10.2980/21-2-3686.

Cole, W.E., and Amman, G.D. 1980. Mountain pine beetle dynamics in lodgepole pine forests, Part 1: course of an infectation. USDA For. Serv. Intermountain Research Station. Research Paper **INT-89**. 56 pp.

Collins, B.J., Rhoades, C.C., Hubbard, R.M., and Battaglia, M.A. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. For. Ecol. Manage. **261**(11): 2168–2175. doi:10.1016/j.foreco.2011.03.016.

Cullingham, C.I., Cooke, J.E.K., Dang, S., Davis, C.S., Cooke, B.J., and Coltman, D.W. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. Mol. Ecol. **20**(10): 2157–2171. doi:10.1111/j.1365-294X.2011.05086.x.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., and Wotton, M.B. 2001. Climate change and forest disturbances. Bioscience **51**(9): 723–734. doi:10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2.

Despain, D.G. 1983. Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. Ecology **64**(2): 231–234. Available from https://www.jstor.org/stable/1937070.

Dhar, A., and Hawkins, C.D.B. 2011. Regeneration and growth following mountain pine beetle attack : A synthesis of knowledge. BC J. Ecosyst. Manag. **12**(2): 1–16. Available from http://jem.forrex.org/index.php/jem/article/ view/22/84.

Edburg, S.L., Hicke, J.A., Brooks, P.D., Pendall, E.G., Ewers, B.E., Norton, U., Gochis, D., Gutmann, E.D., and Meddens, A.J.H. 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. Front. Ecol. Environ. **10**(8): 416–424. doi:10.1890/110173.

Edwards, M., Krawchuk, M.A., and Burton, P.J. 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. For. Ecol. Manage. **338**: 163–175. doi:10.1016/j.foreco.2014.11.011.

Gärtner, S.M., Bokalo, M., Macdonald, S.E., and Stadt, K. 2014. Variation in post-wildfire regeneration of boreal mixedwood forests: Underlying factors and implications for natural disturbance-based management. New For. **45**(2): 215–234. doi:10.1007/s11056-013-9404-6.

Goodsman, D.W., Erbilgin, N., and Lieffers, V.J. 2012. The impact of phloem nutrients on overwintering mountain pine beetles and their fungal symbionts. Environ. Entomol. **41**(3): 478–486. doi:10.1603/EN11205.

Griffin, J.M., Turner, M.G., and Simard, M. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. For. Ecol. Manage. **261**(6): 1077–1089. doi:10.1016/j.foreco.2010.12.031.

Hart, S.A., and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. CRC. Crit. Rev. Plant Sci. **25**(4): 381–397. doi:10.1080/07352680600819286.

Hart, S.A., and Chen, H.Y.H. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol. Monogr. **78**(1): 123–140. doi:10.1890/06-2140.1.

Heath, R., and Alfaro, R.I. 1990. Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle: A case study. J. Entomol. Soc. Br. Columbia **87**: 16–21. Available from http://cfs.nrcan.gc.ca/publications?id=3074.

Hubbard, R.M., Rhoades, C.C., Elder, K., and Negron, J. 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. For. Ecol. Manage. **289**: 312–317. doi:10.1016/j.foreco.2012.09.028.

Johnson, E.A. 1992. Fire and vegetation dynamics: Studies from the North American boreal forest. *Edited by* R.S. Barnes, H.J. Birks, E.F. Connor, and R.T. Paine. Cambridge University Press. 129 pp.

Klutsch, J.G., Negrón, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., and Caissie, R. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (Dendroctonus ponderosae Hopkins) outbreak in Colorado. For. Ecol. Manage. **258**(5): 641–649. doi:10.1016/j.foreco.2009.04.034.

Logan, J.A., Régnière, J., and Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. **1**(3): 130–137. doi:10.1890/1540-9295(2003)001[0130:ATIOGW]2.0.CO;2.

Lotan, J.E., Brown, J.K., and Neuenschwander, L.F. 1985. Role of fire in lodgepole pine forests. *In* Lodgepole pine, the species and it management Symposium proceedings. *Edited by* D. Baumgartner et al. Washington State University, Pullman. pp. 133–152.

Lotan, J.E., and Critchfield, W.B. 1990. Pinus contorta Dougl. ex. Loud. *In* Silvics of North America, Agricultur. *Edited by* R.M. Burns and B.H. Honkala. Washington, DC. pp. 302–315. doi:10.1094/PHYTO-95-0284.

McCambridge, W.F., Edminster, C.B., and Morris, M.J. 1982. Herbage production under ponderosa pine killed by the mountain pine beetle in Colorado. USDA For. Serv. Rocky Mountain Forest and Range Experiment Station. Research Note **RM-416**: 1-3.

McIntosh, A.C.S., and Macdonald, S.E. 2013. Short-term resistance of ecosystem properties and processes to simulated mountain pine beetle attack in a novel region. Ecosphere **4**(6): 68. doi:10.1890/ES12-00344.1.

Morehouse, K., Johns, T., Kaye, J., and Kaye, M. 2008. Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests. For. Ecol. Manage. **255**(7): 2698–2708. doi:10.1016/j.foreco.2008.01.050.

Morris, J.L., Mustaphi, C.J.C., Carter, V.A., Watt, J., Derr, K., Pisaric, M.F.J., Anderson, R.S., and Brunelle, A.R. 2015. Do bark beetle remains in lake sediments correspond to severe outbreaks? A review of published and ongoing research. Quat. Int. **387**: 72–86. doi:10.1016/j.quaint.2014.03.022.

Muir, P.S., and Lotan, J.E. 1985. History and serotiny of Pinus contorta in Western Montana. Ecology **66**(5): 1658–1668.

Natural Resources Canada. 2017. Mountain pine beetle (factsheet). Available from http://www.nrcan.gc.ca/forests/fire-insects-disturbances/top-insects/13397 [accessed 25 August 2018].

Nealis, V.G., and Peter, B. 2008. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests. Canadian Forest Service, Pacific Forestry Centre, Information Report **BC-X-417**: 31 pp.

Ono, H. 2004. The mountain pine beetle: Scope of the problem and key issues in Alberta. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 62–66.

Parker, A.J. 1986. Persistence of lodgepole pine forests in the Central Sierra Nevada. Ecology **67**(6): 1560–1567. Available from http://www.jstor.org/stable/1939086 .

Pec, G.J., Karst, J., Sywenky, A.N., Cigan, P.W., Erbilgin, N., Simard, S.W., and Cahill, J.F. 2015. Rapid increases in forest understory diversity and productivity following a mountain pine beetle (Dendroctonus ponderosae) outbreak in pine forests. PLoS One **10**(4): 1–16. doi:10.1371/journal.pone.0124691.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. Bioscience **58**(6): 501–517. doi:10.1641/B580607.

Rees, D.C., and Juday, G.P. 2002. Plant species diversity on logged versus burned sites in central Alaska. For. Ecol. Manage. **155**: 291–302. doi:10.1016/S0378-1127(01)00566-7.

Rhoades, C.C., McCutchan, J.H., Cooper, L.A., Clow, D., Detmer, T.M., Briggs, J.S., Stednick, J.D., Veblen, T.T., Ertz, R.M., Likens, G.E., and Lewis, W.M. 2013. Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response. Proc. Natl. Acad. Sci. **110**(5): 1756–1760. doi:10.1073/pnas.1221029110.

Rice, A.V., Thormann, M.N., and Langor, D.W. 2008. Mountain pine beetle-associated blue-stain fungi are differentially adapted to boreal temperatures. For. Pathol. **38**(2): 113–123. doi:10.1111/j.1439-0329.2007.00525.x.

Roe, A.L., and Amman, G.D. 1970. The mountain pine beetle in lodgepole pine forests. USDA For. Serv. Intermountain Research Station. Research Paper **INT-71**: 26 pp. doi:10.5962/bhl.title.68786.

Royo, A.A., and Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. **36**(6): 1345–1362. doi:10.1139/x06-025.

Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., and Taylor, S.W. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. Can. Entomol. **142**(5): 415–442. doi:10.4039/n08-CPA01.

Safranyik, L., Shrimpton, D., and Whitney, H. 2002. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service, Pacific Forestry Centre. Forestry Technical Report **1**: 23 pp.

Sibold, J.S., Veblen, T.T., Chipko, K., Lawson, L., Mathis, E., and Scott, J. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. Ecol. Appl. **17**(6): 1638–1655.

Simberloff, D. 2011. Native Invaders. *In* Encyclopedia of biological invasions. *Edited by* D. Simberloff and R. Rejmanek. University of California Press, Berkeley, CA. pp. 472–475.

Stone, W.E., and Wolfe, M.L. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. Vegetation **122**(1): 1–12. doi:10.1007/BF00052811.

Stuart, J., Agee, J., and Gara, R. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. Can. J. For. Res. **19**: 1096–1104.

Taylor, S.W., and Carroll, A.L. 2004. Disturbance, forest age, and mountain pine beetle outbreak in BC: A historical perspective. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 41–51.

Teste, F.P., Lieffers, V.J., and Landhäuser, S.M. 2011a. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecol. Appl. **21**(1): 150–162. doi:10.1890/09-1881.1.

Teste, F.P., Lieffers, V.J., and Landhäusser, S.M. 2011b. Viability of forest floor and canopy seed banks in pinus contorta var. latifolia (pinaceae) forests after a mountain pine beetle outbreak. Am. J. Bot. **98**(4): 630–637. doi:10.3732/ajb.1000252.

Vyse, A., and Navratil, S. 1985. Advances in lodgepole pine regeneration. *In* Lodgepole pine, the species and its management. *Edited by* D. Baumgartner, R. Krebill, J. Arnott, and G. Weetman. Washington State University, Spokane. pp. 173–186.

Waring, R.H., and Pitman, G.B. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. Ecology **66**(3): 889–897. Available from http://www.jstor.org/stable/1940551.

Whitehead, R.J., Russo, G.L., Hawkes, B.C., and Armitage, O.B. 2007. A silvicultural assessment of 10 lodgepole pine stands after partial cutting to reduce susceptibility to mountain pine beetle. Natural Resources Canada, Canadian Forest Service, Canadian Wood Fibre Centre, Victoria, BC. 48 pp.

Whitehead, R.J., Safranyik, L., Russo, G.L., Shore, T.L., and Carroll, A. 2004. Silviculture to reduce landscape and stand susceptibility to the mountain pine beetle. In Mountain Pine Beetle Symposium: Challenges and Solutions. Edited by T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 233–244.

Wilson, B. 2004. An overview of the mountain pine beetle initiative. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone.

Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 3–9.

Chapter 2: Beyond Beetle – Natural regeneration after mountain pine beetle attack in lodgepole pine forests of west-central Alberta

2.1 Introduction

Lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) is a widespread conifer that can be found throughout western North America (Muir 1993). It is an early seral, shade-intolerant species that is able to grow on a variety of forest sites (Amman and Schmitz 1988), including nutrient poor sites where other conifers are unable to grow (Axelson et al. 2010). Lodgepole pine has adapted to a fire dominated disturbance regime (Amman and Schmitz 1988) and regenerates quickly and vigorously following stand-replacing disturbances when there is full sunlight, mineral soil seedbeds, and sufficient heat to open the serotinous or semi-serotinous cones and release seed (Lotan et al. 1985, Amman and Schmitz 1988, Lotan and Critchfield 1990, Muir 1993, Axelson et al. 2009). There is variation in serotiny throughout the range of lodgepole pine (Gendreau-Berthiaume et al. 2018) and even within populations.

Mountain Pine Beetle (*Dendroctonus ponderosae* Hopkins; Coleoptera: Scolytidae; MPB), is a bark beetle native to western North America that has historically been limited to small and scattered outbreaks in western North American pine forests, typically reaching no further than the southern portion of the eastern slopes of the Rocky Mountains in Canada, just east of the Alberta-British Columbia (BC) border (Ono 2004). A combination of extensive, homogenous stands of mature lodgepole pine, plus warmer winters due to climate change, which has increased brood survival (Ono 2004, Raffa et al. 2008), has resulted in the largest known outbreak in recorded history in BC and an unprecedented wave of MPB into Alberta (Axelson et al. 2009, Cigan et al. 2015). MPB has spread east into central and northern Alberta (Nealis and Peter 2008), and further north within BC (Ono 2004). As a result, Western Canada's pine forests have had millions of hectares (ha) affected (Carroll and Safranyik 2004, Raffa et al. 2008). With continuing climate change there is great risk of population growth continuing to increase (Morris et al. 2015) and this devastating bark beetle continuing its journey eastward through Alberta's pine forests and into Saskatchewan.

When MPB attacks a stand, the forest undergoes changes, only some of which are understood. When a stand is first attacked, there are no obvious visual changes and the needles remain green (green attack stage). Within 2-3 years the needles turn red (red attack stage), and by

4-5 years after attack the needles drop (grey attack stage). These canopy changes can alter light, microclimate, nutrients, and soil moisture, which can influence tree regeneration and understory vegetation.

While lodgepole pine forests throughout Alberta are adapted to stand-replacing fires, they are not adapted to a disturbance like that caused by MPB. Pine regeneration after MPB is likely to be impeded by: lack of a seed source, unsuitable regeneration microsites, and competing vegetation – and these could vary with site type. It is unknown which factors are the most influential to determine whether natural regeneration will occur or not in a stand post-MPB in Alberta. MPB attacks differ from fire since the killed trees are left standing, the cones are not exposed to heat from fire, and the forest floor is left undisturbed (Burton 2008). A favourable seedbed, such as mineral soil, is important for lodgepole pine regeneration, but after MPB attack, litter layers remain intact. While the forest floor experiences little change for at least 10 years after MPB attack (Astrup et al. 2008), litter depth increases (Klutsch et al. 2009) due to needle cast. The presence of a thick forest floor and thick feathermoss layer, which are common forest floor substrates in lodgepole pine forests in Alberta, can inhibit pine regeneration post-MPB (Astrup et al. 2008, McIntosh and Macdonald 2013).

Natural regeneration of lodgepole pine following MPB attack will also be hampered by lack of seed supply. Without fire, cones will not typically open unless ambient temperatures are sufficiently high. As stand death due to MPB progresses, branches and cones will fall to the ground; there, shading from the residual canopy and understory vegetation can prevent cones from being exposed to sufficiently high temperatures to open (Roe and Amman 1970, Axelson et al. 2009). However, after MPB-induced mortality, some cones may begin to open in the canopy (Teste et al. 2011a).

Lodgepole pine has been seen regenerating under its own canopy on edaphically limiting sites, dry and rocky sites, or xeric sites where other conifers are unable to establish (Safranyik et al. 2002, Sibold et al. 2007, Axelson et al. 2010, Kayes and Tinker 2012) and self-perpetuating lodgepole pine stands can occur in some areas (Stuart et al. 1989, Muir 1993, Hawkes et al. 2004). This suggests that the requirements for open areas, heat, and mineral soil for regeneration are not absolute. Given that vegetation varies with site moisture and nutrients, and MPB attack severity varies by vegetation type (Cole and Amman 1980), it seems that sites of differing qualities (in terms of moisture and nutrients) may respond differently to the effects of MPB. Poorer quality (moisture and nutrient limited) sites typically have less understory vegetation that could shade out new seedlings. In contrast, sites with more nutrients and moisture often have more ground vegetation present, which may be released after MPB-induced canopy mortality, inhibiting pine regeneration.

Regeneration of a forest stand after MPB-attack can be variable; while MPB typically acts as a stand-releasing disturbance, under certain circumstances, it may also act as a stand-replacing disturbance. Many sites have shown a pulse of growth of shade-tolerant, later-successional species that are left in the understory, resulting in a re-organization of tree composition driven by release of advance regeneration and surviving pine trees (Sibold et al. 2007, Axelson et al. 2009, de Ville 2013). Previous research found that in most MPB-attacked lodgepole pine forests in BC, pine was replaced by pre-existing, suppressed, shade-tolerant species (Roe and Amman 1970, Heath and Alfaro 1990, Astrup et al. 2008, Axelson et al. 2009). Pine regeneration under a MPB-killed canopy typically occurs in areas where MPB is a common disturbance, in stands where the substrate is suitable for regeneration, consisting of a thin organic layer rather than dominated by living feathermosses (Sharpe et al. 2017). These stands may be already somewhat adapted to MPB and the cones may therefore not be fully serotinous (Sharpe et al. 2017). However, the pine regeneration that occurs in these areas tends to be of low stem density, either occurring in only a portion of sites or comprising a low quantity relative to the amount of pine in the canopy prior to attack. For these reasons, evidence suggests most MPB-attacked lodgepole pine forests will regenerate to mixed stands. However, the majority of Alberta has large expanses of older lodgepole pine-dominated stands on its landscape that are not adapted to MPB, and many of which have little in the way of advance regeneration of other species. While previous studies have examined the potential future tree composition post-MPB West of the Rocky Mountains, in BC, the potential for and mechanisms driving pine regeneration post-MPB in Alberta, where forests differ environmentally and climatically from historical MPB habitat, are still unknown.

We need to better understand the impacts of this new disturbance agent on lodgepole pine forests in Alberta to help determine potential long-term implications. The main objectives of this study were to: 1) assess the potential for natural regeneration after MPB attacks across a range of lodgepole pine ecosite types throughout west-central Alberta, and 2) determine stand and site variables that best explain the occurrence and density of pine regeneration in the grey attack stage. We collected overstory and understory data in MPB-attacked stands throughout a variety of ecosites within west-central Alberta. I expected that lodgepole pine regeneration would only occur in areas with high mortality, where there would be sufficient light to open cones deposited on the forest floor. In addition, I expected that regeneration would be better on poorer ecosites, because there would be less competition from other vegetation. I also expected that little or no regeneration would occur in areas with high cover of moss on the forest floor, since this is known to be an unsuitable regeneration microsite. This information can help forest managers determine whether a more hands on approach is needed to return these post-MPB forests to lodgepole pine.

2.2 Methods

2.2.1 Study Area and Experimental Design

Natural regeneration of lodgepole pine and other tree species was examined in lodgepole pine forests post-MPB across a range of ecosites and natural subregions in west-central Alberta, primarily southwest of Grande Prairie, Alberta (55°10'47.000" N, 118°53'06.000" W, 669 meters above sea level). Sites were sampled in the Lower Foothills, Lower Boreal Highlands, and Boreal Mixedwood natural subregions (Figure 2-1) (Natural Regions Committee 2006), and included a variety of ecosite types (Appendix 2-1). The regional climate in this area is humid-continental (Natural Regions Committee 2006). The area receives an average of 445 mm of precipitation per year, has an average of 117 frost free days per year, and has a mean daily average of -13.6°C during the coldest month and 16.2°C during the warmest month (Based on data from 1981-2010) (Environment Canada 2018).

Sites were chosen based on the following criteria: ≥ 70% pine trees in the canopy, ≥ 50% of pine trees at the grey attack stage (attacked between 2007 and 2009), no MPB-management measures in place, advance regeneration present at ≤ 400 stems per hectare (5-meter spacing), including all species, and sites representing as broad a range of ecosites as possible. Stands sampled were a minimum of 200 m apart to minimize spatial autocorrelation. We also ensured that sites were a minimum of 80 m away from roads to reduce impacts of artificial canopy openings and edge effects.

MPB attacks in Alberta between 2007 and 2009 were mapped on ArcGIS and sites were chosen based upon the criteria above, as well as aerial imagery from 2014 and 2015, and accessibility by road. While 203 sites were initially identified as possibilities for sampling, 170 of those sites were either inaccessible or it was determined based on visiting the site that it did not meet the criteria. Typically, sites were rejected for sampling because they had less than 70% pine in the canopy or less than 50% of the pine was in the grey attack stage. Sites were sampled in 2014, 2015, and 2016, which was 6 – 9 years after MPB attack.

Canopies were dominated by even-aged lodgepole pine, over a range of MPB-induced mortality (52% to 100% of pine in grey-attack stage), and trees ranged in height from ~12 to 34 meters. While vegetation and ground cover can vary by ecosite, *Populus tremuloides* (Michx.) and *Picea glauca* ((Moench) Voss) were commonly interspersed in the canopy. *Picea mariana* ((Mill.) Britton, Sterns & Poggenb.), *Populus balsamifera, Larix laricina* ((Du Roi) K. Koch), and *Betula papyrifera* (Marshall) were also occasionally interspersed in the canopy. While ground vegetation varied by site, *Shepherdia canadensis* ((L.) Nutt.), *Arctostaphylos uva-ursi* ((L.) Spreng.), *Rosa acicularis* (Lindl.), and *Rubus idaeus* (L.) were frequently the dominant understory species. Sites were commonly dominated by low shrubs, followed by forbs and graminoids. There was limited cover of lichen, mineral soil, and wood cover, although lichens were dominant on the poorest sites; leaf litter dominated the ground in many stands while needle litter cover was found in low to moderate levels in most stands. The amount of healthy and dead moss cover varied substantially between stands, but when moss was present, there tended to be more healthy moss compared to dead moss.

2.2.2 Data Collection

In sites selected for sampling, a centre point was established in a location that was central in the stand and representative of the composition and structure of that particular MPB-killed stand. Slope, aspect, and elevation were recorded, and stand size was visually estimated. Sample areas were established in circles of 10 m and 20 m radii, radiating from the centre point. At each site, the height of two average sized pine in the canopy was measured using a hypsometer (Vertex). A prism plot was established at the centre point. A #3 prism was used to assess basal area (m^2/ha), while recording the diameter at breast height (DBH), live or dead status, and the species for each tree within that area. All advance regeneration (trees > 1 m but not reaching the subcanopy) was recorded in the 20-meter radius plot, including species, median height of each species, and estimated density of each species. Ground cover type and understory vegetation were recorded in the 10-meter radius plot. Ground cover types included: feather moss, lichen, bare ground, leaf litter, needle litter, decayed wood, and other. Understory vegetation categories included: tall shrubs (typically >1m tall), low shrubs (typically <1m tall), forbs, and graminoids. Ground and understory vegetation cover were recorded as percentage categories (<10%, 10-25%, 25-50%, 50-75%, and >75%), and midpoints were calculated for each category. The condition of the moss was also noted in terms of whether it was green, 10-40% dead, 40-60% dead, or >60% dead. From this and the percent cover of moss I calculated the percent cover of green (healthy) and brown (dead) moss (e.g. 10-25% moss cover (midpoint = 17.5%), 10-40% brown (midpoint = 25% brown and therefore 75% green), brown moss cover = 17.5% cover * 0.25 brown = 4.4% and green moss cover = 17.5% cover * 0.75 green = 13.1%). Total cover of herbaceous vegetation was summed. Ecosite (Beckingham and Archibald 1996, Beckingham et al. 1996, Moisey et al. 2012) was classified based on understory vegetation present. The 20-meter radius plot was given a quick visual inspection for regeneration, then four 1x1 meter seedling plots were established within one canopy tree radius circle from plot centre (one in each quadrat); these plots were selectively placed in open areas that were most likely to have pine seedlings present. Locations selected for the seedling plots were as open as possible, with as little vegetation and as much exposed ground as possible, to minimize competition and maximize suitable microsites for seedlings. We sampled in this way because of the very low occurrence of any pine seedlings over the range of sites and wanted to determine the best-case scenario for post-MPB pine regeneration. Seedlings were ≤9 years old, typically ≤50 cm, which we presumed was young enough to be new regeneration since MPB attack; seedlings detected were often ≤ 5 years of age. Counts of annual height increments were used to estimate age of seedlings. In each of the seedling plots, all post-MPB seedlings present were recorded, including all species. Counts of any seedlings observed outside the quadrats were also recorded.

2.2.3 Assessment of Serotiny

Cones were collected in 2015 and 2016 to assess serotiny (represented by cone openness). In 2015, a minimum of 10 closed cones were collected from within 15 cm of the ground and a minimum of 30 closed cones were collected on downed trees from areas elevated at least 1 m above the ground. In 2016, as many cones as possible were collected, aiming for a minimum of 100 cones from within 15 cm of the ground, and a minimum of 30 cones from approximately 1 meter above the ground. There were a few exceptions where cones were rare at a site and fewer cones were collected. Cones were collected from a minimum of three trees, and the youngest cones possible were collected. Cones were brought to the lab where they were left at ~21 C with a fan blowing on them for approximately 72 hours to ensure they were dry and open if the resin on the scales had already broken prior to collection. The number of cones in each category of cone openness was visually estimated and recorded (adapted from Teste et al. 2011a) as follows: closed (included where only a few scales were open), <25% open, 25%-50% open, 50%-75% open, or fully open (75%-100% open). Naturally occurring cone openness was then determined for each site by averaging the cone openness of ground and elevated cones of a site together and comparing that value to the mean for the year in which the cones were collected. A categorical variable was created to indicate whether the cone openness of a site was high or low, relative to the mean for each year.

To determine the potential for cones to open I conducted a heating experiment. Cones that were still fully closed after the 72 hours at room temperature – and that had been collected from the elevated locations – were heated in an oven with the temperature set to 40°C for one hour, after which they were scored for the degree of openness, using the same categories as described above. The temperature was then raised by increments of 5 degrees every hour (up to 60°C), with scoring taking place after each hour. Cones were removed when they became fully open. Two sites did not have any fully closed cones and were not able to be included in this experiment. A maximum of 30 cones from each site were included in the heating experiment.

2.2.4 Data Analysis

2.2.4.1 Potential Explanatory Variables

Cone heating was used to indicate the potential for cone openness at a variety of temperatures that may occur in a site, given an open canopy that allows the sun to heat the cones below. To examine differences in potential cone openness among sites types I used a mixed effect model using the lme function in nlme (Pinheiro et al. 2016). Temperature, site quality, and the temperature*site quality interaction were considered fixed effects while site was included as a random effect. The residuals were visually assessed for conformity to assumptions of normality and homogeneity of variance. When temperature, site quality, or temperature*site quality interaction had a significant effect on cone openness (α=0.05), lsmeans was used to conduct pairwise post-hoc tests to look for differences among temperatures within site quality groups and differences among site quality groups within temperatures (Lenth 2016). Tukey-adjusted α-values were used (family wise α=0.05).

I used generalized linear models (GLMs) to examine which explanatory variables best explain lodgepole pine regeneration post-MPB across sites. The response variable was the count of pine seedlings in all candidate models. Potential explanatory variables included a variety of ground and vegetation cover variables, tree and advance regeneration variables, site influence variables, and cone openness variables (Appendix 2-2). Categorical variables in GLM models in R result in the creation of “dummy” variables, one representing each level within the categorical variable. Advance regeneration was presented both as density based solely on the spacing of each species, and density that accounted for the spacing and median height of each species. The potential direct incident radiation was calculated from slope, latitude, and folded aspect, which I also determined (McCune and Keon 2002, McCune 2007). Ecosites were grouped into poor (a, b), medium (c, d), and rich (e, f) site quality groups, regardless of natural subregion; the ‘poor’ category was used as the reference. Ecosite scores were estimated for each ecosite based on its position on the edatopic grid (e.g. Nutrient Regime B (column 2 from the left) = 2, Moisture Regime Mesic (row 4 from the top) = 4, so 2 + 4= ecosite score 6). Average cone openness per site at 50°C and 55°C had the largest amount of variation and both were therefore included as potential explanatory variables. Since a t-test revealed that naturally occurring cone openness at both ground and elevated levels were significantly different between 2015 and 2016 (p=0.0003 and p=1.707e-05 respectively), naturally occurring cone openness for each site was organized into a cone openness category as described above (high or low, relative to the mean for each year).

The candidate explanatory variables were grouped into four categories to streamline the variable selection process: ground influence (forb cover, graminoid cover, green (healthy) moss cover, etc.), tree/canopy influence (total basal area, live/dead basal area, basal area by species, etc.), advance regeneration influence (broadleaf density, conifer density, pine density, etc.), and site influence (site quality, radiation, elevation, etc.; Appendix 2-2). Spearman correlation coefficients were examined for each category prior to analysis. Individual effects of each explanatory variable within a category were examined, and their correlations with one another. When any two variables were strongly correlated ($\geq|0.7|$), the variable that had a stronger influence on pine seedling count (determined by whichever had a stronger correlation with the count of pine seedlings) was retained for the exhaustive exploration of candidate models, and the other variable was removed prior to analysis. Variables with no correlations with other variables were also retained for analysis.

2.2.4.2 Model Selection

The influence of the various explanatory variables within each category was examined through exhaustive screening of candidate models using glmulti (Calcagno 2013), a wrapper for glm(), in the R environment Version 3.4.3 (R Core Team 2017). This approach compares multiple candidate explanatory variables and evaluates their importance to the model, using an information-theoretic approach. It generates all possible candidate model formulas, passes these to an R fitting function, and returns the best approximating models based on the smallest Akaike Information Criterion values (AIC) (Burnham and Anderson 2002, Calcagno and Mazancourt 2010). Only main effects (without interactions) were included, candidate models were compared using an AIC value corrected for small sample sizes (AICc) to account for small sample size (Burnham and Anderson 2002), and family was set to Poisson to account for the count data.

Models within 2 AICc were considered equally supported, so MuMIn (Barton 2018) was used to do model averaging on all models that were within 2 AICc points of the best model (within each category separately) to ensure that the optimal set of variables had been selected in the model with the lowest AICc for each category. MuMIn (Barton 2018) was also used to determine the relative importance of each variable in the best candidate model for each category. Glmulti (Calcagno 2013) was used to determine the Akaike weight (w_i) for each model. Coefficient estimates were examined for each continuous variable and each level of categorical explanatory variables from the best approximating final model for each category. The residuals for the best glm model for each category were visually assessed to ensure assumptions were met. Explanatory variables from the best model in each category were then combined in a final model and the methods described above were used to determine, overall, the variables that best explained lodgepole pine regeneration post-MPB.

2.2.4.3 Model Selection with Cone Openness Subset

There were no data on cone openness potential from the heating experiment for two sites because no closed cones were collected at them. Thus, I was unable to include cone openness as a potential explanatory variable in the model selection procedure described above, which included all sites. To determine the importance of cone openness as an explanatory variable, I constructed models using the subset of sites (n=31) for which there was completed data for all explanatory variables.

The same model selection methods described above were used to assess models including cone openness as an explanatory variable through two different approaches. First, the cone openness variables were added to the tree/canopy influence category. I then determined if any of the cone openness variables was a top variable and would be included in the best model for the tree/canopy category and for the final, overall, model. Secondly, using just the subset of 31 sites for which I had cone openness data, I compared the final model (using the explanatory variables from the final best model created using the entire set of sites) with ones to which each cone openness explanatory variable had been added, individually; this allowed me to determine if any of the cone openness variables improved the model. AICc values were used for all comparisons.

2.3 Results

Many plots (58%) had no lodgepole pine seedling recruitment; pine seedlings were only found on 14 of 33 sites. Where seedlings were present, seedling counts in the four - 1 m^2 plots ranged from 1-8 individuals (Figure 2-2). Spruce (black and white), trembling aspen, paper birch, and some balsam poplar and tamarack seedlings (or saplings) were also seen (Appendix 2-3). Where pine seedling regeneration occurred, mean seedling count (per four 1 m^2 plots) was 3.2 (s.d. = 2.5). Mineral soil and decayed wood are known for being favoured regeneration seedbeds, but in our sites, mineral soil (bare ground) and decayed wood often covered none or less than 10% of the 10-m radius area examined.

2.3.1 Explanatory Variables

Model selection for each category resulted in a few explanatory variables that best explained what influenced pine regeneration. From there, the overall most influential explanatory variables were determined. Some of the explanatory variables in the top models had positive associations with pine regeneration (e.g., conifer advance regeneration density and pine advance regeneration density) while the majority were negatively associated with pine regeneration (Tables 2-1 and 2-2).

While forb, graminoid, and green moss had a negative association with pine regeneration at the category level, none were influential overall. Top models in this category also indicated that brown moss, low shrubs, and bare ground had a negative association with pine regeneration, while lichen cover had a positive association with pine regeneration.

Pre-existing trees, measured as either overstory basal area or density of advanced regeneration, impacted pine regeneration in a variety of ways. Basal area had a negative association with pine regeneration, regardless of whether it was total basal area, living trees only, broadleaf trees, or spruce trees. The mean total basal area of all canopy trees (living and dead) was 26.8 m^2/ha (SD=12.9) and the mean basal area of all live trees was 5.6 m^2/ha (SD=5.3). The mean basal area of broadleaf trees was 0.4 m^2/ha (SD=1.6) and the mean basal area of spruce (black and white, living and dead), which was found in the canopy of less than a quarter of all sites, was 0.9 m^2/ha (SD=2.2). Species of advance regeneration included spruce (black and white), paper birch, balsam poplar, trembling aspen, lodgepole pine, and subalpine fir (Appendix

2-3). Birch and aspen were the most common broadleaf advance regeneration species and spruce (black and/or white) was the most common species of conifer advance regeneration. Conifer advance regeneration was found in approximately 90% of sites and averaged 190 stems per hectare (sph) when present (ranging from 25 to 322 sph); it had a positive association with pine regeneration. Broadleaf advance regeneration was found in approximately 70% of sites and averaged 140 sph when present (ranging from 25 to 482 sph); it had a negative association with pine regeneration. Low levels of lodgepole pine advance regeneration were found in approximately 40% of sites (sph ranged from 25-237); it was positively associated with pine regeneration.

Twelve poor, six medium, and 15 rich sites were examined. Pine seedlings were most likely to be found on poor quality sites, while pine did not regenerate well on rich sites (Figure 2-3). Elevation and the site size were negatively associated with pine regeneration.

Temperature and site quality had a significant interaction that impacted cone openness (Table 2-3). While cone openness increased as temperature increased in all sites, differences between site quality began to appear at 55°C; openness was lowest in rich sites (47%) and highest in poor sites (55%; Figure 2-4). This trend remained through 60°C (openness was ~9% higher in poor sites), at which temperature the experiment finished.

2.3.2 Model Selection

The best model for pine regeneration for each category of explanatory variables and the best final combined model contained one to four explanatory variables each (Table 2-4). The best final model, which included site quality, pine advance regeneration density, broadleaf advance regeneration density, and spruce basal area (Tables 2-4 and 2-2) was:

g(x) = 1.2268 + 0.1364(medium site quality) – 1.4434(rich site quality) + 0.0008(pine advance regeneration) – 0.0144(broadleaf advance regeneration) – 0.3677(spruce basal area)

where g(x) is the logit function of the predicted count of pine seedlings. All variables included in this final model significantly influenced pine regeneration post-MPB, although medium site quality was no different than poor site quality, which was included as the reference category (Table 2-2). The final best model run using the subset of data from sites for which I had cone openness data (n=31) was not improved by adding that explanatory variable; the model without cone openness was only marginally better than either the model that included cone openness separated into low/high (Δ AICc = 2.56) or cone openness potential at 50°C (Δ AICc = 2.63; Tables 2-4 and 2-5).

Explanatory variables selected in the final best model had a variety of impacts on pine regeneration. Rich, as compared to poor (the reference category), ecosites had negative associations with pine regeneration, and medium site quality had positive associations with pine regeneration, although it was no different than poor site quality (Table 2-2). Broadleaf advance regeneration had a negative association with pine regeneration post-MPB (Tables 2-1 and 2-2). Pine advance regeneration seemed to have the opposite effect being more abundant on sites that also had higher counts of pine seedlings (Tables 2-1 and 2-2). While spruce was present in the canopy in only six sites, it had a negative association with pine regeneration post-MPB (Table 2-2).

2.4 Discussion

I found natural pine regeneration in less than half of the MPB-killed stands and none of the stands had regeneration that would be considered sufficient to produce a stand similar to the one that was killed. As very little regeneration was seen, a bias was placed in site selection for seedling surveys to increase the likelihood of finding pine seedlings and to determine what might happen in the best-case scenario. Due to this bias, these pine seedling counts are not representative of regeneration on the overall site, and therefore cannot be scaled up to a per hectare estimate. Even with our approach where we purposely placed plots in places where we were most likely to find pine seedlings (i.e., open areas that were less heavily vegetated) search efforts yielded very few seedlings. This poor regeneration is likely due to unsuitable conditions for germination and establishment plus excessive competition from other vegetation. Lodgepole pine is adapted to regenerate following stand-replacing disturbances such as fire, which produce very different conditions from those found in these forests following disturbance by MPB. After MPB-attack, standing dead trees may result in shading of the forest floor which may reduce the chance that cones will receive enough heat to open and for pine seedlings to establish. Our results concur with other studies in Alberta (McIntosh and Macdonald 2013) and BC (Astrup et al. 2008) that showed limited pine recruitment post-MPB. While MPB-killed stands in Colorado have reported sufficient regeneration to eventually adequately stock the forest, lodgepole pine regeneration was only seen in 50% of plots (Collins et al. 2011). Post-MPB regeneration in stands west of the Rocky Mountains in BC tends to vary and may regenerate to lodgepole pine (Alfaro et al. 2015), or they may not (Astrup et al. 2008). However, the studies in BC and Colorado suggested that advance regeneration of more shade tolerant species already present in the stand will most likely replace the pine as the dominant species in the future canopy (Astrup et al. 2008, Collins et al. 2011, Edwards et al. 2015), which could shift species composition on the entire landscape away from pine towards already-present species. For this reason, we avoided stands that were sufficiently stocked with advance regeneration – these stands weren't of the highest concern from a management and future development perspective as they will eventually become adequately stocked. In Alberta, many lodgepole pine forests do not have much advance regeneration, and therefore this is not an option for them to develop adequately stocked forests in the future. A future stand-replacing event, such as fire, could result in a pulse of pine regeneration.

2.4.1 Explanations for regeneration, or lack thereof

As expected, competing vegetation, including from forbs, graminoids, and low shrubs negatively impacted pine regeneration. This is likely to due their ability to outcompete pine seedlings, using up available resources. Vegetation cover limits space on the forest floor that is suitable for pine regeneration. Green moss also negatively impacted pine regeneration, as it is a poor microsite for germination and establishment. Astrup et al. (2008) also found that moss layers in BC inhibited pine regeneration post-MPB. Unlike fire, MPB is known to leave the forest floor untouched for at least 10 years after attack, resulting in unfavourable substrates being available (Astrup et al. 2008). Undisturbed forest floors were seen in this study as there had been no ground disturbance. Thick layers of residual forest floor have been seen to negatively impact pine regeneration in Alberta; fire removes much of this layer to expose mineral soil, promoting dense conifer regeneration (Sharpe et al. 2017). While we initially thought that pine may be able to regenerate as the canopy opened up and moss died due to increased light penetration, it seemed that dying/dead moss also negatively impacted pine seedlings. The death of moss on these sites is likely due to dry conditions and increased light reaching the forest floor; the conditions that caused the moss to die might have also been unfavourable for pine seedling establishment. Pine seedlings need a reliable water supply in their first growing season and are therefore susceptible to drought in the early stages as they initially have a shallow root system that has not yet expanded to depths where there is an adequate water supply (Lotan 1964). Additionally, the moss likely grew on richer sites, and residual vegetation in these sites may have outcompeted pine seedlings.

Almost three quarters of sites had broadleaf advance regeneration (primarily aspen with some birch) in the understory. As expected, broadleaf advance regeneration negatively impacted pine regeneration, even though densities were low. This is likely to due their ability to outcompete pine seedlings and use up available resources, as well as by creating leaf litter which may smother germinants. As the canopy dies and resources (light, nutrients, moisture) are released, advance regeneration could take advantage of this, showing release growth (Oboite 2018), further hampering pine regeneration. Broadleaf species seemed to be released from competition and outcompeted pine regeneration in our stands. Many of our pine dominated sites were adjacent to aspen dominated stands, which could allow aspen suckers to establish as the MPB-killed canopy opens up and additional resources become available.

Spruce advance regeneration was present in the vast majority of sites but did not negatively impact pine regeneration. This is likely because the low density of spruce advance regeneration in the sites that we selected for study did not outcompete pine seedlings. While shade-tolerant species, such as spruce, are often found below the canopy of early successional species, the species present below the canopy can vary between stands. Stands in BC have been seen to have predominately subalpine fir regenerating post-MPB, but no lodgepole pine, most likely due to different species responses to canopy influence (Astrup et al. 2008).

Canopies can influence what happens in the understory of a stand, including regeneration. Overstory basal area, especially spruce, negatively impacted pine regeneration. This was the case even though spruce was not very common in the canopy. Overstory shading, which can be measured as total basal area, can limit lodgepole pine regeneration post-MPB (Astrup et al. 2008). This makes sense as lodgepole pine is known to be a shade-intolerant species, and shade from an existing canopy can prevent sufficient light from reaching the forest floor.

The other major factor influencing regeneration of lodgepole pine was the site type; sites that were more nutrient rich and moister had poorer regeneration, while regeneration seemed to be more common on nutrient and moisture poor sites. Rich sites tend to have heavy vegetation and already established tree species; thus vegetation competition likely partially explains the poor regeneration on these sites. Pine is shade intolerant and not well adapted to dealing with competition from already established vegetation. After fire, pine tends to grow quickly so that it can become established before heavy competing vegetation can establish on the site. In drier and poorer sites, there is less competing vegetation and this would allow higher levels of pine regeneration. Lichen cover, and conifer and pine advance regeneration were also positively associated with pine regeneration. Poorer quality sites are more likely to have higher lichen cover and pine advance regeneration. Initially it was surprising that conifer advance regeneration had this influence, but this can most likely be explained by the inclusion of pine in this variable. It seems unlikely that there was a direct positive influence of pine advance regeneration on new establishment of pine. Rather, the existence of lodgepole pine advance regeneration was indicative of site conditions that were suitable for pine establishment, especially as pine advance regeneration was present in low densities. The sites with higher levels of lichen cover tended to be the more nutrient and moisture limited sites with relatively open canopies. Thus, the lower levels of competing vegetation and higher levels of light reaching the forest floor likely gave pine a chance to regenerate without fire and explain the higher levels of pine regeneration on these sites.

Interestingly, elevation also negatively impacted pine regeneration post-MPB. There is a variety of explanations for this. As the majority of the richer ecosites were found in the lower foothills, these ecosites may have been at higher elevations. Thus, it is possible that this reduced pine regeneration was partially due to the higher levels of vegetative competition in these sites, rather than elevation itself. Alternatively, higher elevation areas may experience higher severity fires (Stretch et al. 2016), possibly due to more frequent lightning; serotiny strength tends to be higher in areas that experience more frequent and severe fires (Buma et al. 2013). If higher elevation areas have more strongly serotinous cones, this could explain why post-MPB regeneration is lower at higher elevations; cones in these areas may need higher temperatures to open. This could be exacerbated by the generally cooler temperatures at higher elevation.

2.4.2 Cone Openness

While cone openness did not improve the model explaining pine regeneration, it did not make it substantially worse. This indicates that it may be somewhat important for pine regeneration, although it may not be one of the top explanatory variables. While serotinous cones are considered an adaptation that allows fire to reset a canopy to lodgepole pine (Muir and Lotan 1985), solar radiation can sometimes cause sufficient heat to melt the cone resin and open cones, resulting in lodgepole pine regeneration, even without fire (Teste et al. 2011a, Edwards et al. 2015). However, radiation did not seem to be a good explanatory variable in any of our top models, likely since most of the sites were relatively flat, so the differences in incoming radiation were small.

A closer inspection of cone openness potential indicated that site quality and temperature interacted to impact how much cones opened. Cones began to open more fully at lower temperatures in poor quality sites compared to high quality sites, indicating they do not need as much heat to open them fully. This concurs with our finding that poorer/drier sites were more likely to have pine regeneration present. Additionally, since poor quality sites often have a more open canopy for sunlight to penetrate through to the ground, higher cone openness at lower temperatures (temperatures that can be achieved by sunlight hitting the ground) may be an adaptation reflective of pine's ability to regenerate under its own canopy in some nutrient poor sites. Alternately, this may be an environmental response and cones in poorer sites may not have enough resources to produce thicker resin, which holds the cone scales together.

Stronger serotiny (higher temperatures required to open cones) in richer sites would help ensure cones stay closed until a higher temperature event, such as fire or stand-replacing disturbance, occurs. This is most likely an adaptation that would prevent cones from opening in undisturbed, or only mildly disturbed, richer sites while there is excessive competition from understory vegetation that would prevent seedling establishment. Closed cones also maintain seed viability within them, which is lost soon after the cone opens. Waiting for a stand-replacing disturbance would keep the cones closed until competition was eliminated and suitable regeneration microsites were created for the pine seedlings to germinate and establish. It also means that populations of lodgepole pine on rich sites are poorly adapted to MPB.

Understanding cone opening following MPB is especially important since MPB-killed stands experience branch breakage as trees die; this results in more cones falling from the canopy and being buried in or below the moss, compared to live stands (Teste et al. 2011a). Almost half of the seed bank can be released within 6 years of MPB attack; these released seeds are subject to loss of viability if no adequate seedbed is present for regeneration but they also face the risk of seed predation from squirrels and ground vertebrate species (Teste et al. 2011a). The closed cones that become covered by moss create a small forest floor seedbank, indicating that fire or anthropogenic disturbance is needed soon after MPB-attack for normal levels of regeneration to occur (Teste et al. 2011a).

2.4.3 Future Stand Composition

While advance regeneration densities were low for all species, they still impacted pine regeneration post-MPB and can help shape the future composition of a stand. In Colorado, Collins et al. (2011) found that post-bark beetle forest recovery may depend more heavily on advance regeneration that established prior to an outbreak than new seedling establishment. Advance regeneration of varying species may be found in stands post-MPB attack; aspen advance regeneration was found in stands in Colorado (Stone and Wolfe 1996, Collins et al. 2011) and Wyoming (Kayes and Tinker 2012), while aspen, lodgepole pine, and other conifer advance regeneration were found at varying densities in BC (Alfaro et al. 2015). Spruce and aspen advance regeneration were present in the vast majority of sites, indicating that they may be present in the future canopy in post-MPB stands in Alberta, even if at low densities. A transition to spruce, a shade-tolerant species, is something that happens naturally in these stands, so MPB may speed up this process and reduce the amount of lodgepole pine on the landscape. However, the low densities at which advance regeneration was found indicates that these post-MPB stands may not become fully stocked with any species, and a lack of burning of these stands may negatively impact lodgepole pine seed abundance and viability over time, and therefore future pine regeneration. Additionally, richer sites are just as capable of growing spruce and aspen as lodgepole pine, and these sites will readily shift away from lodgepole pine. This is of concern since aspen, like lodgepole pine, is an early successional species; a transition to this species may indicate that this forest will take a new trajectory. The transition from lodgepole pine to an aspen dominated canopy might have long term repercussions since broadleaf litter creates more favourable conditions for herbaceous vegetation, increases soil pH, increases rates of nutrient cycling, and decomposes more quickly (Hart and Chen 2006) compared to needle litter. The forest floor conditions may end up quite different following an aspen dominated canopy compared to when pine dominated the stand, and these areas may eventually no longer be hospitable to pine until a fire or logging disturbance.

Seed sources are important for future regeneration after disturbances. In poor quality sites, lodgepole pine cones may open immediately after MPB with high enough ground temperatures, indicating that there may be a seed source present in these sites and this is therefore not the cause of reduced pine regeneration. It also indicates that in richer sites with less cone opening, there may be more of a seedbank remaining in closed cones, which may still contain viable seeds when the next fire eventually burns through the area. Saying that, large durations of time between MPB-induced pine death and fire may negatively impact pine regeneration. Although serotinous cones are an adaptation to fire, historically a fire has burnt a stand regularly. Not only is there a risk of cone viability being reduced over time (Edwards et al. 2015), but pine germination capacity may be reduced by the time a fire comes through (Teste et al. 2011b), which indicates that the future composition may shift away from pine.

Trees killed by bark beetles may increase fuel build up in stands (Hicke et al. 2012), making them more susceptible to increased fire intensity. However, moisture held in the living canopy of partially killed stands may prevent burning in these stands – a lack of fire may hinder pine regeneration. Alternatively, increased fire intensity may increase the risk of fallen cones being consumed in a fire (Edwards et al. 2015), which can also prevent pine regeneration. As the climate becomes warmer and drier, fires and beetle outbreaks may increase in frequency and intensity, which may help pine regenerate (Briggs et al. 2015). On the other hand, re-occurring MPB epidemics might result in a shift away from pine, to other species such as aspen and spruce.

2.5 Conclusion

Limited natural lodgepole pine regeneration was seen post-MPB in the sites we surveyed in west-central Alberta. Fewer than half of sites assessed had any evidence of regeneration and when regeneration was observed the densities were far below full stocking. A lack of suitable regeneration microsites, competition from ground vegetation and broadleaf advance regeneration, shading from spruce in the canopy, and rich ecosites all seem to hinder pine regeneration. A lack of seed source most likely also hindered pine regeneration; few cones opened at temperatures that would likely be experienced on the ground beneath a canopy. Poor quality sites with pre-existing pine advance regeneration seem to be the most likely areas to see post-MPB pine regeneration; this can be attributed to their relatively open canopies, less vegetative competition and perhaps less strong serotiny. The future canopy composition of these stands post-MPB will likely shift away from lodgepole pine and towards greater abundance of species present as advance regeneration (broadleaf species and spruce) in the stand prior to MPB-attack. This information can help prioritize areas for management decisions regarding rehabilitation and intervention in Alberta.

Table 2-1. Direction of influence for all potential explanatory variables that were included in the top model in each category and for the final, overall, best model. See also Table 2-4.

Category	Explanatory Variable [i]	Direction of Influence
Ground	forb	Negative
	graminoid	Negative
	green_moss	Negative
	brown_moss	Negative
	low	Negative
	bare	Negative
	lichen	Positive
Tree/canopy	BA_live	Negative
	BA_total	Negative
	BA_spruce	Negative
	BA_bl	Negative
Advance Regeneration	DA _con	Positive
	DA _Pl_h	Positive
	DA_bl	Negative
Site [ii]	sqmedium	Negative
	sqrich	Negative
	elevation	Negative
	size	Negative
Final [ii]	sqmedium	Negative
	sqrich	Negative
	DA _Pl_h	Positive
	DA_bl	Negative
	BA_spruce	Negative
	DA _con	Positive
	BA_live	Negative

[i] See Appendix 2-2 for variable descriptions.

[ii] The ‘sqpoor’ category for site quality was used as the reference

Table 2-2. Coefficients for the explanatory variables in the generalized linear models predicting lodgepole pine regeneration post-MPB in west-central Alberta. Explanatory variables from the best model in each category, including the best overall model, are included, including the "dummy" variables created for each level of categorical variables. Relative importance is relative to other variables included in the top models within a given category. Also given is the standard error and significance (Significance codes: <0.0001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1) for each variable.

Category	**Explanatory Variable** [i]	**Coefficient Estimate (β)**	**Standard Error**	**Relative Importance**	**Pr(>|z|)**
Ground	Intercept	1.8390	0.3402	-	6.48e-08 ***
	forb	-0.0317	0.0085	1.00	0.000174 ***
	graminoid	-0.0184	0.0079	0.87	0.019051 *
	green_moss	-0.0137	0.0059	1.00	0.020930 *
Tree/canopy	Intercept	0.8316	0.1955	-	2.11e-05 ***
	BA_live	-0.0904	0.0363	1.00	0.0127 *
	BA_spruce	-0.3096	0.1829	0.83	0.0905 .
Advance Regeneration	Intercept	-0.2009	0.5325	-	0.706007
	DA _Pl_h	0.0010	0.0004	1.00	0.011095 *
	DA_bl	-0.0139	0.0040	1.00	0.000561 ***
	DA _con	0.0041	0.0024	0.55	0.086884 .
Site [ii]	Intercept	1.0116	0.1741	-	6.20e-09 ***
	sqmedium	-0.7239	0.3941	1.00	0.0662 .
	sqrich	-2.3334	0.5294	1.00	1.05e-05 ***
Final [ii]	Intercept	1.2268	0.2914	-	2.56e-05 ***
	sqmedium	0.1364	0.4510	1.00	0.762339
	sqrich	-1.4434	0.5740	1.00	0.011920 *
	DA _Pl_h	0.0008	0.0004	0.34	0.051833 .
	DA_bl	-0.0144	0.0039	1.00	0.000199 ***
	BA_spruce	-0.3677	0.1758	1.00	0.036503 *

[i] See Appendix 2-2 for variable descriptions.

[ii] The 'sqpoor' category for site quality was used as the reference category

Table 2-3. Results (p-value) from a one-way ANOVA comparing cone openness at six temperatures: ~21, 40, 45, 50, 55, and 60 °C, in three different site quality groups. See also Figure 2-4.

Temperature	**Site Quality**	**Temperature*Site Quality**
<.0001	0.4701	**<.0001**

Table 2-4. The best approximating candidate models for each of the four categories of explanatory variables (all models within 2 AICc points of the best model are included), indicating which explanatory variables best explained lodgepole pine regeneration (seedling counts) post-MPB in west-central Alberta. Models within each category were compared using AIC corrected for small sample sizes (AICc) and AICc weights (AICc w_i). The best model for each category had the lowest AICc value within that category (shown in bold). Explanatory variables from the top model in each category were combined to determine the top variables overall, in the final best model (best, overall, model shown in bold).

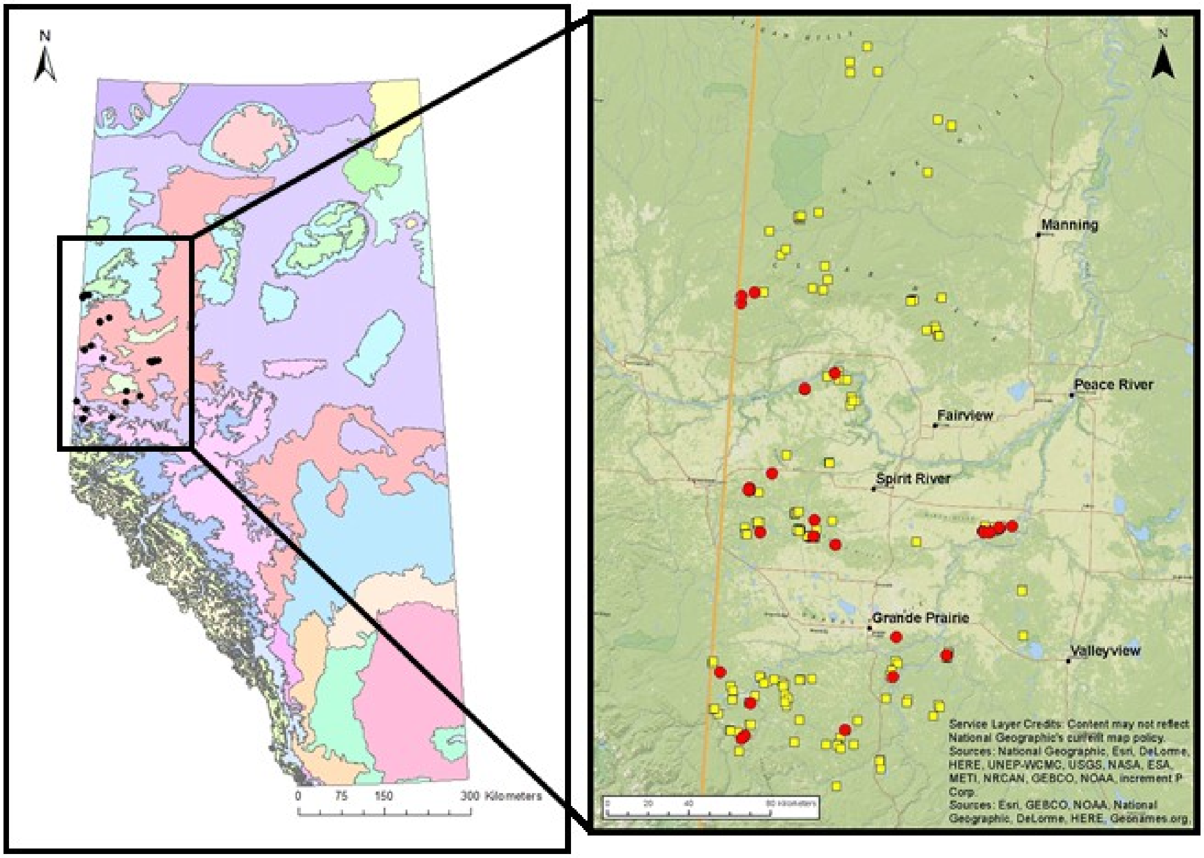
Category	**Model Structure** [i]	**AICc**	**W*i* AICc**
Ground	**1 - forb - graminoid - green_moss**	**124.56**	**0.059**
	1 - forb - graminoid - brown_moss - green_moss	124.58	0.057
	1 - forb - brown_moss - green_moss	125.94	0.029
	1 - forb - graminoid - bare - brown_moss - green_moss	126.05	0.027
	1 - low - forb - graminoid - brown_moss - green_moss	126.09	0.027
	1 - forb - graminoid + lichen - green_moss	126.30	0.024
Tree/canopy	**1 - BA_live - BA_spruce**	**133.07**	**0.243**
	1 - BA_live - BA_spruce - BA_bl	133.40	0.207
	1 - BA_live	135.06	0.090
Advance Regeneration	**1 + DA _Pl_h - DA_bl + DA _con**	**94.149**	**0.505**
	1 + DA _Pl_h - DA_bl	94.573	0.409
Site	**1 - sq**	**113.90**	**0.383**
	1 - sq - elevation	115.62	0.162
	1 - sq - size	115.72	0.154
Final	**1 - sq + DA _Pl_h - DA_bl - BA_spruce**	**84.572**	**0.093**
	1 - sq - DA_bl - BA_spruce	85.164	0.069
	1 - sq + DA _con - DA_bl - BA_spruce	85.310	0.065
	1 - sq - DA_bl - BA_live - BA_spruce	85.781	0.051

[i] See Appendix 2-2 for variable descriptions.

Table 2-5. A comparison of AICc values (AIC corrected for small sample size) of the best final model without cone openness to the same model with inclusion of four different measures of potential cone openness. Models were constructed using the subset of sites for which cone openness data were available (n=31). This comparison indicates whether adding cone openness improved the final model explaining lodgepole pine seedling counts post-MPB in west-central Alberta. See Table 2-4.

Cone Openness	**Model Structure** [i]	**AICc**	**Δ AICc**
Without Cone Openness	**1 - sq + DA _Pl_h - DA_bl - BA_spruce**	**81.42**	**0**
Openness Category (lh)	1 - sq + DA _Pl_h - DA_bl - BA_spruce + CO_lh	83.98	2.56
Openness @ 50°C	1 - sq + DA _Pl_h - DA_bl - BA_spruce - CO_50	84.05	2.63
Openness @ 55°C	1 - sq + DA _Pl_h - DA_bl - BA_spruce + CO_55	84.75	3.33

[i] See Appendix 2-2 for variable descriptions.



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Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org.

Figure 2-1. The 33 sites that fit the criteria (black circles on the left and red circles on the right) and 170 sites that were not sampled fully (yellow squares) either due to being inaccessible (n=56) or not fitting the criteria (n=114), throughout various natural subregions in west-central Alberta, as surveyed in 2014, 2015, and 2016. Natural subregions surveyed included Boreal Mixedwood, Lower Boreal Highlands, and Lower Foothills (Natural Regions Committee 2006).

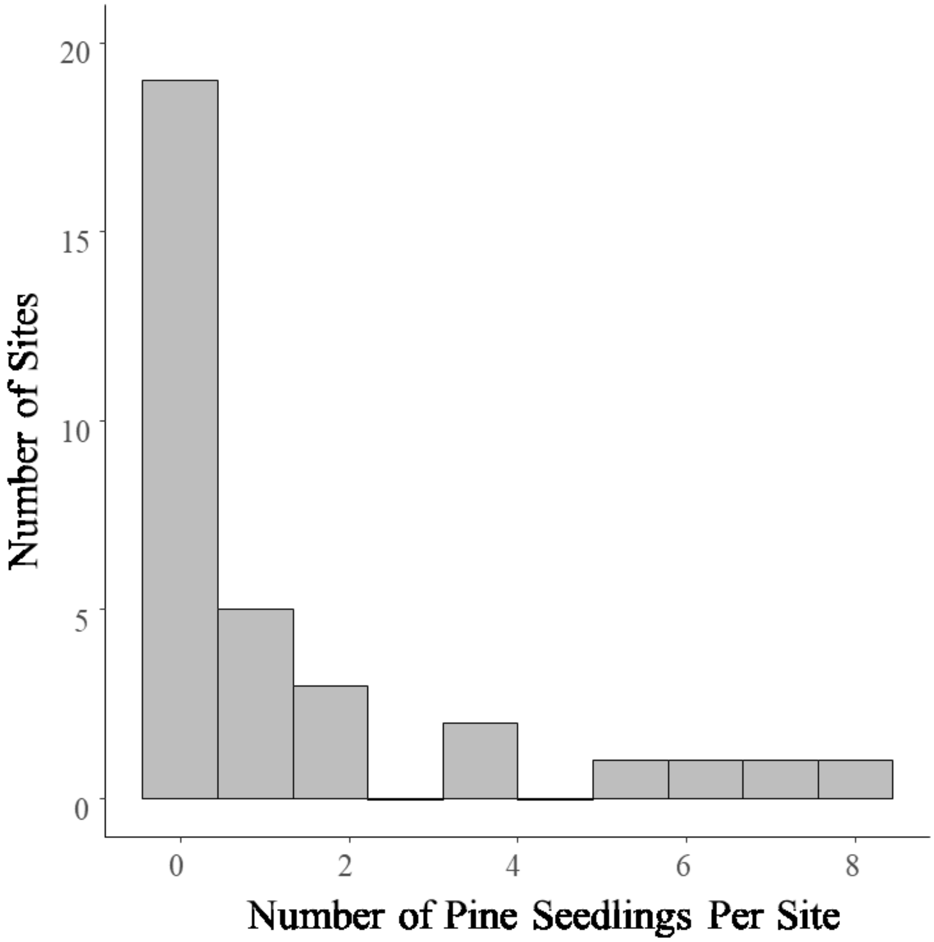

Figure 2-2. The frequency distribution of number of lodgepole pine seedlings found per site (including the four 1x1m seedling plots), throughout MPB-killed stands in west-central Alberta.

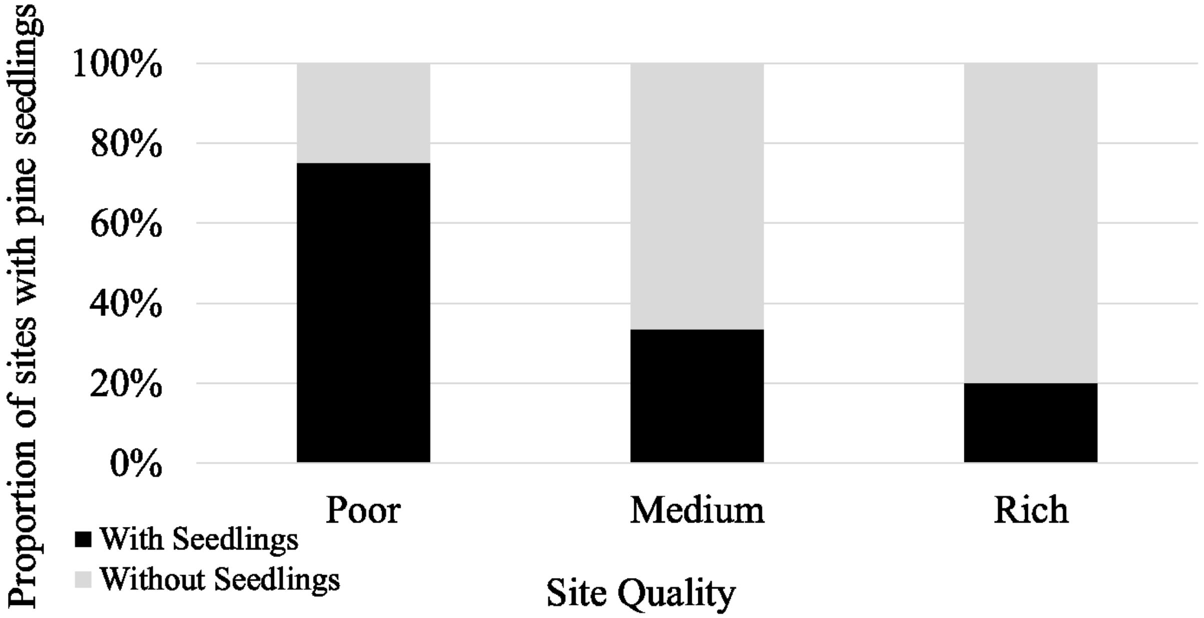

Figure 2-3. The proportion of sites with presence of at least one lodgepole pine seedling (black) and those without (grey), in the poor, medium, and rich site categories. See Appendix 2-2 for information regarding which ecosite types were in each category.

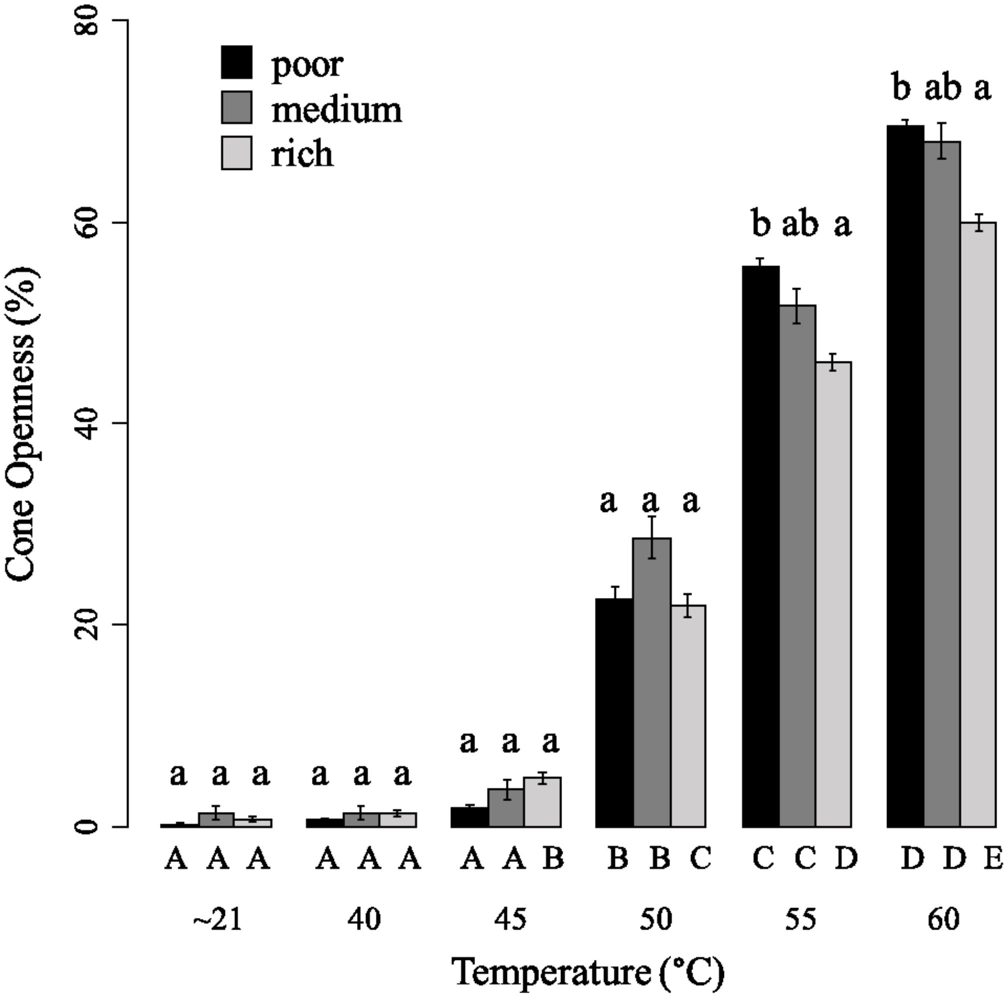

Figure 2-4. Percent cone openness at six temperatures: room temperature (~21), 40, 45, 50, 55, and 60 °C, for three different site quality groups. Cone openness was determined by the amount that cones opened during a heating experiment; cones were placed in an oven at 40°C and the temperature was raised in 5-degree increments after one hour at each temperature, until cones had been exposed to 60°C or cones had fully opened. Upper-case letters (A-E) below signify differences among temperatures within a site quality group and lower-case letters (a, b) above signify differences between site quality groups within a temperature.

Literature Cited

Alfaro, R.I., van Akker, L., and Hawkes, B. 2015. Characteristics of forest legacies following two mountain pine beetle outbreaks in British Columbia, Canada. Can. J. For. Res. **45**: 1387–1396. doi:10.1139/cjfr-2015-0042.

Amman, G.D., and Schmitz, R.F. 1988. Mountain pine beetle: Lodgepole pine interactions and strategies for reducing tree losses. Ambio **17**(1): 62–68. doi:10.2307/4313420.

Astrup, R., Coates, K.D., and Hall, E. 2008. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. For. Ecol. Manage. **256**(10): 1743–1750. doi:10.1016/j.foreco.2008.07.025.

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. For. Ecol. Manage. **257**(9): 1874–1882. doi:10.1016/j.foreco.2009.01.047.

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2010. Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. For. Chron. **86**(1): 87–99. doi:10.5558/tfc86087-1.

Beckingham, J.D., and Archibald, J.H. 1996. Field guide to ecosites of Northern Alberta. Natural Resources Canada, Canadian Forest Service, Nothern Forestry Centre. Special Report **5**.

Beckingham, J.D., Corns, I.G.W., and Archibald, J.H. 1996. Field guide to ecosites of west-central Alberta. UBC Press, Vancouver, BC. 380 pp.

Briggs, J.S., Hawbaker, T.J., and Vandendriesche, D. 2015. Resilience of ponderosa and lodgepole pine forests to mountain pine beetle disturbance and limited regeneration. For. Sci. **61**(4): 689–702. doi:10.5849/forsci.14-192.

Buma, B., Brown, C.D., Donato, D.C., Fontaine, J.B., and Johnstone, J.F. 2013. The impacts of changing disturbance regimes on serotinous plant populations and communities. Bioscience **63**(11): 866–876. doi:10.1525/bio.2013.63.11.5.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. *In* Ecological Modelling, 2nd edition. Springer, Verlag, New York. doi:10.1016/j.ecolmodel.2003.11.004.

Barton, K. 2018. MuMIn: Multi-Modal Inference. R package version 1.40.4. Available from https://CRAN.R-project.org/package=MuMIn.

Burton, P.J. 2008. The mountain pine beetle as an agent of forest disturbance. BC J. Ecosyst. Manag. **9**(3): 9–13. Available from http://jem.forrex.org/index.php/jem/article/viewArticle/402.

Calcagno, V. 2013. glmulti: Model selection and multimodel ingerence made easy. R package version 1.0.7. Available from https://CRAN.R-project.org/package=glmulti.

Calcagno, V., and Mazancourt, C. De. 2010. glmulti : An R Package for easy automated model selection with (Generalized) Linear Models. J. Stat. Softw. **34**(12): 1–29. doi:10.18637/jss.v034.i12.

Carroll, A.L., and Safranyik, L. 2004. The bionomics of the mountain pine beetle in lodgepole pine forests: establishing a context. *In* Mountain Pine Beetle Symposium: Challenges and

Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 21–32.

Cole, W.E., and Amman, G.D. 1980. Mountain pine beetle dynamics in lodgepole pine forests, Part 1: course of an infectation. USDA For. Serv. Intermountain Research Station. Research Paper **INT-89**. 56 pp.

Collins, B.J., Rhoades, C.C., Hubbard, R.M., and Battaglia, M.A. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. For. Ecol. Manage. **261**(11): 2168–2175. doi:10.1016/j.foreco.2011.03.016.

Edwards, M., Krawchuk, M.A., and Burton, P.J. 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. For. Ecol. Manage. **338**: 163–175. doi:10.1016/j.foreco.2014.11.011.

Environment Canada. 2018. Canadian Climate Normals 1981-2010 Station Data. Available from http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=2718&autofwd=1 [accessed 28 February 2018].

Gendreau-Berthiaume, B., Macdonald, S.E., and Stadt, J.J. 2018. Importance of the canopy in determining on-going regeneration and stand successional development in lodgepole pine forests. J. Veg. Sci. **29**(2): 213–225. doi:10.1111/jvs.12622.

Hart, S.A., and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. CRC. Crit. Rev. Plant Sci. **25**(4): 381–397. doi:10.1080/07352680600819286.

Hawkes, B., Taylor, S., Stockdale, C., Shore, T., Alfaro, R., Campbell, R., and Vera, P. 2004. Impact of mountain pine beetle on stand dynamics in British Columbia. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 177–199.

Heath, R., and Alfaro, R.I. 1990. Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle: A case study. J. Entomol. Soc. Br. Columbia **87**: 16–21. Available from http://cfs.nrcan.gc.ca/publications?id=3074.

Hicke, J.A., Johnson, M.C., Hayes, J.L., and Preisler, H.K. 2012. Effects of bark beetle-caused tree mortality wildfire. For. Ecol. Manage. **271**: 81–90. doi:10.1002/jgrg.20078.

Kayes, L.J., and Tinker, D.B. 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. For. Ecol. Manage. **263**: 57–66. doi:10.1016/j.foreco.2011.09.035.

Klutsch, J.G., Negrón, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., and Caissie, R. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (Dendroctonus ponderosae Hopkins) outbreak in Colorado. For. Ecol. Manage. **258**(5): 641–649. doi:10.1016/j.foreco.2009.04.034.

Lenth, R.V. 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Softw. **69**(1): 1–33. doi:10.18637/jss.v069.i01.

Lotan, J.E. 1964. Initial germination and survival of lodgepole pine on prepared seedbeds. USDA For. Serv. Intermountain Research Station. Research Paper **INT-29**: 1–8.

Lotan, J.E., Brown, J.K., and Neuenschwander, L.F. 1985. Role of fire in lodgepole pine forests. *In* Lodgepole pine, the species and it management Symposium proceedings. *Edited by* D. Baumgartner et al. Washington State University, Pullman. pp. 133–152.

Lotan, J.E., and Critchfield, W.B. 1990. Pinus contorta Dougl. ex. Loud. *In* Silvics of North America, Agricultur. *Edited by* R.M. Burns and B.H. Honkala. Washington, DC. pp. 302–315. doi:10.1094/PHYTO-95-0284.

McCune, B. 2007. Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. J. Veg. Sci. **18**(2002): 751–754. doi:10.1658/1100-9233(2007)18%5B751:IEOIRA%5D2.0.CO;2.

McCune, B., and Keon, D. 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. **13**(4): 603–606. doi:10.1111/j.1654-1103.2002.tb02087.x.

McIntosh, A.C.S., and Macdonald, S.E. 2013. Potential for lodgepole pine regeneration after mountain pine beetle attack in newly invaded Alberta stands. For. Ecol. Manage. **295**: 11–19. doi:10.1016/j.foreco.2012.12.050.

Moisey, D., Young, J., Lawrence, D., Stone, C., and Willoughby, M.G. 2012. Guide to range plant community types and carrying capacity for the dry and central mixedwood subregions in Alberta. 7th edition. Alberta Environment and Sustainable Resource Development, Lands Division. Pub. No. **T/276**.

Morris, J.L., Mustaphi, C.J.C., Carter, V.A., Watt, J., Derr, K., Pisaric, M.F.J., Anderson, R.S., and Brunelle, A.R. 2015. Do bark beetle remains in lake sediments correspond to severe outbreaks? A review of published and ongoing research. Quat. Int. **387**: 72–86. doi:10.1016/j.quaint.2014.03.022.

Muir, P. 1993. Disturbance Effects on Structure and Tree Species Composition of Pinus Contorta in Western Montana. Can. J. For. Res. **23**: 1617–1625.

Muir, P.S., and Lotan, J.E. 1985. Disturbance History and Serotiny of Pinus contorta in Western Montana. Ecol. **66**(5): 1658–1668.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. *Compiled by* D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. **1/005**.

Nealis, V.G., and Peter, B. 2008. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests. Canadian Forest Service, Pacific Forestry Centre, Information Report **BC-X-417**: 31 pp.

Oboite, F.O. 2018. Growth of understory spruce following mountain pine beetle attack and recalibration and validation of the Mixedwood Growth Model for black spruce. PhD thesis, Dept. of Renewable Resources, University of Alberta.

Ono, H. 2004. The mountain pine beetle: Scope of the problem and key Issues in Alberta. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 62–66.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team. 2016. _nlme: Linear and Nonlinear Mixed Effects Models_. Available from http://cran.r-project.org/package=nlme.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. Bioscience **58**(6): 501–517. doi:10.1641/B580607.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Roe, A.L., and Amman, G.D. 1970. The mountain pine beetle in lodgepole pine forests. USDA For. Serv. Intermountain Research Station. Research Paper **INT-71**: 26 pp. doi:10.5962/bhl.title.68786.

Safranyik, L., Shrimpton, D., and Whitney, H. 2002. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service, Pacific Forestry Centre. Forestry Technical Report **1**: 23 pp.

Sharpe, M., Hwang, H., Schroeder, D., Ryu, S.R., and Lieffers, V.J. 2017. Prescribed fire as a tool to regenerate live and dead serotinous jack pine (Pinus banksiana) stands. Int. J. Wildl. Fire **26**(6): 478–484. doi:10.1071/WF17046.

Sibold, J.S., Veblen, T.T., Chipko, K., Lawson, L., Mathis, E., and Scott, J. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. Ecol. Appl. **17**(6): 1638–1655.

Stone, W.E., and Wolfe, M.L. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. Vegetation **122**(1): 1–12. doi:10.1007/BF00052811.

Stretch, V., Gedalof, Z., Cockburn, J., and Pisaric, M.F.J. 2016. Sensitivity of reconstructed fire histories to detection criteria in mixed-severity landscapes. For. Ecol. Manage. **379**: 61–69. doi:10.1016/j.foreco.2016.08.009.

Stuart, J., Agee, J., and Gara, R. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. Can. J. For. Res. **19**: 1096–1104.

Teste, F.P., Lieffers, V.J., and Landhäuser, S.M. 2011a. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecol. Appl. **21**(1): 150–162. doi:10.1890/09-1881.1.

Teste, F.P., Lieffers, V.J., and Landhäusser, S.M. 2011b. Viability of forest floor and canopy seed banks in pinus contorta var. latifolia (pinaceae) forests after a mountain pine beetle outbreak. Am. J. Bot. **98**(4): 630–637. doi:10.3732/ajb.1000252.

de Ville, N. 2013. Forest light and structure in relation to disturbances: comparing mountain pine beetle, wildfire and salvage logging. MRM thesis, School of Resource and Environmental Management, Simon Fraser University.

Appendices

Appendix 2-1. The ecosite types visited, in each of the natural subregions (Natural Regions Committee 2006). Poor sites included ecosite types ‘a’ and ‘b’, medium sites included ecosite types ‘c’ and ‘d’, and rich sites included ecosite types ‘e’ and ‘f’ (Beckingham and Archibald 1996, Beckingham et al. 1996, Moisey et al. 2012).

Boreal Highlands (BH)	**Boreal Mixedwood (BM)**	**Lower Foothills (LF)**
c (Labrador tea-mesic Pl-Sb)	a (Lichen Pj)	d (Labrador tea-mesic Pl-Sb)
	b (Blueberry Pj-Aw)	e (Low-bush cranberry Pl)
	e (dogwood)	f (Bracted honeysuckle Pl)

Appendix 2-2. A description of each explanatory variable that was included in the model selection process, including whether they were continuous or categorical.

Category	Variable	Data Type	Description
Ground	tall	Continuous	Percent cover of tall shrubs
	low	Continuous	Percent cover of low shrubs
	forb	Continuous	Percent cover of forbs
	graminoid	Continuous	Percent cover of graminoids
	lichen	Continuous	Percent cover of lichens
	bare	Continuous	Percent cover of bare ground/mineral soil
	leaf_litter	Continuous	Percent cover of leaf litter
	needle_litter	Continuous	Percent cover of needle litter
	wood	Continuous	Percent cover of wood, regardless of decay class
	total_veg	Continuous	Percent cover of all vascular ground vegetation combined (shrubs, forbs, graminoids)
	green_moss	Continuous	Percent cover of green (healthy) moss
	brown_moss	Continuous	Percent cover of brown (dead) moss
Tree/canopy	BA_total	Continuous	Basal area of all trees (live and dead)
	BA_live	Continuous	Basal area of all live trees

Category	Variable	Data Type	Description
Tree/canopy	BA_dead	Continuous	Basal area of all dead trees
	BA_Pl_live	Continuous	Basal area of all live pine trees
	BA_Pl_dead	Continuous	Basal area of all dead pine trees
	BA_bl	Continuous	Basal area of all broadleaf trees (live and dead)
	BA_spruce	Continuous	Basal area of all spruce trees (live and dead)
Advance Regeneration	DA_bl_h	Continuous	The density of advance regeneration for all broadleaf species, based on spacing and median height
	DA_bl	Continuous	The density of advance regeneration for all broadleaf species
	DA _con_h	Continuous	The density of advance regeneration for all conifer species, based on spacing and median height
	DA _con	Continuous	The density of advance regeneration for all conifer species
	DA _Pl_h	Continuous	The density of advance regeneration for pine, based on spacing and median height
	DA _Pl	Continuous	The density of advance regeneration for pine
	DA_con_nopl_h	Continuous	The density of advance regeneration for all conifer species except pine, based on spacing and median height
	DA_con_nopl	Continuous	The density of advance regeneration for all conifer species except pine

Category	Variable	Data Type	Description
Site	size	Continuous	The size of the pine stand that was killed by MPB (ha)
	radiation	Continuous	The potential direct incident radiation, based on slope, aspect, and latitude
	elevation	Continuous	The elevation (meters above sea level) of the site
	sq	Categorical	Groups of ecosites (3) representing site quality (moisture and nutrients) (see Appendix 2-1).
	eco_score	Continuous	Ecosite score – based on the nutrients and moisture of a site; estimated from location of ecosite on edatopic grid
Cone Openness*	CO_50	Continuous	Cone openness (percent open) potential of pine cones collected from ~ 1 meter of the ground, after being heated to 50°C
	CO_55	Continuous	Cone openness (percent open) potential of pine cones collected from ~ 1 meter of the ground, after being heated to 55°C
	CO_lh	Categorical	Naturally occurring cone openness category: Low or high; determined by averaging pine cone openness of ground and elevated cones for each site and comparing that value to the mean for the year (2015 or 2016) in which the cones were collected.

* Cone openness was included only for a subset of 31 sites (two sites did not have closed cones and could therefore not be included in the heating experiment)

Appendix 2-3. The number of sites with seedlings or advance regeneration of a variety of species, found in MPB-killed stands throughout west-central Alberta.

Species	**# sites with seedlings**	**# sites with advance regeneration**
Pine	14	13
Spruce*	20	29
Tamarack	1	0
Subalpine fir	0	1
Aspen	14	9
Birch	3	14
Poplar	3	3

* Includes both black and white spruce

Chapter 3: Impacts of simulated mountain pine beetle attack and salvage logging on understory vegetation seven years post-treatment in lodgepole pine stands in west-central Alberta

3.1 Introduction

Natural disturbances are important for driving successional change in forests through their effects on vegetation, the environment, and resource availability. The disturbance regime of an area can be dominated by natural or anthropogenic disturbances that vary in size and intensity. Less intense disturbances are stand-releasing/modifying while more intense ones are stand-replacing/initiating. Forests are adapted to the natural disturbance regime they have historically experienced. Alberta's lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) forests are primarily adapted to stand-replacing fire disturbance due to wildfire (Sibold et al. 2007). Mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Coleoptera: Scolytidae; MPB) is a bark beetle that is native to western North America, including British Columbia (BC) (Ono 2004). MPB consumes the phloem of pine trees, which girdles and kills them (Safranyik et al. 2002), and acts as a stand-releasing disturbance (Axelson et al. 2010). However, a recent (since 2006) range expansion of MPB eastward from BC has led to an unprecedented MPB outbreak in Alberta (Nealis and Peter 2008).Various interacting factors including host requirements, increased beetle density, escape from predators, and warmer weather patterns due to climate change have resulted in increased brood survival (Raffa et al. 2008), have allowed the beetles to expand their distribution (Nealis and Peter 2008). This is leading to a shift in the disturbance regime of Alberta's lodgepole pine forests to include MPB attack. With continuing climate change, there is a great risk of population growth continuing to increase (Morris et al. 2015). Thus, there is a great risk of this devastating bark beetle continuing its journey further eastward through Alberta's pine forests and beyond across Canada's boreal jack pine forests. Compounding the effects of this novel management issue is the common practice of salvage logging MPB-attacked stands in Alberta (ASRD 2007), which shifts the type of disturbance from stand-modifying to a stand replacing/initiating disturbance. The potential long-term impacts of MPB attack and post-attack forest management, specifically salvage logging, remain unknown.

Differing disturbance types can result in different forest understory plant communities (Rees and Juday 2002) and this can have long lasting effects on subsequent forest communities (Chapin et al. 2004). Unlike stand-replacing disturbances such as fire, a stand-modifying disturbance like MPB kills the overstory but does not directly disturb the understory or forest floor (Burton 2008); remaining vegetation acts as a biological legacy, strongly influencing the future successional trajectory of a forest stand. These impacts can vary with the severity of attack.

The effects of overstory mortality on the understory environment and vegetation following MPB attack will also vary over time. Changes to the overstory are not seen within the first year after attack while needles are still green (green-attack), but after 1-3 years needles turn red (red-attack), and within 4-5 years of attack needles have fallen (grey-attack). Overstory mortality and time post-attack will affect conditions in the understory such as light, soil moisture and nutrients, soil temperature, available space, and competition; in turn, these conditions will indirectly affect understory vegetation abundance, composition, and distribution (Stone and Wolfe 1996, Barbier et al. 2008, Axelson et al. 2009, Pec et al. 2015). The environmental changes resulting from tree death and needle loss following MPB can result in a release of understory vegetation due to compensatory responses (Edwards et al. 2015, Pec et al. 2015), increasing both abundance and density of understory vegetation, accompanied by a change in composition. These changes can also result in increased density and cover of species already present in the understory; these can begin to dominate the understory, preventing seedling regeneration and hindering successional development (Royo and Carson 2006). Increases in light, space, moisture, and nutrients following MPB-caused canopy death in Utah released existing understory vegetation and facilitated establishment of new vegetation (Stone and Wolfe 1996). McCambridge et al. (1982) also found changes to understory vegetation in grey attack stands in Colorado. Initial studies by McIntosh and Macdonald (2013) and Klutsch et al. (2009) found understory vegetation did not respond immediately, and exhibited resistance to MPB attack in red-attack stage. This apparent understory vegetation resistance may be temporary and as stands transition into grey-attack stage, understory vegetation changes may become more pronounced.

Although studies have begun to emerge in Alberta concerning the response of understory vegetation to MPB attacks (McIntosh and Macdonald 2013, Pec et al. 2015), no long-term studies have yet been conducted. This study quantifies the responses of understory vegetation to a gradient of simulated MPB-induced canopy death to determine what epidemic level attacks in Alberta, where MPB is a novel management issue, might mean for understory diversity in grey-attack forests. The main objective of this study was to measure effects of MPB attack and salvage logging on forest understory vegetation and resources in stands in west-central Alberta that were subjected to a simulated MPB attack treatment, in order to determine the most likely future forest structure and successional pathways. I expected to find increases in light, litterfall, soil moisture, and available soil nutrients along the gradient of increasing disturbance, and I anticipated that these would be associated with increasing vegetation abundance and diversity. The results of this study will be useful for informing forest management planning regarding the need for rehabilitation of lodgepole pine forests in Alberta following MPB attack.

3.2 Methods

3.2.1 Study Area and Experimental Design

The study area was located southeast of Robb, Alberta (53°13'17.9148" N, 116°59'1.5972" W, 1,130 meters above sea level) in the Upper Foothills Natural Subregion (Natural Regions Committee 2006) on a fairly flat area, and the studied forest stands were classified as ecosite UF e1.1 – Pl/green alder/feathermoss (Beckingham et al. 1996). The area was dominated by lodgepole pine of approximately 110–120 years old, with trees ranging from 22-24 meters in height (McIntosh and Macdonald 2013). The regional climate in this area is temperate continental (Natural Regions Committee 2006). The area receives an average of 507.9 mm of precipitation per year and has a mean daily average of -9.2°C during the coldest month and 14.4°C during the warmest month (Environment Canada 2018).

The study was set up as a repeated measures randomized block design in 2008. It contained three replicate blocks, each comprised of four 0.48 ha (60-m x 80-m) plots that underwent different treatments. Each treatment plot contained nine nested sampling points set up in a systematic grid (a minimum distance of 20 m between sampling points) in which we collected data on a variety of forest structure, vegetation, and abiotic variables (n=3 blocks, each with 4 treatment plots, each with 9 sampling points = 108 sampling points). Each sampling point had a 1x1 m permanent plot (quadrat) established for understory vegetation, and trees were tagged within an 8-m radius. Treatments, applied in 2009, represented a gradient of disturbance intensity and included: an untreated control, moderate mortality (50% kill), high mortality (100% kill), and salvage logged. The 50% and 100% kill treatments were achieved by subjecting trees to glyphosate-induced girdling to mimic MPB attack while clearcutting simulated salvage logging (McIntosh and Macdonald 2013). Treatments were randomly assigned to plots within the blocks, except for the salvage logging which was located in the plot closest to the road in order to reduce impacts from the machines used to apply the treatment (McIntosh and Macdonald 2013).

Simulated MPB kill was achieved by chemically girdling trees with glyphosate (N-(phosphonomethyl)glycine), a systemic herbicide, which can be used as a desiccant, defoliation aid, and growth retardant (Baylis 2000). Glyphosate inhibits the enzyme 5-enolpyruvylshikimate 3-phosphate synthase, which blocks aromatic amino acid production, affecting protein synthesis; photosynthesis is reduced and chlorophyll is degraded (Baylis 2000). Trees were injected with herbicide capsules (Glyphosate 0.15 grams per capsule, EZ-Ject sytem, ArborSystems, Omaha, NE; http://www.ezject. com/) equally spaced around the circumference of the tree near the base of the bole. For trees with a 10–20 cm diameter at breast height (DBH) the rate was 1 capsule per 5 cm DBH, while smaller trees were injected with 1 capsule per 3 cm DBH (McIntosh and Macdonald 2013). In the high severity (100% kill) treatment, all trees >10 cm DBH were injected while in the moderate severity (50% kill) treatment, every third tree >10 cm DBH was injected; this recognized that there would be some glyphosate transfer to neighbouring trees (McIntosh and Macdonald 2013).

Harvesting was completed by West Fraser Timber Company in July and August 2009. A feller-processor unit was used for stump-side processing with in-situ de-limbing (debris and cones left on site), and there was no site preparation or planting (McIntosh and Macdonald 2013). All trees were cut, and trees were not injected with glyphosate prior to harvesting.

3.2.2 Data Collection

Data were collected one year prior to treatment as a reference (2008), in the year of treatment (2009), one year post-treatment (2010), five years post-treatment (2014), and most recently seven years post-treatment (2016) to determine longer term effects of simulated MPB attacks in Alberta. The exceptions were that overstory stem data were not collected in the year of treatment, and were collected four, instead of five, years post-treatment (See Appendix 3-1). Canopy cover data were, additionally, collected three and four years post-treatment. No overstory data were collected in the salvage logged treatment (because all the trees were harvested). Dead woody material and forest floor depth data were not collected five years post-treatment. Soil moisture data were collected using an alternate method in 2016. Data collected in 2008, 2009, and 2010 were reported on previously (McIntosh and Macdonald 2013).

3.2.2.1 Overstory

Data were collected from all overstory trees (dbh ≥ 5 cm and height > 1.3 m) in 8-m radius circular plots (0.02 ha) at each of the 108 sample points. Species, live/dead status, crown vigour of live trees (healthy=no to a few red needles, declining=intermediate amount to all red needles), and decay class of dead trees (1=recently dead with fine branches; through 5=all bark and branches gone) were recorded. DBH was measured for all trees that had a DBH greater than 5 cm and a height of more than 1.3 m. A hypsometer (Vertex) was used to measure height for a subsample of trees, including a minimum of two trees in each of the upper, mid, and lower canopy. Stem density (tph) and basal area (m^2/ha; BA) were assessed by crown vigour class (healthy, declining, and dead).

The percent canopy cover was determined using hemispherical photographs (digital Nikon Coolpix 4500 with a FC-E8 (0.21x) fisheye converter lens). Photos were taken at the peak of the growing season in mid-July. The camera was levelled on a tripod at approximately 1.3 meters above the forest floor, and the bottom of the camera was oriented towards North. Auto-bracketing was used at -3, 0, and +3 to achieve optimal light settings, and a timer was used to eliminate the risk of movement while the photograph was being taken. The canopy photographs were analyzed using SLIM (Spot Light Intercept Model Version 3.02a). Batch processing was used; separate batches were created for plots and colour thresholds were manually adjusted for each batch. Once gap fraction ratio was calculated for each quadrat, it was subtracted from 100 to determine the percent canopy cover at that sampling point.

3.2.2.2 Above-ground

Dead woody material (DWM) was measured along an 8-m transect originating from each sampling point using the line intersect method (Van Wagner 1968, 1982, Brown 1974, Brown et al. 1982). The direction of the transect was randomly selected during the establishment of the experiment and the same direction was used each year that sampling occurred. At each point of intersection, the diameter of the DWM was measured with calipers. DWM pieces were categorized into diameter size class categories: 0-0.5, 0.5-1.0, 1-3, 3.5, 5-7, and >7 cm (McRae et al. 1979, Van Wagner 1982). DWM of all size classes were counted within the first two meters of the transect, only pieces of DWM that were greater than 3 cm in size were counted between 2 and 4 m along the transect, and only DWM that was greater than 7 cm were counted between 4 and 8 m along the transect. Diameter, length, and decay class (Classes 1-5, based on Table 8.1 in VRI 2007) were measured for all pieces greater than 7 cm along the entire 8 meter transect. The biomass (Mg ha^{-1}) of DWM was calculated for each size class, using values for *Pinus contorta* in the Central Alberta Foothills (Nalder et al. 1997). Biomass for large pieces of DWM (>7 cm diameter) was calculated separately for sound (decay classes 1-3) and rotten (decay classes 4-5) downed wood (Delisle and Woodard 1988). Total biomass was calculated for all, small (0-7 cm), and large (>7 cm) pieces of DWM.

At each sampling point, percent cover was visually estimated to the nearest percent within 1-m x 1-m quadrats for all vascular plant species, the common forest floor mosses and for general ground cover types (all mosses, all lichens, litter, coarse woody debris, exposed soils, and rock; see Appendix 2 for full species list). A general walk through census was conducted in each of the 12 plots to account for any species present that were not recorded in the quadrats. Plant species diversity (Shannon Index, Magurran 1988) and richness were calculated for each quadrat, and total percent of vegetation cover was calculated by summing individual covers of each species, including bryophytes. Total cover could exceed 100% due to vertical overlapping of some species. Vegetation richness was also calculated for each plot (data were combined from the quadrats and the census). Percent cover and richness were calculated for each different vegetation group (forbs, shrubs, graminoids, and bryophytes) for each quadrat. Forest floor (Fibric/Humic layers) thickness (mm) was measured in each of the four corners of each quadrat.

3.2.2.3 Below-ground

Spot measurements of soil moisture were taken adjacent to each sampling point using a FieldScout TDR 300 soil moisture meter (Spectrum Technologies, Inc.). The top forest floor layer was scraped to the side so that the bottom of the probe was flush against the mineral soil, and the volumetric water content mode for standard soils was used to determine the percent soil moisture content in the root zone, at a depth of approximately 15 cm. Moisture measurements were taken four times during the growing season, once each month from June to September in 2016.

Plant root simulator (PRS®) probe ion exchange membranes (Western Ag Innovations, Inc., SK, Canada) were used to measure soil nutrient availability. Nutrients adsorbed by the probes included both cations (NH_4^+, K^+, Ca^{2+}, Mg^{2+}, etc.) and anions (NO_3^-, SO_4^{2-}, etc.). Four pairs of cation and anion probes were installed at each understory quadrat, with one pair in each corner. The probes were placed vertically so that the top of the probe was at mineral soil level so that nutrients were collected from the root zone (at a depth of approximately 10 cm). These soil nutrient probes were left for the duration of the growing season (mid-June to mid-September) before being removed and cleaned thoroughly with de-ionized water. The four cation and anion pairs from each quadrat were combined as one sample and sent to Western Ag for analysis of nutrient supply rates. Nutrients that commonly had supply rates below the minimum detection limit (at least 50% of plots) were excluded from analysis (NO_3N (n=336/540<MDL), Cu (n=470/540<MDL), Pb (n=332/540<MDL), and Cd (n=440/540<MDL)).

3.2.3 Data Analyses

3.2.3.1 Univariate Analyses

Analyses of univariate response variables (e.g. canopy cover, soil moisture, species cover, richness, diversity, and individual nutrients) were conducted by repeated measures mixed effect ANOVA models using the lme function in nlme (Pinheiro et al. 2016) using R Version 3.2.2 (R Core Team 2015). Treatment and time (repeated measure) were considered fixed variables while block and plot were considered nested random effects. Normality and homogeneity of variance of residuals were assessed visually for all models. Outliers were removed where present and log or square root transformations were applied when necessary. Residuals were visually assessed again post-transformation. Where significance of an individual response variable to treatment or treatment*time interaction was indicated (α=0.05), lsmeans (Lenth 2016) was used to conduct pairwise post-hoc tests to look for treatment effects among years for each treatment and among treatments for each year. Comparisons were made among all treatments (except salvage logged for overstory variables) and among all years (except BA was only compared between one year pre-treatment and seven years post-treatment, moisture was only compared among months seven years post-treatment, and plot level species richness was only compared among treatments seven years post-treatment to examine if differences due to treatments had arisen at that time). If year but not treatment or a treatment*year interaction was significant, lsmean post-hoc tests were used to compare among years for all treatments combined (except year was replaced with month in 2016 for soil moisture). Tukey-adjusted α-values were used for all post-hoc comparisons (family wise α=0.05). For overstory variables, salvage logged was excluded from analyses due to a lack of overstory present in the stands post-treatment.

3.2.3.2 Multivariate Analyses

For multivariate analysis of vegetation composition, only the 27 most common species (species found in at least 5% of the plots) were considered. Ecodist was used to fit the vegetation species abundance data to a Bray-Curtis distance index (Goslee and Urban 2007). Ape (version 4.1) was then used to apply a Principal Coordinate Analysis (PCoA) to the vegetation distance matrix, with no correction (Paradis et al. 2004). The PCoA was plotted to visualize variation in community composition at the plot level. The capscale function in Vegan was used to extract the eigenvalues from this distance matrix to calculate the proportion of variance explained by each axis (Oksanen et al. 2017). PCoA scores were extracted and rearranged to overlay successional vectors to visualize the trajectory of how the plant communities changed within each treatment over time.

A distance based redundancy analysis (dbRDA) was used on the understory vegetation to determine whether understory vegetation communities were significantly different between treatments and years. This was done using the capscale function in Vegan, using the Bray-Curtis distance index (Oksanen et al. 2017). This constrained ordination was first applied to all years to see if there was a treatment*year interaction, then each year individually to see differences between treatments within each year. Significance of the dbRDA model terms were assessed using 999 permutations.

An Indicator Species Analysis (Dufrêne and Legendre 1997) was conducted in PC-ORD 5.10 to identify species that showed a particular affinity for a given treatment in a given year (McCune and Mefford 2006). Default settings, including a Monte Carlo test with 1000 randomizations, were used to assess significance of species as an indicator.

3.3 Results

3.3.1 Above-ground

As expected, there was an increase in dead trees and a decline in healthy trees over time post-treatment in both the MPB-killed treatments (Tables 3-1, 3-2). By seven years post-treatment, tree density and basal area (BA) of trees were representative of the treatments applied; there were more healthy trees in the control than the 50% kill, with the least in the 100% kill, and there were more dead trees in the 100% kill compared to the 50% kill or control (Table 3-2; Figure 3-1). The density and BA of declining trees increased in the control and 50% kill between one year prior to treatment and seven years post-treatment, while there was no difference over time in the 100% kill (Table 3-2; Figure 3-1).

Canopy cover did not change over time in the control and it was temporarily reduced three years post-treatment in the 50% kill; in the 100% kill it showed a significant decline by three years post-treatment and then remained there (Table 3-1, 3-2). By seven years post-treatment, canopy cover was lower in the 100% kill than the 50% kill and the control, which did not differ from one another (Table 3-2).

As expected, changes in DWM over time from the pre-treatment to seven years post-treatment time period were minor and the only significant differences among treatments were differences in the salvaging logging treatment (Table 3-1, 3-3). The biomass of small pieces (0-7 cm) of DWM increased temporarily after the salvage logging; this was primarily due to changes in the biomass of the smaller pieces (0-3 cm diameter) (Table 3-3). The biomass of larger (> 5 cm diameter) and rotten DWM showed minor variation over time, irrespective of treatment (Table 3-4).

There were some temporary changes in ground cover, but minimal differences were visible seven years post-treatment. There was some variation in litter cover over time within each treatment but the only significant treatment effects, again, were due to the difference between the salvage logging and the other treatments (Table 3-2). There was minimal rock and mineral soil cover found in any of the plots in any of the years, and so these variables were not further examined.

Vegetation richness and diversity were both impacted by treatment and time (Table 3-1). As expected, more severe treatments had larger increases in richness, which occurred along the gradient of treatment intensity. There were 47 species found one year before treatment and 66 species found seven years post-treatment across all treatments (Figure 3-2; Appendix 2). Vegetation richness per quadrat increased in the 50% and 100% kill seven years after treatment relative to previous years but decreased in the salvage logged plots during the year of treatment and remained low the following year before gradually increasing five and seven years post-treatment (Table 3-2). One year post-treatment, richness was lower in salvage logged compared to the 100% kill, while the other two treatments were intermediate; by seven years post-treatment, the salvage logged areas had higher richness compared to the control, while both MPB-killed treatments had intermediate levels (Figure 3-2). Shannon diversity showed only minor variation among years in the control and 50% kill, but in the 100% kill diversity was higher seven years post-treatment relative to all other years. In salvage logged plots, diversity decreased during the year of treatment, where it remained until seven years post-treatment when it returned to pre-treatment levels (Table 3-2). Total species richness per plot (based on the quadrats and the survey) seven years post-treatment did not differ among treatments (Table 3-1). Graminoid richness increased over time in the 100% kill and salvage logged treatments such that by five and seven years post-treatment it differed among treatments following the gradient of disturbance intensity (i.e., lowest in the control, higher in the 50% then 100% kill, highest in the salvage logged treatment) (Table 3-2). Both forb and shrub richness also increased over time in the 100% kill while in the salvage logged treatment they decreased during the year of, and one year after, treatment before returning to (shrubs) or exceeding (forbs) pre-treatment levels by seven years post-treatment (Table 3-2). There were no differences in shrub or forb richness among treatments (Table 3-2). Bryophyte richness varied slightly over time in the control, 50% kill, and 100% kill but decreased in the salvage logged treatment during the year of and one year post-treatment, before gradually increasing until by seven years post-treatment it had surpassed pre-treatment levels (Table 3-2). The only significant treatment effect on bryophyte richness was that it was lower in the salvage logged treatment one year post-treatment.

While I anticipated that vegetation cover would increase with canopy removal or tree mortality, total vegetation cover varied over time in all treatments, including the control; the only notable treatment effect was that cover declined post-treatment with salvage logging; in the year of and one year post-treatment it was lower than in the other treatments but those differences disappeared thereafter (Tables 3-1, 3-2). Different vegetation types responded differently. Graminoid cover did not change over time in the control or 50% kill, but increased in the other two treatments such that by five and seven years post-treatment it followed the gradient of treatment intensity (Figure 3-3c). While shrub cover did not change over time in the control or either of the MPB-attack levels, forb and bryophyte cover showed minor variations over time in those treatments (Figure 3-3a, b, d). Shrub, forb, and bryophyte cover were impacted the most heavily by salvage logging, declining one year post-treatment at which time they were lower than in the other treatments. Cover of all three subsequently increased in the salvage logged treatment such that there were no differences among treatments by seven years post-treatment (Figure 3-3a, b, d). In the year of treatment through five years post-treatment, bryophyte cover was lowest in salvage logged, relative to the other treatments.

Vegetation compositional changes also followed the gradient of treatment intensity, with the most compositional changes in the salvage logged treatment. The PCoA solution required 30 axes to explain 100% of the variance, but the first two axes explained 46.1% of the variation (30.6% and 15.6% for axes 1 and 2, respectively) (Figure 3-4). Successional vectors overlaid on this PCoA showed that the salvage logging resulted in the largest amount of change, especially immediately post-treatment. Between five and seven years post-treatment the composition began to return to the direction from which it originated (Figure 3-4). The 100% kill experienced the next largest amount of change, in the same direction as salvage logged, but not to the same extent (Figure 3-4). The 50% kill only experienced a slightly larger change in community composition than the control (Figure 3-4). A dbRDA indicated community composition was affected by a significant interaction between treatment and year (p=0.023). Examination of differences between treatments in individual years indicated no difference between treatments one year pre-treatment, but there were significant differences between treatments one year through seven years post-treatment (Figure 3-5a-d). While vegetation communities overlapped in the pre-treatment year (2008) (Figure 3-5a), one year post-treatment (2010) showed salvage logged to be quite different from the other three treatments which were still fairly similar to one another (Figure 3-5b). Five years post-treatment (2014) salvage logged was still quite different from the other three treatments, but control was starting to become even more different from salvage logged (Figure 3-5c). By seven years post-treatment (2016) there was no overlap between the treatments; salvage logged and control were the most different from one another with the 50% kill and 100% kill intermediate between them but closer to the control (Figure 3-5d).

An indicator species analysis showed that seven years post-treatment several species were affiliated with particular treatments, mostly notably with salvage logging. *Pinus contorta*, various grass and forb species, and *Polytrichum commune* were indicators of the salvage logging treatment, while common feathermoss species were indicators of the control (Table 3-5).

3.3.2 Below-ground

Soil moisture was not significantly different between treatments seven years post-treatment (Tables 3-1, 3-5). Although the time by treatment interaction was significant for forest floor depth, subsequent analyses showed no significant differences between treatments in any year; there was a decrease in depth over time in all treatments, including the control (Tables 3-1, 3-2).

Differences in individual nutrient supply rates among treatments occurred occasionally, mostly in the year of, or immediately post-treatment and these primarily reflected the gradient of disturbance intensity with the salvage logged treatment being most notably different from the control (Tables 3-1, 3-2). These included short-term post-treatment increases in Ca, Mg and P supply rates (Table 3-2). Other nutrient supply rates experienced minor variations among treatments (Tables 3-1, 3-2). There were temporary increases in Mn supply rates in the lower severity treatments (control and 50% kill), NH_4-N supply rates in the control and salvage logged treatments, and S supply rates in salvage logged treatment (Table 3-2; Figure 3-6). For other nutrients responses were delayed; seven years post-treatment there were increased K supply rates in the salvage logged treatment, declines in Mn supply rates in the higher severity treatments (100% kill and salvage logged), declines in S supply rates in the control and simulated-MPB treatments, and declines in B supply rates in all treatments (Table 3-2).

Other nutrient supply rates were only impacted by year, not treatment (Table 3-1). These short-term changes occurred either during the year of treatment, or immediately afterwards and by seven years post-treatment, supply rates had returned to pre-treatment levels (Fe and Zn) or decreased below pre-treatment levels (Al) (Table 3-4).

3.4 Discussion

The results of this study suggest that mortality of lodgepole pine stands due to simulated mountain pine beetle attack is likely to result in increased understory vegetation richness, limited changes to cover, and a change in vegetation composition along the gradient of treatment intensity; these changes, in turn, will likely influence the ensuing succession of a stand. The observed vegetation changes support our hypothesis that by seven years post-treatment the previously-observed resistance to simulated MPB attack had disappeared with the magnitude of vegetation response varying with the severity of attack. Stands that are not completely killed by MPB (moderate mortality) may not experience substantial understory impacts and may not be able to overcome the ecological inertia, while high severity attack and salvage logging had greater impacts on the canopy and thus on the understory environment and vegetation. Simulated salvage logging, in particular, is likely to result in dramatic changes to the understory, notably much increased abundance of early-successional shade-intolerant species. I did not, however, see the expected increase in soil moisture and nutrients following the higher intensity mortality treatments; I attribute this to compensatory responses by vegetation in these treatments.

3.4.1 Effects of the treatments

Canopy cover, density and basal area (BA) responded as expected, all declining as a result of the simulated MPB treatments. Surprisingly, I observed a decrease in BA of healthy trees in all stands, even in the control. This likely reflects natural senescence of these mature lodgepole pine stands as well as windthrow. During the year of treatment and one year after, extreme wind events were recorded, which caused some blow-down (McIntosh and Macdonald 2013). Interestingly, reductions in canopy cover were less pronounced than the changes in live density and BA. Thus, while standing dead trees lose their needles as they transition to the "grey attack" stage, they still have an ecologically important shading effect on the understory through the effects of their trunks and branches.

Changes to downed woody material (DWM) and litter cover were not as pronounced as expected; logging slash resulted in an increase in small (< 3 cm diameter) pieces in the salvage logged treatment while large pieces (> 7 cm) of DWM increased in all treatments, including the control. This is likely due to natural mortality of trees and blow-down (McIntosh and Macdonald 2013). Klutsch et al. (2009) also found no differences in DWM between infested and uninfested plots 4-7 years post-attack. Other previous studies found increased DWM within a decade after disturbance (Page and Jenkins 2007, Briggs et al. 2015) due to MPB-killed snags having fallen by then. Mitchell and Preisler (1998) estimated that within 6 years of MPB-attack 10% of MPB-killed trees had fallen, and by 12 years post-attack 80% of MPB-killed trees had fallen. It seems that in our study seven years post-treatment there had not yet been substantial fall down of dead, treated trees.

While others have found increases in litter after MPB (Page and Jenkins 2007, Klutsch et al. 2009, Griffin et al. 2011), I saw temporary increases in all treatments. This likely reflects the mortality that was occurring in all stands, as mentioned above. The increase in litter cover in all treatments was most likely due to needles falling as trees experienced mortality (Cigan et al. 2015) and from extreme wind. Increases in salvage logged areas was likely due to logging slash or damage to understory vegetation.

3.4.2 Understory vegetation responses

Understory richness increased along the gradient of treatment intensity, as expected, but only the simulated salvage logging treatment had a significant effect on understory cover. Compositional changes also reflected the gradient of treatment intensity with the strongest and most immediate responses observed in the salvage logging treatment with the next strongest being in the 100% kill; however by seven years post-treatment there was some evidence that the community composition in the salvage logged plots was beginning to show recovery towards the pre-disturbance condition. The previously observed resistance of understory vegetation seen during the red-attack stage seemed to have lessened once the trees reached the grey-attack stage.

Seven years post-treatment, understory vegetation richness increased along a gradient of disturbance intensity (control, 50% kill, 100% kill, salvage logged). This is similar to the increased richness along a gradient of tree mortality found by Pec et al. (2015) in Alberta. In a study in Utah, Stone and Wolfe (1996) found the highest understory vegetation richness in stands of moderate mortality; this was potentially attributable to the fact that the highest mortality sites were also wet with dense graminoid cover. This suggests potential confounding of site conditions and mortality level that would influence vegetation responses.

Different vegetation types responded differently to the varying disturbance levels. Only graminoid richness increased along the gradient of disturbance intensity, although forb and shrub richness increased slightly after the high severity MPB disturbance and forb richness increased after salvage logging. Similar to our results for graminoids, but in contrast to our results for forbs, previous studies, which did not separate forbs and graminoids, have found notable increases in herbaceous, vascular species richness (including forbs and graminoids) after harvesting (Pykälä 2004, Hart and Chen 2008) and after MPB-induced mortality (Pec et al. 2015). Our results for shrub richness in the 50% kill agree with Pec et al. (2015) who also found shrub richness to be resistant to changes resulting from MPB-induced tree mortality. Bryophyte richness did not appear to be impacted by the simulated MPB treatments but it decreased immediately after salvage logging. This is similar to findings by Astrup et al. (2008), who found that the moss dominated forest floor did not change after MPB-attack. It also aligns well with findings by Hart and Chen (2008) who found a decline in non-vascular species diversity after harvesting.

Vegetation cover doesn't always have strong responses to disturbances. Seven years after treatment, total vegetation cover did not appear to be impacted by MPB; it decreased immediately after salvage logging but then recovered. Our results for vegetation responses are similar to Klutsch et al. (2009) who found no changes to vegetation cover after MPB attack, and to Griffin et al. (2013) who found decreased vegetation cover following salvage logging in Wyoming.

Cover of forbs, bryophyte, and shrubs cover did not change with the MPB-related treatments, while graminoid cover increased. These results are fairly similar to previous studies. Klutsch et al. (2009) found no changes in cover for any understory vegetation type within seven years after MPB. Pec et al. (2015) found no changes in shrubs, possibly indicating an ecological resistance to the impacts of MPB. Stone and Wolfe (1996) found higher abundance of graminoids after MPB-attack. Some other studies found contrasting results; shrubs and forbs increased after MPB attack (Kovacic et al. 1985, Stone and Wolfe 1996). Salvage logging, in contrast to MPB attack, had much more dramatic effects; shrub, forb, and bryophyte cover decreased immediately after salvage logging. Graminoid cover, however, increased after salvage logging, eventually surpassing pre-treatment levels. Our results contrast with studies that found increased cover of herbaceous, vascular species (Bock and van Rees 2002, Pykälä 2004, Hart and Chen 2008) and shrub cover after harvesting (Bock and van Rees 2002). It is possible that I did not see an increase of shrubs and forbs because of the dramatic increase in graminoids seen in our results, which may have outcompeted other species. Our results for bryophyte cover, however, are similar to those of Bock and Van Rees (2002) who found decreased bryophyte cover following harvesting.

Seven years post-treatment, differences in vegetation composition were emerging between the treatments, and the treatments had different indicator species associated with each of them. As expected, indicator species in the control were comprised of *Hylocomium splendens* and *Pleurozium schreberi*, shade obligate understory feather moss species that are characteristic of mature lodgepole pine dominated forests in this region. Just as these moss species were indicative of the control in this study, Edwards et al. (2015) found the most notable change in understory vegetation species after MPB-attack was a loss of *P. schreberi* cover, which they attributed to an opening of the canopy accompanying tree mortality resulting in a loss of moisture from the forest floor. After treatments were applied, the loss of moss cover was offset by increases in other species, which differed between the difference severities of mortality. The 50% kill was characterized by *Cornus canadensis* and the 100% kill was characterized by *Aralia nudicaulis*, both of which are often found in the understory in lodgepole pine forests in this region. Previous studies have found that understory vegetation communities after insect-induced mortality tend to exhibit a shift in dominance of species that were already present in the understory prior to disturbance (Ehrenfeld 1980, Hart and Chen 2006). Interestingly, the 100%

kill treatment was also characterized by the prominence of *Rosa acicularis* and *Rubus pubescens*, which are shade-intolerant species common in post-disturbance communities (Hart and Chen 2006). This concurs with previous studies that found increased abundance of vascular understory species following insect-attack that resulted in shifts in understory vegetation composition (Stone and Wolfe 1996, Hart and Chen 2006).

Simulated salvage logging resulted in the most indicator species seven years post-treatment, characterized by primarily shade-intolerant, early-successional species that are common after disturbances and in open areas. Indicator species of the salvage logging treatment in our study included: *Chamerion angustifolium*, *Calamagrostis* spp., *Leymus innovatus*, *Polytrichum commune*, *Pinus contorta*, and *Vaccinium caespitosum*. This is similar to Hart and Chen (2008), who also found many herbaceous indicator species following harvesting. Interestingly, the salvage logging resulted in a shift in the moss community with the feather mosses (*H. splendens* and *P. schreberi*) being replaced by *P. commune*, a bryophyte species that is often found in disturbed areas that can continue to photosynthesize even in hot, dry conditions (Callaghan et al. 1978). This is similar to previous studies that found harvesting reduced feathermosses, which were replaced with vascular species and tolerant bryophytes (Bock and Van Rees 2002, Hart and Chen 2006).

While there was an initial resistance of understory vegetation to the impacts of MPB (McIntosh and Macdonald 2013), some changes in vegetation richness, cover, and composition began to emerge five years after treatment. This is somewhat similar to other studies that also found changes to understory vegetation composition within five years of attack (McCambridge et al. 1982, Kovacic et al. 1985, Pec et al. 2015). Interestingly, by seven years post-treatment, vegetation composition in the salvage logged treatment showed evidence that the community had begun to slowly return in the direction of pre-treatment composition. This supports observations by Rydgren et al. (1998) that within five years, changes to understory vascular plants resulting from less severe ground disturbances were no longer evident.

In the MPB treatments, the canopy cover did not change much, and perhaps the changes in the light environment were not sufficient to result in much response in the understory vegetation. Previous studies that found changes to understory vegetation after a disturbance attributed it to increased resources, including availability of soil nutrients, soil moisture, and light

(Stone and Wolfe 1996, Hart and Chen 2006, Pec et al. 2015). Piña (2013) found increased transpiration of residual trees after simulated MPB-attack. The remaining living trees and understory vegetation may have been released from below-ground competition, allowing them to take up more water and nutrients, thus, compensating for those effects.

Environmental changes that occur following MPB-induced mortality impact the understory to varying degrees. As tree mortality increases, the amount of light that penetrates to the forest floor increases. Combined with reduced competition for resources, this may have been sufficient to allow new species to establish. The environmental changes due to our simulated-MPB treatments, like those due to other insect outbreaks, were not severe, however; this likely explains the relatively minor responses in understory vegetation. Even in the 100% kill treatment, the standing dead overstory may have provided enough shade to sustain and/or release some of the shade-tolerant species already established in the understory. Likewise, in the 50% kill treatment minor changes to resource and light availability were enough to release pre-existing shade-tolerant species. Stone and Wolfe (1996) speculated that with low levels of canopy mortality residual vegetation might outcompete any potential new species; this could explain the minimal vegetation changes observed in our 50% kill.

As compared to the simulated-MPB treatments, the simulated salvage logging resulted in a much more dramatic change to the environment as well as direct disturbance/damage of the vegetation. Previous studies that also found changes to post-harvest understory vegetation attributed this to stress from increased exposure to solar radiation, increased ground-level air temperatures, decreased moisture, and increased competition from pioneer and released shade-intolerant species, including a reduction in feathermosses (Bock and Van Rees 2002, Edwards et al. 2015). Shade-intolerant and disturbance adapted species became prominent in the salvage logged treatment by seven years post-treatment; this likely explains the apparent recovery of vegetation cover and the large change in species composition. Increased resources combined with reduced competition in the 100% kill and salvage logging treatment likely allowed the establishment of new shade-intolerant species, including graminoids. Many of the species that were associated with the salvage logging treatment have below-ground rhizomes that allow them to survive disturbances and thrive when competition is reduced. Other species, specifically *Polytrichum commune*, regenerate through spores which can easily colonize new areas, especially when ground disturbance may have created suitable regeneration and establishment conditions.

3.4.3 Below-ground effects of simulated MPB treatment and salvage logging

Soil moisture did not respond as expected; it did not differ between treatments seven years after treatment. Other studies found soil moisture increased after MPB attack; this can be attributed to reduced precipitation interception due to needle fall and reduced moisture uptake accompanying tree mortality (Kovacic et al. 1985, Dhar and Hawkins 2011, Piña 2013). Compensatory moisture uptake by understory vegetation (Cigan et al. 2015, Pec et al. 2015) and surviving residual trees (Piña 2013) likely explain why stronger moisture responses were not seen.

Effects of the treatments on soil nutrient availability were weak and inconclusive. We had expected an increase in soil nutrient availability due to reduced uptake by trees, increased decomposition due to warmer and moister soils, and increased litter inputs. Results were likely more pronounced in the salvage logged treatment due to the complete loss of canopy and therefore greater changes in environment. The temporary increase of some nutrients (Ca, Mg, P, NH_4-N) in the salvage logged treatment, and slightly in the MPB treatments in some cases, are somewhat similar to other studies. Bock and Van Rees (2002) found nutrient rich material was deposited during harvesting, increasing availabilities of some nutrients (Mg and Ca). Previous studies (Cigan et al. 2015, Pec et al. 2015) found elevated concentrations of macronutrients (N, P, K, and Mg) in needles of MPB-killed pine; increased needle fall and root loss resulted in a flush of nutrients shortly after MPB-induced canopy mortality. Residual vegetation can compensate for increased soil nutrient availabilities by increasing their uptake (Hubbard et al. 2013, Rhoades et al. 2013, Cigan et al. 2015), reducing the amount remaining in the soil (Klutsch et al. 2009). This compensatory response likely explains the vegetation changes accompanied by minimal changes to soil nutrients and moisture. Increased graminoid cover in the salvage logging treatment likely shaded the ground, resulting in cooler soils and lower decomposition rates, rendering environmental conditions similar to the other treatments, which still had shading from standing trees (dead and alive).

Vegetation in higher severity treatments, where vegetation changes were more noticeable, likely used up more Mn. Increased graminoid cover in the salvage logging plots likely increased litter inputs, resulting in increased K supply rates. This contrasts with a study by Bock and Van Rees (2002), who found decreased K availability after harvesting, which they attributed to greater mobility of this nutrient. The differences in B availability that emerged are likely due to newer probes being used five and seven years post-treatment; B is not completely desorbed from nutrient probes during regeneration and may have been present at elevated background levels in the older probes used during earlier years (Western Ag, Personal Communication). For other nutrient availabilities, the results mostly show variation over time in all treatments, including the control. Temperatures and precipitation play important roles in nutrient cycling, so inter-annual variation may impact nutrient cycling more heavily than the impacts of MPB-disturbance do.

3.4.4 Long-term implications of vegetation changes

These changes in understory vegetation may have long term implications for the future of a stand. Our results suggest that understory vegetation can show resistance up to a certain threshold of MPB-caused canopy death; relatively minor changes were observed in the understory environment and vegetation when canopy mortality was low to moderate (≤50%). Interestingly, many stands in Alberta experienced such lower levels of mortality (see Chapter 2). If surviving pine trees can benefit from a release of resources in these low mortality stands they may continue on their current successional trajectories without severe negative consequences from MPB-attack. Similarly, Edwards et al. (2015) found that trait composition remained similar post-MPB as prior to attack; however, they speculate that this will result in the pine dominated canopy shifting to already-present shade-intolerant species, and suggest that fire is required to reset the forest to pine after MPB attacks. In stands that experience higher severity MPB-attack, understory changes, resulting from released residual species and new species establishment, may outcompete new tree seedlings, hinder pine regeneration, and alter the future composition of the overstory, resulting in changes to the successional trajectories.

While the long term impacts of MPB in Alberta are still unknown, previous studies have found that environmental and compositional changes to understory vegetation resulting from disturbances, including MPB-attack, can last up to 25 years or even possibly longer (Dykstra and Braumandl 2006, Hart and Chen 2006, Griffin et al. 2011).

Salvage logging can hinder forest recovery after a disturbance; some species may experience reduced regeneration due to the interacting effects of two consecutive disturbances (MPB and salvage logging) (Lindenmayer et al. 2004). Salvage logging may disperse pine cones, create good regeneration microsites, and provide enough light for pine regeneration, but graminoids may outcompete pine in these stands. *Calamagrostis* has been shown to suppress tree regeneration (Lieffers et al. 1993, Royo and Carson 2006); it can create a dense understory near the soil surface which prevents light from reaching the forest floor and can prevent other species from establishing (Royo and Carson 2006). This suggests that salvage logging has the potential to alter successional trajectories.

3.5 Conclusion

The magnitude of vegetation response varied with the severity of disturbance; simulated salvage logging resulted in the largest changes, then the high severity mortality, then the low severity mortality, then the control. While lower severity MPB resulted in minor changes to the understory vegetation, high severity MPB attacks and salvage logging resulted in increased vegetation richness, accompanied by a change in composition that was primarily due to increased graminoid richness and cover and the establishment of shade-intolerant species. Standing dead trees provided some protection for the understory environment, limiting the vegetation changes that occurred after MPB-attack compared to salvage logging, which had much more dramatic and immediate, although mostly temporary, environmental impacts. Vegetation was able to take advantage of increased soil moisture and soil nutrients, compensating for their increases.

These results indicate that there may be some resistance of understory vegetation up to a certain threshold of canopy death resulting from MPB-attack; while forbs and shrubs may be somewhat resistant to MPB impacts, there were minor increases in richness in the 100% kill as shade-intolerant species were able to establish. Many stands in Alberta have experienced lower levels of mortality, and these stands will most likely remain on their current successional trajectories without severe negative consequences from MPB-attack. However, shade-intolerant species that are released from competition after higher severity MPB-attack may outcompete tree seedlings, potentially delaying pine regeneration and altering the future composition of the overstory. Salvage logging may result in pine cone dispersal, good regeneration microsites, an initial reduction in competing vegetation, and increased light for pine regeneration, however, vegetation that is released from competition, especially graminoids, has the potential to outcompete pine in these stands. If competition after salvage logging is severe, it may hinder sufficient pine regeneration from occurring, altering successional trajectories of these stands. Otherwise, pine may regenerate sufficiently after salvage logging.

Further research on a variety of site types in Alberta would be beneficial since vegetation responses are likely to differ among rich and poor sites. Longer term studies would be beneficial to examine further changes that may arise from this new disturbance type over time. Overall, this study has provided novel insights concerning the understory responses to MPB that can be applied to informing the management of lodgepole pine forests in Alberta; understory vegetation resistance in stands with low levels of MPB-induced mortality indicate that these stands are of less concern, whereas stands with high levels of MPB-induced mortality no longer have a pine dominant canopy and experience changes in understory vegetation that may prevent pine regeneration. If lodgepole pine stands in Alberta are to be managed after MPB-attacks, the focus should be on stands that have experienced high-severity MPB kill.

Table 3-1. Results (p-values) from linear mixed-effects models for environmental response variables in four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged, one year before treatment (2008), the year of treatment (2009), one year post-treatment (2010), five years post-treatment (2014), and seven years post-treatment (2016). Significant terms are in bold.

Component	Variable	Treatment	Time	Treatment*Time
Overstory	Healthy stems (tph)	**0.0087**	**<.0001**	**<.0001**
	Declining stems (tph) [i]	0.1344	**<.0001**	**<.0001**
	Dead stems (tph)	0.2885	**<.0001**	**<.0001**
	Healthy basal area +	0.1797	**<.0001**	**<.0001**
	Declining basal area	0.2150	**<.0001**	**0.0001**
	Dead basal area +	0.0802	**<.0001**	**<.0001**
	Canopy cover (%)	0.1357	**<.0001**	**<.0001**
DWM biomass	Class 1: diameter < 0.5 cm *	0.1631	**<.0001**	**<.0001**
	Class 2: diameter 0.5-1 cm *	0.1411	**<.0001**	**0.0010**
	Class 3: diameter 1-3 cm +	**0.0420**	**0.0009**	**0.0001**
	Class 4: diameter 3-5 cm	0.1942	0.1763	0.1195
	Class 5: diameter 5-7 cm	0.3453	**0.0160**	0.9135
	Total 0-7 cm diameter	0.2462	**0.0002**	**0.0232**
	Class 6: diameter > 7 cm (rotten) +	0.7331	**<.0001**	0.5145
	Class 6: diameter > 7 cm (sound) **	0.5879	**<.0001**	0.8078
	Class 6: diameter > 7 cm (total) **	0.7510	**0.0002**	0.5442
Understory	Understory Vegetation Richness (per quadrat)	0.2439	**<.0001**	**<.0001**
	Understory Vegetation Richness [ii] (per plot)	0.1462	-	-
	Graminoid Richness	**0.0095**	**<.0001**	**<.0001**
	Shrub Richness	0.2916	**<.0001**	**0.0018**

Component	Variable	Treatment	Time	Treatment*Time
Understory	Forb Richness	0.5066	**<.0001**	**0.0017**
	Bryophyte Richness	**0.0153**	**<.0001**	**<.0001**
	Total Vegetation Cover	**0.0138**	**0.0001**	**<.0001**
	Graminoid Cover **	**0.0132**	**<.0001**	**<.0001**
	Shrub Cover **	0.3003	0.2945	**0.0001**
	Forb Cover	0.1061	**0.0035**	**<.0001**
	Bryophyte Cover	**0.0012**	**<.0001**	**<.0001**
	Understory Vegetation Diversity	0.3611	**<.0001**	**0.0034**
	Litter cover	**0.0071**	**<.0001**	**0.0076**
	Wood Cover	0.6647	**<.0001**	0.3746
	Species Composition †	**0.001**	**0.001**	**0.023**
Below Ground	Moisture [ii]	0.6884	**<.0001**	0.5283
	Forest Floor (FH) depth	0.1176	**<.0001**	**0.0173**
	Nutrient Supply: NH_4-N +*	0.9573	**<.0001**	**0.0453**
	Nutrient Supply: Ca	0.1853	**<.0001**	**0.0486**
	Nutrient Supply: Mg +	0.0538	**<.0001**	**0.0477**
	Nutrient Supply: S	0.5581	**<.0001**	**0.0373**
	Nutrient Supply: K +	0.6854	0.0747	**0.0116**
	Nutrient Supply: Mn +	0.8913	**<.0001**	**0.0205**
	Nutrient Supply: P +	0.3315	**<.0001**	**0.0011**
	Nutrient Supply: B *	0.1877	**<.0001**	**0.0273**
	Nutrient Supply: Fe +	0.9719	**<.0001**	0.6103
	Nutrient Supply: Zn +*	0.6202	**0.0001**	0.5058
	Nutrient Supply: Al	0.5394	**<.0001**	0.5382

* Log transformed

** Square root transformed

\+ Removed outlier(s)

[i] Declining stems were those that were unhealthy but not yet dead

[ii] Only data from 2016, time was month (where applicable)

† Differences in species composition were analyzed using a distance-based redundancy analysis

Table 3-2. LSmean values (standard error) for environmental response variables in four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged, one year before treatment (2008), the year of treatment (2009), one year post-treatment (2010), five years post-treatment (2014), and seven years post-treatment (2016). Upper case letters signify significant differences among treatments within a year and bolded, lower case letters signify significant differences among years within a treatment. See also Table 3-1.

Variable	**Year**	**Control**	**50% Kill**	**100% Kill**	**Salvage Logged**
OVERSTORY					
Healthy Stems (tph)	2008	1059 (79) **y**	1006 (79) **z**	1120 (79) **z**	-
	2010	1133 (79) C **y**	785.2 (79) B **y**	485.2 (79) A **y**	-
	2013	592.6 (79) B **x**	359.3 (79) AB **x**	169.3 (81) A **x**	-
	2016	542.6 (79) B **x**	369.7 (80) AB **x**	156.6 (80) A **x**	-
Declining Stems (tph) [i]	2008	193 (63) **x**	108 (64) **x**	122 (63)	-
	2010	40 (79) **x**	97 (63) **x**	182 (62)	-
	2013	428 (62) **y**	338 (62) **y**	194 (63)	-
	2016	410 (63) B **y**	263 (62) AB **y**	131 (63) A	-
Dead Stems (tph)	2008	828 (197) **x**	689 (197) **x**	748 (197) **x**	-
	2010	939 (197) **xy**	780 (197) **x**	819 (197) **x**	-
	2013	1011 (197) **y**	989 (197) **y**	1589 (197) **y**	-
	2016	1096 (197) **y**	1048 (197) **y**	1641 (197) **y**	-

Variable	**Year**	**Control**	**50% Kill**	**100% Kill**	**Salvage Logged**
Canopy cover (%)	2008	62.0 (3.0)	61.9 (3.0) **z**	60.2 (3.0) **z**	-
	2009	60.6 (3.0)	59.7 (3.0) **yz**	57.6 (3.0) **yz**	-
	2010	64.1 (3.0)	61.1 (3.0) **yz**	60.0 (3.0) **z**	-
	2012	57.8 (3.0)	51.7 (3.0) **x**	51.4 (3.0) **xy**	-
	2013	58.2 (3.0) AB	64.9 (3.0) B **z**	51.3 (3.0) A **xy**	-
	2014	58.6 (3.0)	54.3 (3.0) **xy**	49.6 (3.0) **x**	-
	2016	58.9 (3.0) B	58.9 (3.0) B **xyz**	45.1 (3.0) A **x**	-
UNDERSTORY					
Vegetation Richness	2008	9.4 (1.0)	10.2 (1.0) **x**	10.9 (1.0) **x**	11.9 (1.0) **y**
	2009	9.4 (1.0)	10.3 (1.0) **x**	11.0 (1.0) **x**	8.4 (1.0) **x**
	2010	10.0 (1.0) AB	10.4 (1.0) AB **x**	11.7 (1.0) B **x**	7.6 (1.0) A **x**
	2014	9.7 (1.0)	11.0 (1.0) **xy**	12.4 (1.0) **x**	13.5 (1.0) **y**
	2016	11.1 (1.0) A	12.8 (1.0) AB **y**	14.4 (1.0) AB **y**	16.5 (1.0) B **z**
Graminoid Richness	2008	0.4 (0.1)	0.6 (0.1)	0.6 (0.1) **x**	0.7 (0.1) **x**
	2009	0.3 (0.1)	0.7 (0.1)	0. 7 (0.1) **x**	0.4 (0.1) **x**
	2010	0.4 (0.1)	0.7 (0.1)	0.6 (0.1) **x**	0.7 (0.1) **x**
	2014	0.4 (0.1) A	1.0 (0.1) AB	1.3 (0.1) B **y**	1.6 (0.1) B **y**
	2016	0.6 (0.1) A	1.0 (0.1) AB	1.3 (0.1) B **y**	2.0 (0.1) C **y**

Variable	**Year**	**Control**	**50% Kill**	**100% Kill**	**Salvage Logged**
Shrub Richness	2008	2.4 (0.3)	2.7 (0.3)	2.7 (0.3) **x**	3.2 (0.3) **y**
	2009	2.2 (0.3)	2.9 (0.3)	2.6 (0.3) **x**	2.0 (0.3) **x**
	2010	2.4 (0.3)	3.0 (0.3)	2.9 (0.3) **xy**	2.3 (0.3) **x**
	2014	2.4 (0.3)	2.9 (0.3)	3.1 (0.3) **xy**	3.7 (0.3) **y**
	2016	2.5 (0.3)	3.4 (0.3)	3.7 (0.3) **y**	4.1 (0.3) **y**
Forb Richness	2008	3.4 (0.7)	3.3 (0.7)	3.8 (0.7) **w**	4.2 (0.7) **xy**
	2009	3.3 (0.7)	3.2 (0.7)	3. 9 (0.7) **wx**	2.8 (0.7) **w**
	2010	3.5 (0.7)	3.2 (0.7)	4.2 (0.7) **wx**	3.6 (0.7) **wx**
	2014	3.7 (0.7)	3.7 (0.7)	4.3 (0.7) **wx**	4.7 (0.7) **yz**
	2016	3.7 (0.7)	3.9 (0.7)	4.7 (0.7) **x**	5.2 (0.7) **z**
Bryophyte Richness	2008	2.9 (0.2) **w**	3.0 (0.2) **wx**	3.4 (0.2) **wx**	3.2 (0.2) **y**
	2009	3.2 (0.2) **wx**	3.0 (0.2) **wx**	3.4 (0.2) **wx**	2.6 (0.2) **x**
	2010	3.3 (0.2) B **wx**	3.0 (0.2) B **wx**	3.5 (0.2) B **wx**	0.7 (0.2) A **w**
	2014	2.9 (0.2) **w**	2.9 (0.2) **w**	3.1 (0.2) **w**	2.2 (0.2) **x**
	2016	4.0 (0.2) **x**	3.7 (0.2) **x**	4.0 (0.2) **x**	3.8 (0.2) **z**
Vegetation Cover (%)	2008	121.1 (10.8) **y**	138.6 (10.8) **xy**	115.0 (10.8) **x**	133.0 (10.8) **z**
	2009	141.2 (10.8) B **yz**	159.5 (10.8) B **yz**	140.1 (10.8) B **xy**	75.1 (10.8) A **y**
	2010	169.1 (10.8) B **z**	167.7 (10.8) B **z**	158.6 (10.8) B **y**	38.4 (10.8) A **x**
	2014	120.1 (10.8) **xy**	137.6 (10.8) **xy**	153.2 (10.8) **y**	127.8 (10.8) **z**
	2016	92.3 (10.8) **x**	114.6 (10.8) **x**	131.6 (10.8) **xy**	112.7 (10.8) **z**

Variable	**Year**	**Control**	**50% Kill**	**100% Kill**	**Salvage Logged**
Shannon Diversity	2008	5.37 (0.72) **xy**	5.83 (0.72) **xy**	6.30 (0.72) **x**	6.76 (0.72) **y**
	2009	5.12 (0.72) **x**	5.81 (0.72) **xy**	6.20 (0.72) **x**	4.85 (0.72) **x**
	2010	5.47 (0.72) **xy**	5.63 (0.72) **x**	6.37 (0.72) **x**	4.10 (0.72) **x**
	2014	5.43 (0.72) **xy**	5.80 (0.72) **xy**	6.98 (0.72) **x**	5.31 (0.72) **x**
	2016	6.63 (0.72) **y**	7.09 (0.72) **y**	8.53 (0.72) **y**	7.74 (0.72) **y**
Litter Cover (%)	2008	42.3 (4.7) **xy**	43.7 (4.6) **xy**	50.2 (4.7) **x**	59.4 (4.7) **x**
	2009	51.8 (4.7) **y**	59.8 (4.6) **z**	62.0 (4.7) **x**	69.8 (4.7) **x**
	2010	55.4 (4.7) A **y**	57.0 (4.6) A **yz**	62.6 (4.7) A **x**	89.1 (4.7) B **y**
	2014	33.1 (4.6) A **wx**	41.9 (4.6) A **x**	51.4 (4.6) AB **x**	66.0 (4.6) B **x**
	2016	20.5 (4.6) **w**	26.7 (4.6) **w**	22.7 (4.6) **w**	29.4 (4.6) **w**
BELOW GROUND					
Forest Floor Depth (mm)	2008	90.2 (6.2) **y**	105.0 (6.2) **y**	88.8 (6.2) **z**	81.6 (6.2) **z**
	2009	63.1 (6.2) **x**	70.9 (6.2) **x**	74.2 (6.2) xy	66.3 (6.2) **y**
	2010	76.0 (6.2) **x**	78.7 (6.2) **x**	82.5 (6.2) **yz**	64.0 (6.2) xy
	2016	70.2 (6.2) **x**	72.9 (6.2) **x**	62.9 (6.2) **x**	52.1 (6.2) **x**
NUTRIENT SUPPLY RATES (micro grams/10 cm^2/summer burial length)					
Ca	2008	1192 (64) **x**	1362 (64) **xy**	1394 (64) **x**	1302 (64) **x**
	2009	1275 (64) **x**	1357 (64) **xy**	1281 (64) **x**	1534 (64) **y**
	2010	1522 (64) **y**	1493 (64) **y**	1648 (64) **y**	1549 (64) **y**
	2014	1277 (64) **x**	1327 (64) **xy**	1450 (64) **xy**	1293 (64) **x**
	2016	1118 (64) **x**	1208 (64) **x**	1317 (64) **x**	1203 (64) **x**

Variable	**Year**	**Control**	**50% Kill**	**100% Kill**	**Salvage Logged**
B	2008	0.88 (0.06) **z**	0.84 (0.06) **z**	0.89 (0.06) **z**	1.02 (0.06) **z**
	2009	0.94 (0.06) **z**	1.11 (0.06) **z**	0.94 (0.06) **z**	1.05 (0.06) **z**
	2010	0.52 (0.06) **y**	0.50 (0.06) **y**	0.49 (0.06) **y**	0.47 (0.06) **y**
	2014	0.21 (0.06) AB **x**	0.19 (0.06) AB **x**	0.26 (0.06) B **x**	0.13 (0.06) A **x**
	2016	0.05 (0.06) **w**	0.07 (0.06) **w**	0.10 (0.06) **w**	0.04 (0.06) **w**
Mg	2008	234.5 (16.1) **x**	268.8 (16.1) **x**	246.4 (16.1) **x**	278.6 (16.1) **x**
	2009	272.5 (16.1) A **xy**	292.1 (16.1) AB **xy**	256.1 (16.1) A **xy**	339.6 (16.1) B **z**
	2010	315.8 (16.1) **z**	312.8 (16.1) **y**	319.6 (16.1) **z**	334.1 (16.1) **yz**
	2014	281.9 (16.1) **yz**	299.7 (16.1) **xy**	292.9 (16.1) **yz**	316.2 (16.1) **xyz**
	2016	251.7 (16.1) **xy**	274.7 (16.1) **xy**	263.7 (16.1) **xy**	295.3 (16.1) **xy**
S	2008	69.9 (23.9) **y**	84.3 (23.9) **yz**	86.7 (23.9) **xy**	53.2 (23.9) **x**
	2009	76.7 (23.9) **y**	100.8 (23.9) **z**	104.3 (23.9) **y**	101.4 (23.9) **z**
	2010	77.3 (23.9) **y**	96.9 (23.9) **z**	98.2 (23.9) **y**	80.7 (23.9) **y**
	2014	63.1 (23.9) **xy**	74.5 (23.9) **xy**	77.5 (23.9) **x**	53.9 (23.9) **x**
	2016	47.1 (23.9) **x**	59.1 (23.9) **x**	74.6 (23.9) **x**	46.3 (23.9) **x**
K	2008	223.0 (25.1)	245.5 (25.1)	219.1 (25.1)	209.7 (25.1) **xy**
	2009	224.2 (25.1)	254.8 (25.1)	232.1 (25.1)	197.9 (25.1) **x**
	2010	198.2 (25.1)	224.4 (25.1)	183.5 (25.1)	196.3 (25.1) **x**
	2014	226.2 (25.1)	209.8 (25.1)	197.8 (25.1)	314.8 (25.1) **z**
	2016	217.7 (25.1)	232.1 (25.1)	223.7 (25.1)	318.6 (25.1) **yz**

Variable	Year	Control	50% Kill	100% Kill	Salvage Logged
Mn	2008	39.1 (6.9) **xy**	55.6 (6.9) **xy**	63.9 (6.9) **yz**	55.7 (6.9) **yz**
	2009	58.0 (6.9) **yz**	61.7 (6.9) **y**	60.1 (6.9) **yz**	65.2 (6.9) **z**
	2010	73.3 (6.9) **z**	70.5 (6.9) **y**	68.0 (6.9) **z**	61.4 (6.9) **z**
	2014	58.4 (6.9) **yz**	49.1 (6.9) **xy**	43.1 (6.9) **xy**	39.0 (6.9) **xy**
	2016	35.6 (6.9) **x**	38.5 (6.9) **x**	28.0 (6.9) **x**	23.3 (6.9) **x**
P	2008	13.2 (2.5)	16.6 (2.5)	19.2 (2.5) **xy**	13.8 (2.5) **x**
	2009	16.9 (2.5)	17.4 (2.5)	15.2 (2.5) **x**	17.9 (2.5) **x**
	2010	15.4 (2.5) A	20.1 (2.5) AB	23.1 (2.5) AB **y**	26.6 (2.5) B **y**
	2014	17.2 (2.5)	17.4 (2.5)	16.8 (2.5) **x**	24.7 (2.5) **y**
	2016	13.6 (2.5)	14.6 (2.5)	15.0 (2.5) **x**	17.5 (2.5) **x**

[i] Declining stems were those that were unhealthy but not yet dead

Table 3-3. LSmean values (standard error) for downed woody material biomass (Mg ha-1) in four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged, one year before treatment (2008), the year of treatment (2009), one year post-treatment (2010), and seven years post-treatment (2016). Upper case letters signify significant differences among treatments within a year and bolded, lower case letters signify significant differences among years within a treatment. See also Table 3-1.

Size Class	**Year**	**Control**	**50% Kill**	**100% Kill**	**Salvage Logged**
1: (0-0.5 cm)	2008	0.16 (0.04) **xy**	0.16 (0.04)	0.19 (0.04)	0.17 (0.04) **x**
	2009	0.26 (0.04) **y**	0.27 (0.04)	0.27 (0.04)	0.56 (0.04) **y**
	2010	0.24 (0.04) A **y**	0.20 (0.04) A	0.21 (0.04) A	0.57 (0.04) B **y**
	2016	0.14 (0.04) **x**	0.20 (0.04)	0.24 (0.04)	0.14 (0.04) **x**
2: (0.5-1 cm)	2008	0.25 (0.08) **xy**	0.30 (0.08)	0.37 (0.08)	0.32 (0.08) **x**
	2009	0.45 (0.08) AB **y**	0.35 (0.08) A	0.45 (0.08) A	0.99 (0.08) B **y**
	2010	0.48 (0.08) **xy**	0.45 (0.08)	0.38 (0.08)	0.89 (0.08) **y**
	2016	0.23 (0.08) **x**	0.30 (0.08)	0.43 (0.08)	0.25 (0.08) **x**
3: (1-3 cm)	2008	1.03 (0.59)	0.99 (0.59)	1.43 (0.59)	1.21 (0.59) **x**
	2009	1.06 (0.59) A	1.06 (0.59) A	1.32 (0.59) AB	4.47 (0.59) B **y**
	2010	1.58 (0.59) A	1.32 (0.59) A	1.36 (0.59) A	4.51 (0.59) B **y**
	2016	0.66 (0.59)	0.77 (0.59)	1.94 (0.59)	1.80 (0.59) **x**
Total Small: (0-7 cm)	2008	11.1 (2.2)	5.8 (2.2)	10.0 (2.2)	8.8 (2.2) **x**
	2009	12.3 (2.2)	8.1 (2.2)	11.7 (2.2)	16.9 (2.2) **y**
	2010	11.6 (2.23)	8.1 (2.2)	10.5 (2.2)	17.4 (2.2) **y**
	2016	10.9 (2.2)	6.3 (2.2)	9.6 (2.2)	8.3 (2.2) **x**

Table 3-4. LSmean values (standard error) for environmental response variables that were impacted by time, but not treatment, one year before treatment (2008), the year of treatment (2009), one year post-treatment (2010), five years post-treatment (2014), and seven years post-treatment (2016). Bolded lower case letters signify significant differences among years, regardless of treatment. See also Table 3-1.

Variable	2008	2009	2010	2014	2016
Wood Cover	16.5 (1.9) **x**	20.2 (1.9) **x**	18.2 (1.9) **x**	24.9 (1.9) **y**	18.4 (1.9) **x**
DWM Class 5: (5-7 cm)	5.5 (0.8) **xy**	7.1 (0.8) **y**	6.3 (0.8) **xy**	**-**	4.8 (0.8) **x**
DWM Class 6: > 7 cm (rotten)	4.2 (1.3) **x**	6.9 (1.3) **y**	8.1 (1.3) **y**	**-**	1.8 (1.3) **x**
DWM Class 6: > 7 cm (sound)	24.9 (6.0) **x**	25.3 (6.0) **x**	30.6 (6.0) **x**	-	41.0 (6.0) **y**
DWM Class 6: > 7 cm (total)	29.1 (7.0) **x**	32.3 (7.0) **xy**	38.8 (7.0) **yz**	-	42.8 (7.0) **z**
Fe	11.6 (0.5) **y**	14.8 (0.5) **z**	6.9 (0.5) **x**	8.9 (0.5) **x**	10.4 (0.5) **y**
Zn	3.6 (0.4) **x**	4.2 (0.4) **xy**	5.3 (0.4) **z**	4.7 (0.4) **yz**	4.5 (0.4) **xy**
Al	69.0 (3.4) **y**	89.0 (3.4) **z**	83.0 (3.4) **z**	56.3 (3.47) **x**	49.4 (3.4) **x**

Table 3-5. Indicator Species Analysis showing which understory plant species are indicators (based on maximum Indicator Values (IV) from a Monte Carlo test based on 1000 randomizations) in four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged, one year prior to treatment (2008) and seven years post-treatment (2016). The observed *IV*, mean and standard deviation of the *IV* from the randomizations, and the *p*-value are reported for significant species (alpha=0.05). Mean percent cover values for each treatment are also shown.

				Indicator Values (*IV*) from Randomization			
Year	Treatment	Species	Cover (%)	Observed *IV*	Mean	SD	P
2008	Salvage Logged	*Chamerion angustifolium*	13.6	37.8	20.7	3.7	0.0010
2016	Salvage Logged	*Pinus contorta*	4.2	69.1	11.3	3.9	0.0002
		Calamagrostis spp	20.7	37.8	21.7	3.8	0.0016
		Leymus innovatus	11.0	29.2	17.0	3.7	0.0096
		Vaccinium caespitosum	2.6	28.4	17.1	3.8	0.0116
		Chamerion angustifolium	11.7	38.7	23.4	3.4	0.0008
		Polytrichum commune	16.7	44.5	25.2	4.0	0.0002
	100% kill	*Rosa acicularis*	7.4	31.2	24.8	3.3	0.0450
		Rubus pubescens	5.8	22.7	15.2	3.8	0.0466
		Aralia nudicaulis	7.6	36.9	16.5	3.8	0.0002
	50% kill	*Cornus canadensis*	12.9	34.3	29.5	2.5	0.0398
	Control	*Hylocomium splendens*	8.9	41.5	23.3	4.3	0.0012
		Pleurozium schreberi	16.7	38.3	30.6	3.5	0.0304

Table 3-6. LSmean values (standard error) for volumetric moisture content (VWC) for all treatments combined for each month during the growing season seven years post treatment (2016). Letters signify significant differences among months, regardless of treatment.

Variable	Month			
	June	July	August	September
Moisture (VWC)	18.3 (0.7) **B**	20.8 (0.7) **C**	15.5 (0.7) **A**	17.7 (0.7) **B**

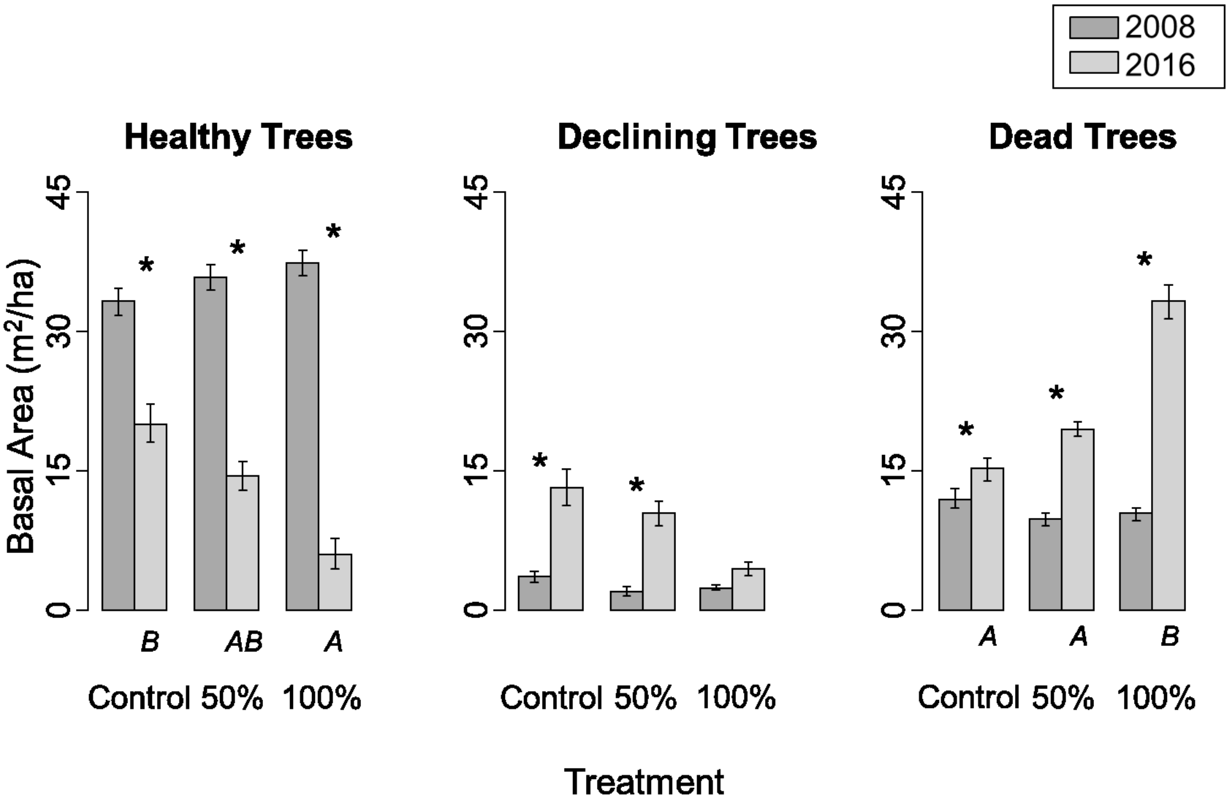

Figure 3-1. Basal area of healthy, declining, and dead trees one year pre-treatment and seven years post-treatment for three treatments: control, 50% simulated mountain pine beetle kill, and 100% simulated mountain pine beetle kill. Asterix (*) above represents differences between years within a treatment and capitalized letters below represent differences among treatments within a year.

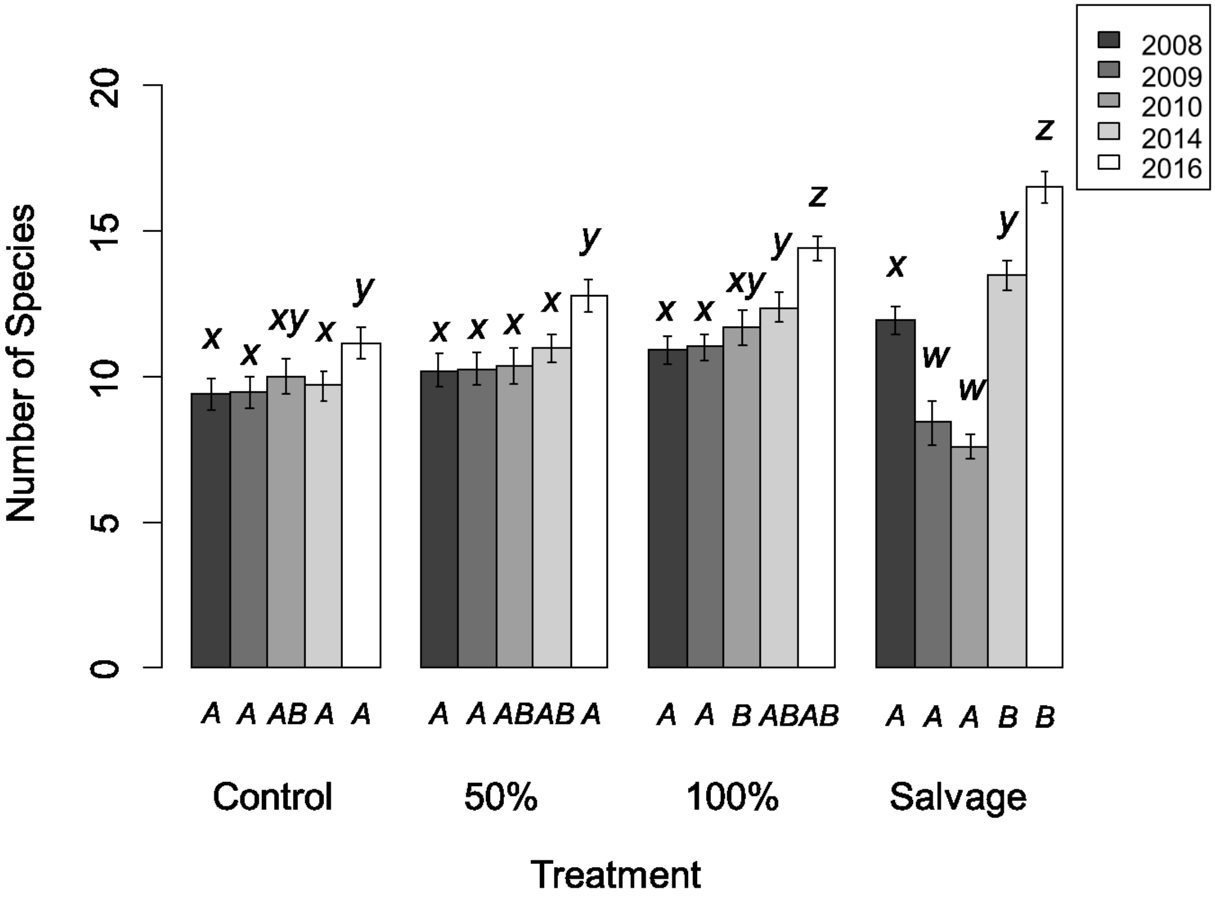

Figure 3-2. Total species richness per quadrat (1 m^2) pre-treatment (2008), the year of treatment (2009), one year post-treatment (2010), five years post-treatment (2014), and seven years post-treatment (2016) for each of the four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged. Small italicized letters above represent significant differences among years within a treatment and capitalized letters below represent significant differences among treatments within a year.

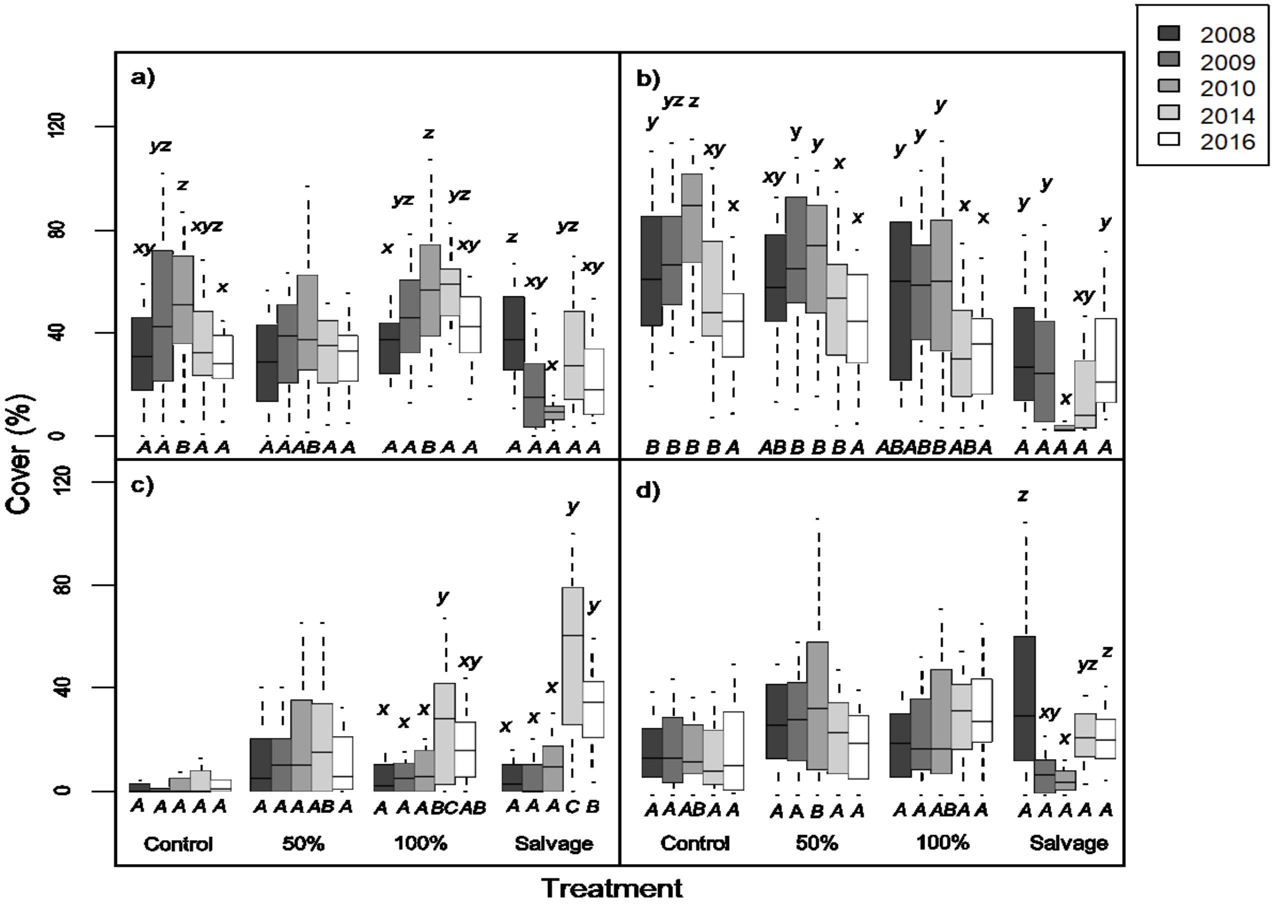

Figure 3-3. The percent cover of a) forbs, b) bryophytes, c) graminoids, and d) shrubs, pre-treatment (2008), the year of treatment (2009), one year post-treatment (2010), five years post-treatment (2014), and seven years post-treatment (2016) in the four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged. Lower case italicized letters above represent significant differences among years within a treatment and capitalized letters below represent significant differences among treatments within a year.

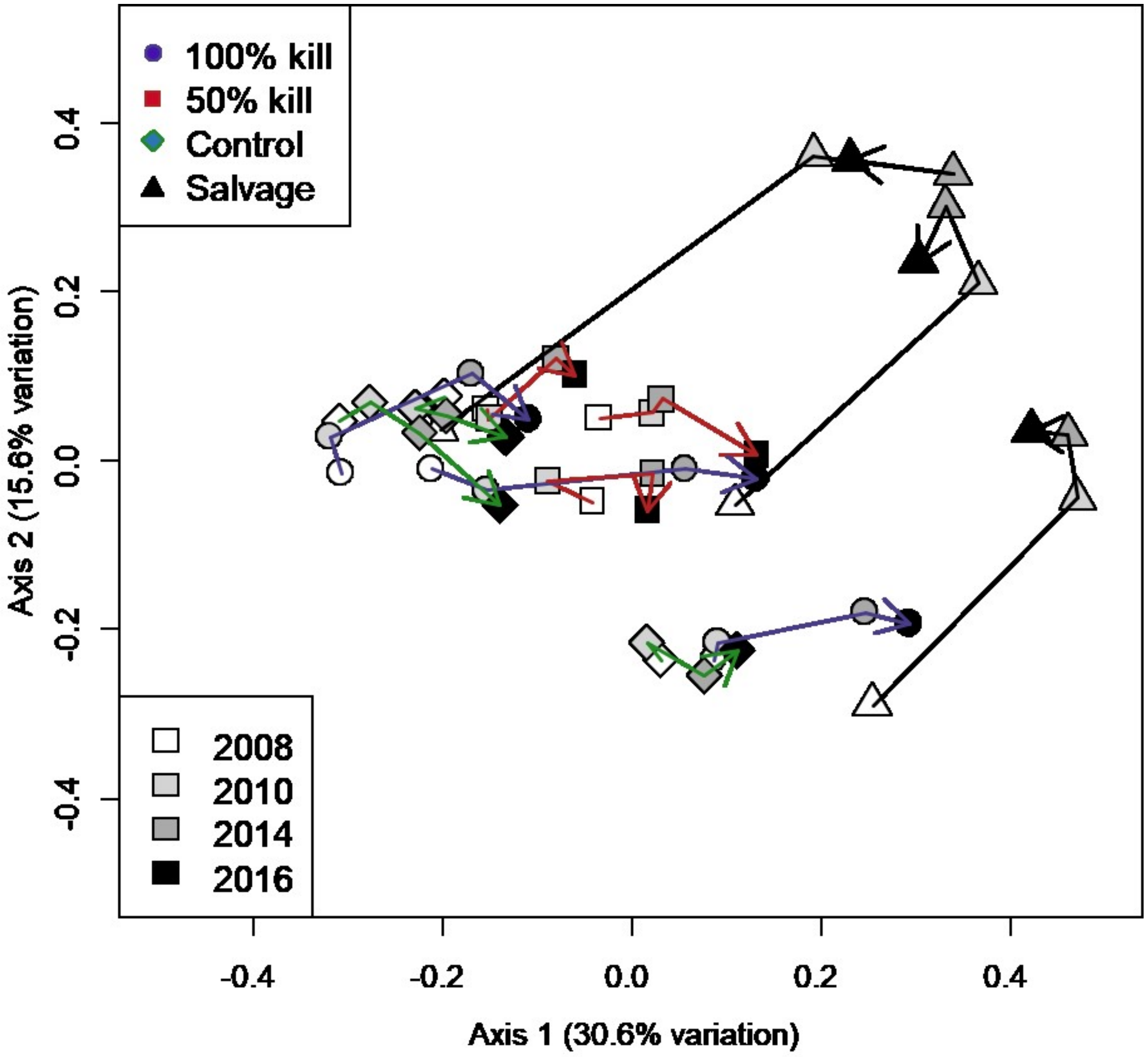

Figure 3-4. A Principal Coordinate Analysis ordination for vegetation species composition (46.1% variance explained on the first two axes) with successional vectors overlaid to show the direction and amount of change in community composition at four time periods: pre-treatment (2008), one year post-treatment (2010), five years post-treatment (2014), and seven years post-treatment (2016), in four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged. Vectors are for a given plot over time, and there were three replicate plots (one in each block) per treatment.

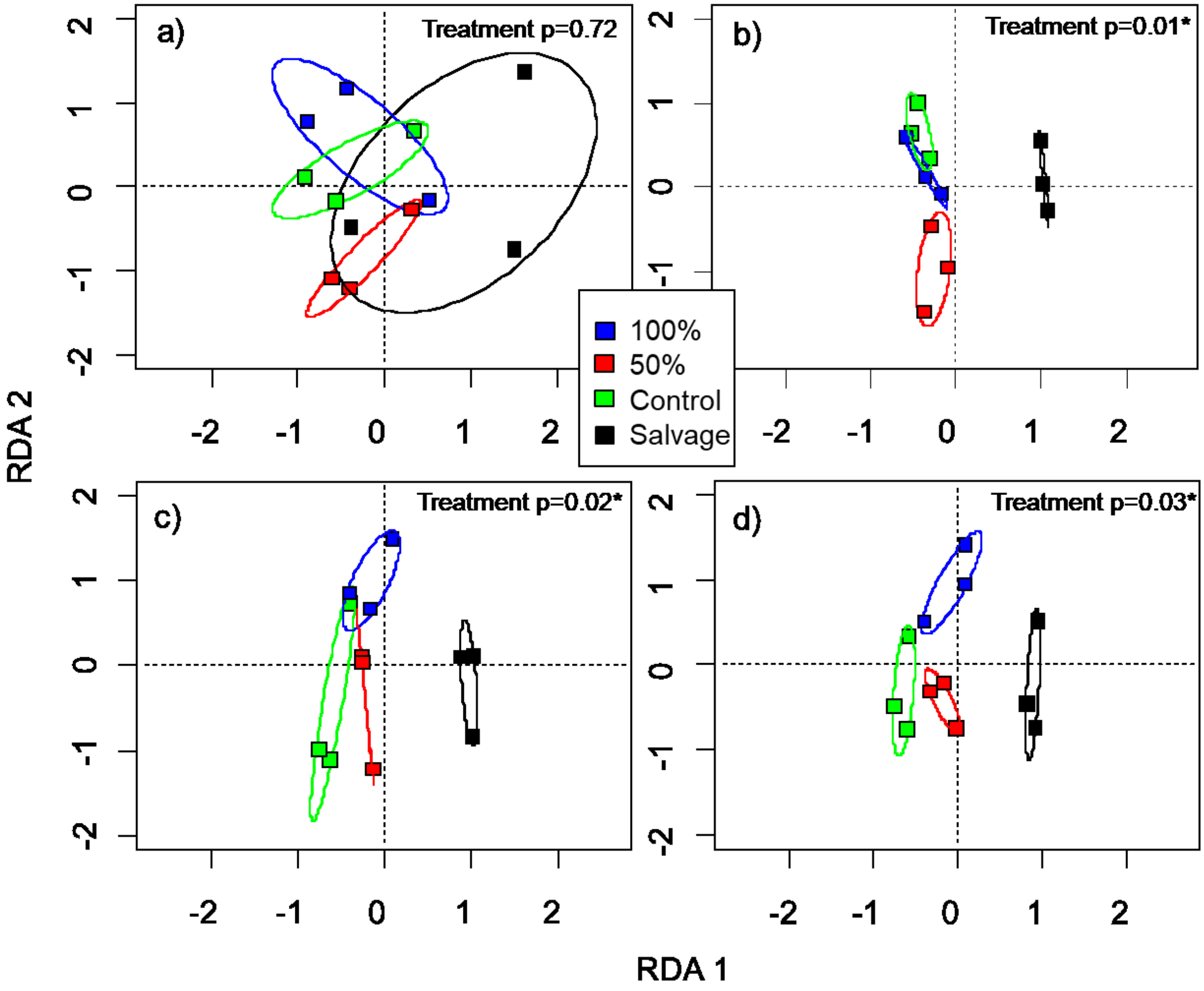

Figure 3-5. A distance-based redundancy analysis (dbRDA) ordination showing changes to vegetation community composition at four time periods: pre-treatment (2008; a), one year post-treatment (2010; b), five years post-treatment (2014; c), and seven years post-treatment (2016; d), for four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged. Ellipses group together plots within a treatment. The p-values indicate whether treatment had a significant effect on vegetation community composition within a year.

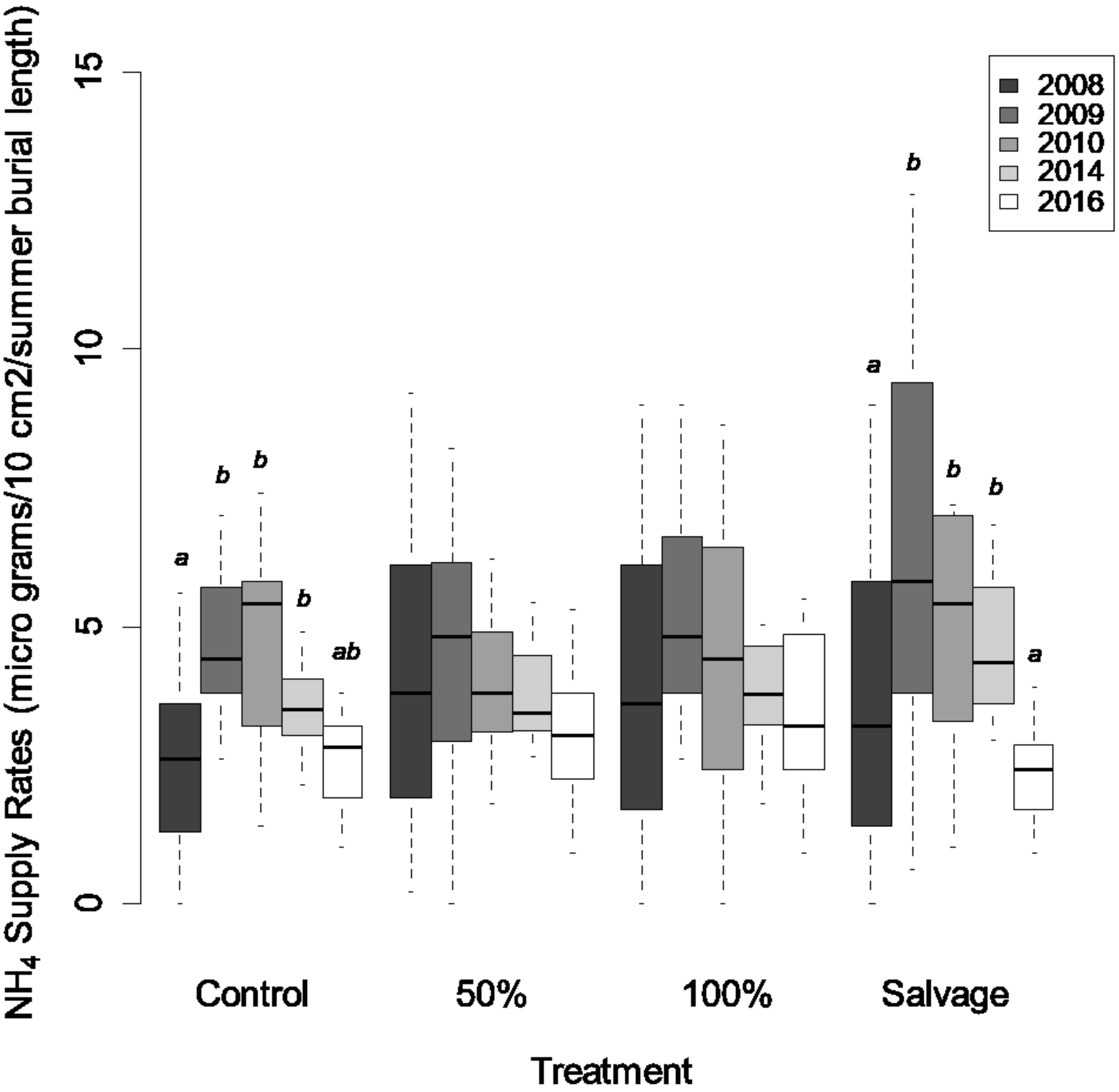

Figure 3-6. NH_4 supply rates pre-treatment (2008), the year of treatment (2009), one year post-treatment (2010), five years post-treatment (2014), and seven years post-treatment (2016) for each of the four treatments: control, 50% simulated mountain pine beetle kill, 100% simulated mountain pine beetle kill, and salvage logged. Small italicized letters above represent significant differences among years within a treatment. No significant differences were found among treatments within years.

Literature Cited

ASRD. 2007. Mountain pine beetle management strategy. Alberta Sustainable Resource Development. Pub. No. **T/154**. 14 pp.

Astrup, R., Coates, K.D., and Hall, E. 2008. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. For. Ecol. Manage. **256**(10): 1743–1750. doi:10.1016/j.foreco.2008.07.025.

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. For. Ecol. Manage. **257**(9): 1874–1882. doi:10.1016/j.foreco.2009.01.047.

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2010. Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. For. Chron. **86**(1): 87–99. doi:10.5558/tfc86087-1.

Barbier, S., Gosselin, F., and Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved-A critical review for temperate and boreal forests. For. Ecol. Manage. **254**(1): 1–15. doi:10.1016/j.foreco.2007.09.038.

Baylis, A.D. 2000. Why glyphosate is a global herbicide: Strengths, weaknesses and prospects. Pest Manag. Sci. **56**(4): 299–308. doi:10.1002/(SICI)1526-4998(200004)56:4<299::AID-PS144>3.0.CO;2-K.

Beckingham, J.D., Corns, I.G.W., and Archibald, J.H. 1996. Field guide to ecosites of west-central Alberta. UBC Press, Vancouver, British Columbia, Canada. 380 pp.

Bock, M.D., and Van Rees, K.C. 2002. Forest harvesting impacts on soil properties and vegetation communities in the Northwest Territories. Can. J. For. Res. **32**(4): 713–724. doi:10.1139/x02-014.

Briggs, J.S., Hawbaker, T.J., and Vandendriesche, D. 2015. Resilience of ponderosa and lodgepole pine forests to mountain pine beetle disturbance and limited regeneration. For. Sci. **61**(4): 689–702. doi:10.5849/forsci.14-192.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Intermountain Forest and Range Experiment Station. General Technical Report **INT-16**: 24 pp. doi:10.1017/CBO9781107415324.004.

Brown, J.K., Oberheu, R.D., and Johnston, C.M. 1981. Handbook for inventorying surface fuels and biomass in the Interior West. USDA For. Serv. Intermountain Forest and Range Experiment Station. General Technical Report **INT-129**: 48 pp.

Burton, P.J. 2008. The mountain pine beetle as an agent of forest disturbance. BC J. Ecosyst. Manag. **9**(3): 9–13. Available from http://jem.forrex.org/index.php/jem/article/viewArticle/402.

Callaghan, T.V, Collins, N.J., and Callaghan, C.H. 1978. Photosynthesis, growth and reproduction of Hylocomium splendens and Polytrichum commune in Swedish Lapland. Strategies of growth and population dynamics of tundra plants 4. Oikos **31**(1): 73–88. Available from http://www.jstor.org/stable/3543386.

Chapin, F.S., Callaghan, T.V, Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G., and Zimov, S.A. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? Ambio **33**(6): 361–365. doi:10.1579/0044-7447-33.6.361.

Cigan, P.W., Karst, J., Cahill, J.F., Sywenky, A.N., Pec, G.J., and Erbilgin, N. 2015. Influence of bark beetle outbreaks on nutrient cycling in native pine stands in western Canada. Plant Soil **390**: 29–47. doi:10.1007/s11104-014-2378-0.

Delisle, G., and Woodard, P. 1988. Constants for calculating fuel loads in Alberta. Canadian Forestry Service, Northern Forestry Centre. Note No. **45**: 3 pp. Available from http://www.cabdirect.org/abstracts/19920662847.html.

Dhar, A., and Hawkins, C.D.B. 2011. Regeneration and growth following mountain pine beetle attack : A synthesis of knowledge. BC J. Ecosyst. Manag. **12**(2): 1–16. Available from http://jem.forrex.org/index.php/jem/article/ view/22/84.

Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. **67**: 345-366.

Dykstra, P.R., and Braumandl, T.F. 2006. Historic influence of the mountain pine beetle on stand dynamics in Canada's Rocky Mountain parks. Canadian Forest Service, Pacific Forestry Centre. MPB Initiative Working Paper **2006-15**: 75 pp.

Edwards, M., Krawchuk, M.A., and Burton, P.J. 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. For. Ecol. Manage. **338**: 163–175. doi:10.1016/j.foreco.2014.11.011.

Ehrenfeld, J. 1980. Understory response to canopy gaps of varying size in a mature oak forest. Bull. Torrey Bot. Club **107**(1): 29–41.

Environment Canada. 2018. Canadian Climate Normals 1981-2010 Station Data. Available from http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=2718&autofwd=1 [accessed 28 February 2018].

Goslee, S.C., and Urban, D.L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. J. Stat. Softw. **22**(7): 1–19.

Griffin, J.M., Simard, M., and Turner, M.G. 2013. Salvage harvest effects on advance tree regeneration, soil nitrogen, and fuels following mountain pine beetle outbreak in lodgepole pine. For. Ecol. Manage. **291**: 228–239. doi:10.1016/j.foreco.2012.11.029.

Griffin, J.M., Turner, M.G., and Simard, M. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. For. Ecol. Manage. **261**(6): 1077–1089. doi:10.1016/j.foreco.2010.12.031.

Hart, S.A., and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. CRC. Crit. Rev. Plant Sci. **25**(4): 381–397. doi:10.1080/07352680600819286.

Hart, S.A., and Chen, H.Y.H. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol. Monogr. **78**(1): 123–140. doi:10.1890/06-2140.1.

Hubbard, R.M., Rhoades, C.C., Elder, K., and Negron, J. 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. For. Ecol. Manage. **289**: 312–317. doi:10.1016/j.foreco.2012.09.028.

Klutsch, J.G., Negrón, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., and Caissie, R. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (Dendroctonus ponderosae Hopkins) outbreak in Colorado. For. Ecol. Manage. **258**(5): 641–649. doi:10.1016/j.foreco.2009.04.034.

Kovacic, D.A., Dyer, M.I., and Cringan, A.T. 1985. Understory biomass in ponderosa pine following mountain pine beetle infestation. For. Ecol. Manage. **13**(1–2): 53–67. doi:10.1016/0378-1127(85)90005-2.

Lenth, R. V. 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Softw. **69**(1): 1–33. doi:10.18637/jss.v069.i01.

Lieffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for Calamagrostis canadensis in boreal forest sites. Can. J. For. Res. **23**: 2070–2077.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A., and Perry, D. 2004. Salvage harvesting policies after natural disturbance. Science **303**: 1303.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

McCambridge, W.F., Edminster, C.B., and Morris, M.J. 1982. Herbage production under ponderosa pine killed by the mountain pine beetle in Colorado. USDA For. Serv. Rocky Mountain Forest and Range Experiment Station. Research Note **RM-416**: 1-3.

McCune, B., and Mefford, M.J. 2006. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach, Oregon, USA.

McIntosh, A.C.S., and Macdonald, S.E. 2013. Short-term resistance of ecosystem properties and processes to simulated mountain pine beetle attack in a novel region. Ecosphere **4**(6): 68. doi:10.1890/ES12-00344.1.

McRae, D.J., Alexander, M.E., and Stocks, B.J. 1979. Measurement and description of fuels and fire behaviours on prescribed burns: A handbook. Canadian Forestry Service, Great Lakes Forest Research Centre. Information Report **O-X-287**: 44 pp.

Mitchell, R.G., and Preisler, H.K. 1998. Fall rate of lodgepole pine killed by the mountain pine beetle in Central Oregon. West. J. Appl. For. **13**(1): 23–26.

Morris, J.L., Mustaphi, C.J.C., Carter, V.A., Watt, J., Derr, K., Pisaric, M.F.J., Anderson, R.S., and Brunelle, A.R. 2015. Do bark beetle remains in lake sediments correspond to severe outbreaks? A review of published and ongoing research. Quat. Int. **387**: 72–86. doi:10.1016/j.quaint.2014.03.022.

Nalder, I.A, Wein, R.W., Alexander, M.E., and de Groot, W.J. 1997. Physical properties of dead and downed round-wood fuels in the boreal forests of Alberta and Northwest Territories. Int. J. Wildl. Fire **27**(9): 1513–1517. doi:10.1139/x97-083.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. *Compiled by* D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. **1/005**.

Nealis, V.G., and Peter, B. 2008. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests. Canadian Forest Service, Pacific Forestry Centre, Information Report **BC-X-417**: 31 pp.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and Wagner, H. 2017. Vegan: Community Ecology Package. R package version 2.4-2. Available from http://cran.r-project.org/package=vegan.

Ono, H. 2004. The mountain pine beetle: Scope of the problem and key issues in Alberta. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 62–66.

Page, W.G., and Jenkins, M.J. 2007. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. For. Sci. **53**(4): 507–518.

Paradis, E., Claude, J., and Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics **20**: 289–290.

Pec, G.J., Karst, J., Sywenky, A.N., Cigan, P.W., Erbilgin, N., Simard, S.W., and Cahill, J.F. 2015. Rapid increases in forest understory diversity and productivity following a mountain pine beetle (Dendroctonus ponderosae) outbreak in pine forests. PLoS One **10**(4): 1–16. doi:10.1371/journal.pone.0124691.

Piña, P.C.P. 2013. Impact of mountain pine beetle attack on water balance of lodgepole pine forests in Alberta. PhD thesis, Dept. of Renewable Resources, University of Alberta.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team. 2016. _nlme: Linear and Nonlinear Mixed Effects Models_. Available from http://cran.r-project.org/package=nlme.

Pykälä, J. 2004. Immediate increase in plant species richness after clear-cutting of boreal herb-rich forests. Appl. Veg. Sci. **7**: 29–34. doi:10.1111/j.1654-109X.2004.tb00592.x.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. Bioscience **58**(6): 501–517. doi:10.1641/B580607.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Rees, D.C., and Juday, G.P. 2002. Plant species diversity on logged versus burned sites in central Alaska. For. Ecol. Manage. **155**: 291–302. doi:10.1016/S0378-1127(01)00566-7.

Rhoades, C.C., McCutchan, J.H., Cooper, L.A., Clow, D., Detmer, T.M., Briggs, J.S., Stednick, J.D., Veblen, T.T., Ertz, R.M., Likens, G.E., and Lewis, W.M. 2013. Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response. Proc. Natl. Acad. Sci. **110**(5): 1756–1760. doi:10.1073/pnas.1221029110.

Royo, A.A., and Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. **36**(6): 1345–1362. doi:10.1139/x06-025.

Rydgren, K., Hestmark, G., and Økland, R.H. 1998. Revegetation following experimental disturbance in a boreal old-growth Picea abies forest. J. Veg. Sci. **9**(3): 763–776. doi:10.2307/3237042.

Safranyik, L., Shrimpton, D., and Whitney, H. 2002. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service, Pacific Forestry Centre. Forestry Technical Report **1**: 23 pp.

Sibold, J.S., Veblen, T.T., Chipko, K., Lawson, L., Mathis, E., and Scott, J. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. Ecol. Appl. **17**(6): 1638–1655.

Stone, W.E., and Wolfe, M.L. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. Vegetation **122**(1): 1–12. doi:10.1007/BF00052811.

VRI. 2007. Vegetation resources inventory: Ground sampling procedures. The Province of British Columbia Ministry of Forests and Range Forest Analysis and Inventory Branch for the Terrestrial Ecosystems Task Force Resources Information Standards Committee. 236 pp.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. For. Sci. **14**: 20–27.

Van Wagner, C.E. 1982. Practical aspects of the line intersect method. Canadian Forestry Service, Petawawa National Forestry Institute. Information Report **PI-X-12**: 11 pp. Available from http://www.floresta.ufpr.br/firelab/artigos/artigo389.pdf.

Appendices

Appendix 3-1. The years in which data were collected for each variable in all quadrats and plots, between one year prior to treatment (2008) and seven years post-treatment (2016). Overstory stem and canopy cover data in salvage logged were only collected one year prior to removal.

Variable/Year	2008	2009	2010	2012	2013	2014	2016
Overstory stems	✓		✓		✓		✓
Canopy cover	✓	✓	✓	✓	✓	✓	✓
Dead Woody Material	✓	✓	✓				✓
Ground cover	✓	✓	✓			✓	✓
FH depth	✓	✓	✓				✓
Vegetation (quadrat level)	✓	✓	✓			✓	✓
Plant richness (plot level) *	✓	✓	✓				✓
Moisture *	✓	✓	✓				✓
Nutrients	✓	✓	✓			✓	✓

The prior data (2008 – 2010) for all variables were analyzed and presented in McIntosh and Macdonald (2013).

* Only 2016 data were analyzed in this study.

Appendix 3-2. A list of plant species, both vascular and non-vascular, found in the plots; nomenclature as per USDA plant database (https://plants.sc.egov.usda.gov/java/). Species in bold were used in community composition analyses.

Growth Form	**Code** [i]	**Scientific Name**	**Common Name**	**Scientific Authority**
Tree	ABBA	*Abies balsamea*	Balsam fir	(L.) Mill.
	PIGL	*Picea glauca*	White spruce	(Moench) Voss
	PIMA	*Picea mariana*	Black spruce	(Mill.) Britton, Sterns & Poggenb.
	PICO	***Pinus contorta***	**Lodgepole pine**	**Douglas ex Loudon**
	POBA	*Populus balsamifera*	Balsam poplar	L.
	POTR	***Populus tremuloides***	**Trembling/quaking aspen**	**Michx.**
Shrub	**ALCR**	***Alnus crispa***	**Green alder**	**(Aiton) Pursh**
	ARUV	*Arctostaphylos uva-ursi*	Bearberry	(L.) Spreng.
	LEGR	***Ledum groenlandicum***	**Common Labrador tea**	**Oeder**
	LOIN	*Lonicera involucrata*	Bracted honeysuckle	(Richardson) Banks ex Spreng.
	RIGL	*Ribes glandulosum*	Skunk currant	Grauer
	ROAC	***Rosa acicularis***	**Prickly rose**	**Lindl.**
	RUAC	*Rubus arcticus* ssp. *acaul*	Dwarf raspberry	L. (Michx.) Focke
	RUID	*Rubus idaeus*	Wild red raspberry	L.
	RUPE	*Rubus pedatus*	Trailing raspberry	Sm.
	RUPU	***Rubus pubescens***	**Dewberry**	**Raf.**
	Saspp [ii]	*Salix* spp	Willow	
	SOSC	*Sorbus scopulina*	Mountain-ash	Greene
	SPBE	***Spiraea betulifolia***	**White spirea**	**Pall.**
	VACA	***Vaccinium caespitosum***	**Dwarf bilberry**	**Michx.**

Growth Form	Code [i]	Scientific Name	Common Name	Scientific Authority
Shrub	VAME	*Vaccinium membranaceum*	Tall bilberry	Douglas ex Torr.
	VAMY	***Vaccinium myrtilloides***	**Common blueberry**	**Michx.**
	VAVI	***Vaccinium vitis-idaea***	**Bog cranberry**	**L.**
	VIED	***Viburnum edule***	**Low-bush cranberry**	**(Michx.) Raf.**
Herb	**ARNU**	***Aralia nudicaulis***	**Wild sarsaparilla**	**L.**
	ARCO	*Arnica cordifolia*	Heartleaf arnica	Hook.
	CAMI	*Castilleja miniata*	Common red paintbrsuh	Douglas ex Hook.
	CHAN	***Chamerion angustifolium***	**Fireweed**	**L. Holub**
	COTR	*Coptis trifolia*	Goldthread	(L.) Salisb.
	COCA	***Cornus canadensis***	**Bunchberry**	**L.**
	EQSY	*Equisetum sylvaticum*	Woodland horsetail	L.
	GABO	*Galium boreale*	Northern bedstraw	L.
	GATRI	*Galium triflorum*	Sweet-scented bedstraw	Michx.
	GAHI	*Gaultheria hispidula*	Creeping snowberry	(L.) Muhl. ex Bigelow
	GOOB	*Goodyera oblongifolia*	Western rattlesnake plantain	Raf.
	HAOR	*Habenaria orbiculata*	Bog orchid	(Pursh) Torr.
	LIBO	***Linnaea borealis***	**Twinflower**	**L.**
	LICO	*Listera cordata*	Heart-leaved twayblade	(L.) R. Br.
	MACA	***Maianthemum canadense***	**Wild lily-of-the-valley**	**Desf.**
	MEPA	*Mertensia paniculata*	Tall lungwort	(Aiton) G. Don
	MINU	*Mitella nuda*	Naked miterwort	L.
	OSDE	*Osmorhiza depauperata*	Spreading sweet-cicely	Phil.

Growth Form	Code [i]	Scientific Name	Common Name	Scientific Authority
Herb	**PEPA**	***Petasites palmatus***	**Palmate-leaved coltsfoot**	**(Aiton) A. Gray**
	PLOR	*Platanthera orbiculata*	Round-leaved orchid	(Pursh) Lindl.
	PYAS	*Pyrola asarifolia*	Common pink wintergreen	Michx.
	PYSE	*Pyrola secunda*	One-sided wintergreen	L.
	STAM	*Streptopus amplexifolius*	Twisted-stalk	(L.) DC.
	TRHY	*Trifolium hybridum*	Alsike clover	L.
	TRPR	*Trifolium pratense*	Red clover	L.
	VIRE	***Viola renifolia***	**Kidney-leaved violet**	**A. Gray**
Graminoid	AGTR	*Agropyron trachycaulum*	Slender wheat grass	Link
	AGSC	*Agrostis scabra*	Hair grass	Willd.
	BRIN	*Bromus inermis*	Smooth brome	Leyss.
	CACA	*Calamagrostis canadensis*	Bluejoint	(Michx.) P. Beauv.
	CAMO	*Calamagrostis montanensis*	Plains reedgrass	Scribn. ex Vasey
	Caspp [iii]	***Calamagrostis* spp**	**Reed grass**	
	CAAN	*Carex aenea*	Bronze sedge	Fern.
	CACO	*Carex concinna*	Northern elegant sedge	R. Br.
	CILA	*Cinna latifolia*	Drooping woodreed	(Trevis. ex Goepp.) Griseb.
	FERU	*Festuca rubra*	Red fescue	L.
	LEIN	***Leymus innovatus***	**Hairy wild rye**	**(Beal) Pilg.**
	PHPR	*Phleum pratense*	Timothy grass	L.
	POPA	*Poa palustris*	Fowl bluegrass	L.

Growth Form	Code [i]	Scientific Name	Common Name	Scientific Authority
Fern	DRAU	*Dryopteris austriaca*	Spiny wood fern	(Jacq.) Woynar ex Schinz & Thell.
	GYDR	*Gymnocarpium dryopteris*	Oak fern	(L.) Newman
Bryophyte	BRST	*Brachythecium starkei*		(Brid.) Schimp.
	DIFU	*Dicranum fuscecens*	Dusky fork-moss	Sm.
	DIPO	***Dicranum polysetum***	**Rugose fork-moss**	**Sw.**
	HYSP	***Hylocomium splendens***	**Stairstep moss**	**(Hedw.) Schimp.**
	PLSC	***Pleurozium schreberi***	**Big red stem moss**	**(Brid.) Mitt.**
	POCO	***Polytrichum commune***	**Common haircap**	**Hedw.**
	PTCR	***Ptilium crista-castrensis***	**Knight's plume**	**(Hedw.) De Not.**
Clubmoss	**LYAN**	***Lycopodium annotinum***	**Stiff club-moss**	**L.**
	LYCL	*Lycopodium clavatum*	Running club-moss	L.
	LYCO	*Lycopodium complanatum*	Ground-cedar	L.
Lichen	CLspp [ii]	*Cladina* spp	Reindeer lichen	
	CRLI		Crustose lichen	
	PEAP	***Peltigera aphthosa***	**Studded leather lichen**	**(L.) Willd.**

[i] The 27 species used in community composition analyses are in bold

[ii] *Cladina* and *Salix* species were only identified to genus

[iii] *Calamagrostis* spp. is a combination of *C. canadensis* and *C. montanensis*

Chapter 4: General Conclusions

This thesis provided insights concerning changes to Alberta's lodgepole pine forests that are being attacked by Mountain Pine Beetle (MPB), a novel management issue in this region.

I found natural pine regeneration in less than half of the MPB-killed stands we surveyed in west-central Alberta. Counts of pine seedlings in these stands were very low (one to eight individuals in the four 1 m^2 plots combined), but this represents a best case scenario. Because of the very low abundances of seedlings observed, we targeted searches to areas we judged most likely to have pine seedlings.

Variables that were the most influential for natural pine regeneration were: site quality, pine advance regeneration, broadleaf advance regeneration, and spruce basal area. Regeneration was much poorer in rich sites (~20% of sites had at least one pine seedling present), likely due to more strongly serotinous cones, dense vegetation that resulted in competition and shade, and low availability of suitable seedbeds. Natural regeneration of pine was more likely to occur in poor sites (~75% of sites had at least one pine seedling present); populations from these sites showed less strong serotiny (cones were 55% open at 55°C), such that cones were more likely to open at lower temperatures achieved by solar radiation near the ground. Additionally, poor quality sites tend to have more open canopies for sunlight to penetrate through to the ground and less vegetative competition; thus, site conditions were likely more suitable for pine regeneration. Although stands with high densities of advance regeneration were avoided, broadleaf (primarily aspen and birch) species and spruce (black and white) were present at low densities in the vast majority of sites visited (70% and 90%, respectively). Broadleaf advance regeneration, while present only at low densities (mean=140 stems per hectare (sph)), had a significant negative effect on density of pine seedlings post-MPB. Pine advance regeneration was only found in 40% of sites (densities ranged from 25-237 sph), however, its presence had a positive association with the presence of pine seedlings. Spruce trees in the canopy were present at low levels (mean basal area (BA)=0.9 m^2/ha), however, canopy spruce BA had a negative association with pine seedling density, which suggests that spruce trees in the canopy hamper pine regeneration.

The broadleaf and spruce advance regeneration, combined with canopy spruce, will likely take advantage of additional light and nutrient resources in MPB-killed stands and dominate the future canopies, albeit at densities far below adequate stocking rates. In stands that transition to a spruce dominated canopy, overstory shading may prevent future pine regeneration. In stands that transition to an aspen dominated canopy, unhospitable conditions for pine regeneration may further develop, including increased understory vegetation, litter, and shade, which may further hinder future pine regeneration in these stands. These scenarios are more likely to occur in richer sites, where there is more moisture and nutrients for tree growth and these species are likely already present. The canopy that develops post-MPB may increase shading of the forest floor and further prevent cones from opening. These richer sites have more strongly serotinous cones, which will likely end up in a forest floor seedbank, further reducing the chance of immediate pine recovery. Thus, pine regeneration on such sites is likely to be minimal until a stand-replacing disturbance occurs. In poorer quality sites, however, which are less suitable for other tree species, pine seedlings may be able to take advantage of increases in soil moisture, soil nutrients, and light; thus, more pine regeneration may occur.

Vegetation responses to simulated MPB-attack varied by treatment, indicating that the severity of attack determines the magnitude of vegetation changes, and therefore the ensuing succession of a stand. Salvage logging showed immediate changes, likely due to damage from heavy machinery and a drastic change in environmental conditions, while the other treatments responded more slowly. Seven years post-treatment, total vegetation richness and diversity increased with disturbance severity, while total vegetation cover was similar among treatments. This was accompanied by a change in species composition in some of the treatments, which can be explained in part by the changes that occurred among vegetation types. Graminoids had the strongest response; richness and cover increased with disturbance intensity. In contrast, forb, shrub, and bryophyte cover seemed to be resistant to changes that occurred after both intensities of MPB mortality. Forb and shrub richness increased in response to only the high mortality MPB treatment. Forb, shrub, and bryophyte cover temporarily decreased following salvage logging before recovering; this was accompanied by changes in species composition. More specifically, the untreated control remained dominated by feathermosses, medium MPB mortality resulted in a minor increase of residual shade-tolerant species, high MPB mortality resulted in an increase of both residual shade-tolerant and new shade-intolerant species, and salvage logging resulted in increased abundance of primarily early successional, shade-intolerant species (including lodgepole pine). These composition changes were most likely due to a release from below-ground competition resulting in an increased availability of soil nutrients, light, and soil moisture. Increases in soil moisture and nutrients, however, were compensated for by increased uptake by vegetation.

The environmental and vegetation changes after simulated salvage logging were quite large; while pine regeneration was found after salvage logging, graminoids have the potential to outcompete pine seedlings. The environmental changes in the simulated-MPB kill treatment followed the gradient of severity. The 100% kill resulted in higher light levels than the 50% kill or control and experienced larger changes in vegetation; still, the standing dead trees after high severity MPB mortality cast substantial shade to the understory. The shade, plus competition from vegetation, may result in limited pine regeneration even after high mortality, which may have long term consequences for pine regeneration. Finally, there may be some resistance of understory vegetation at medium mortality levels, as seen by the minor changes in both the environment and vegetation. Stands that experience lower levels of mortality may remain on their current successional pathways, although tree density in the future may be low.

Overall, the results of this thesis have provided novel insights into vegetation responses to MPB that can be used to help inform management decisions, for example regarding the need for rehabilitation of lodgepole pine sites in Alberta. While higher levels of canopy mortality provided a better understory light environment that might be sufficient to open pine cones, our results show that this effect could be negated by competitive effects arising from the responses of understory vegetation and overstory shading from residual spruce and standing dead. Major competing vegetation included graminoids, which are known to outcompete and suppress pine regeneration, and broadleaf advance regeneration, which even at low densities, negatively influenced pine regeneration. On rich quality sites, especially those that have experienced high MPB mortality, pine regeneration is likely to be poor or delayed. Previous studies have suggested that rich sites tend to have more frequent and severe MPB attacks and they are also more likely to have advance regeneration of trees present. If that advance regeneration is sufficient (e.g., >400 sph) these stands could become fully stocked with another tree species; these fully stocked stands were not common. If advance regeneration is not sufficient, these pine stands on rich sites are likely to experience substantial delays in forest recovery post-MPB and will likely follow altered successional pathways. Many MPB-attacked stands in Alberta experienced less than 50% mortality, and less severe attacks had minimal impacts to the understory environment and vegetation. If the density of residual trees is sufficiently high and the trees can take advantage of improved conditions, then these stands are of minimal concern as they will likely remain on their current successional trajectories. However, if the density is low, pine regeneration will likely still be poor as the light environment will not change much, indicating that these stands will be of higher concern until a stand-initiating disturbance is experienced. Poor quality sites are more likely to see better pine regeneration; they likely have less issues with competing vegetation, their canopies are more naturally open, and they often have advance pine regeneration. Pine regeneration here is more likely after high MPB mortality since there would likely be limited competition for resources. These poor sites may therefore be of less concern as they are fairly likely to continue developing as multi-cohort pine stands even after MPB. The amount of regeneration, however, is likely not enough to satisfy regeneration requirements for wood production. Therefore, rich sites and sites that have experienced high mortality, should be prioritized for lodgepole pine rehabilitation in Alberta. However, further research on a variety of site types in Alberta would be beneficial since vegetation responses are likely to differ among rich and poor sites.

While a stand-replacing event, such as fire, will likely provide the best possible chance of sufficient levels of pine regeneration in MPB-attacked forests, other management options are available. Salvage logging and mechanical scarification can provide suitable conditions for pine regeneration and dispersal of pine cones throughout poorer quality sites. Graminoid cover on richer sites has the potential to limit the quantity of pine regeneration after salvage logging. After salvage logging and site preparation in richer sites, planting and vegetation control could be used as needed.

Literature Cited

Amman, G.D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. J. Econ. Entomol. **65**(1): 138.

Alfaro, R.I., van Akker, L., and Hawkes, B. 2015. Characteristics of forest legacies following two mountain pine beetle outbreaks in British Columbia, Canada. Can. J. For. Res. **45**: 1387–1396. doi:10.1139/cjfr-2015-0042.

Amman, G.D., and Schmitz, R.F. 1988. Mountain pine beetle: Lodgepole pine interactions and strategies for reducing tree losses. Ambio **17**(1): 62–68. doi:10.2307/4313420.

Anhold, J.A., Jenkins, M.J., and Long, J.N. 1996. Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. West. J. Appl. For. **11**(2): 50–53. doi:10.1093/wjaf/11.2.50.

ASRD. 2007. Mountain pine beetle management strategy. Alberta Sustainable Resource Development. Pub. No. **T/154**. 14 pp.

Astrup, R., Coates, K.D., and Hall, E. 2008. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. For. Ecol. Manage. **256**(10): 1743–1750. doi:10.1016/j.foreco.2008.07.025.

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. For. Ecol. Manage. **257**(9): 1874–1882. doi:10.1016/j.foreco.2009.01.047.

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2010. Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. For. Chron. **86**(1): 87–99. doi:10.5558/tfc86087-1.

Barbier, S., Gosselin, F., and Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved-A critical review for temperate and boreal forests. For. Ecol. Manage. **254**(1): 1–15. doi:10.1016/j.foreco.2007.09.038.

Barton, K. 2018. MuMIn: Multi-Modal Inference. R package version 1.40.4. Available from https://CRAN.R-project.org/package=MuMIn.

Baylis, A.D. 2000. Why glyphosate is a global herbicide: Strengths, weaknesses and prospects. Pest Manag. Sci. **56**(4): 299–308. doi:10.1002/(SICI)1526-4998(200004)56:4<299::AID-PS144>3.0.CO;2-K.

Beckingham, J.D., and Archibald, J.H. 1996. Field guide to ecosites of Northern Alberta. Natural Resources Canada, Canadian Forest Service, Nothern Forestry Centre. Special Report **5**.

Beckingham, J.D., Corns, I.G.W., and Archibald, J.H. 1996. Field guide to ecosites of west-central Alberta. UBC Press, Vancouver, BC. 380 pp.

Bock, M.D., and Van Rees, K.C. 2002. Forest harvesting impacts on soil properties and vegetation communities in the Northwest Territories. Can. J. For. Res. **32**(4): 713–724. doi:10.1139/x02-014.

Briggs, J.S., Hawbaker, T.J., and Vandendriesche, D. 2015. Resilience of ponderosa and lodgepole pine forests to mountain pine beetle disturbance and limited regeneration. For. Sci. **61**(4): 689–702. doi:10.5849/forsci.14-192.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Intermountain Forest and Range Experiment Station. General Technical Report **INT-16**: 24 pp. doi:10.1017/CBO9781107415324.004.

Brown, J.K., Oberheu, R.D., and Johnston, C.M. 1981. Handbook for inventorying surface fuels and biomass in the Interior West. USDA For. Serv. Intermountain Forest and Range Experiment Station. General Technical Report **INT-129**: 48 pp.

Buma, B., Brown, C.D., Donato, D.C., Fontaine, J.B., and Johnstone, J.F. 2013. The impacts of changing disturbance regimes on serotinous plant populations and communities. Bioscience **63**(11): 866–876. doi:10.1525/bio.2013.63.11.5.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. In Ecological Modelling, 2nd edition. Springer, Verlag, New York. doi:10.1016/j.ecolmodel.2003.11.004.

Burton, P.J. 2008. The mountain pine beetle as an agent of forest disturbance. BC J. Ecosyst. Manag. **9**(3): 9–13. Available from http://jem.forrex.org/index.php/jem/article/viewArticle/402.

Calcagno, V. 2013. glmulti: Model selection and multimodel ingerence made easy. R package version 1.0.7. Available from https://CRAN.R-project.org/package=glmulti.

Calcagno, V., and Mazancourt, C. De. 2010. glmulti : An R Package for easy automated model selection with (Generalized) Linear Models. J. Stat. Softw. **34**(12): 1–29. doi:10.18637/jss.v034.i12.

Callaghan, T.V, Collins, N.J., and Callaghan, C.H. 1978. Photosynthesis, growth and reproduction of Hylocomium splendens and Polytrichum commune in Swedish Lapland. Strategies of growth and population dynamics of tundra plants 4. Oikos **31**(1): 73–88. Available from http://www.jstor.org/stable/3543386.

Carroll, A.L., and Safranyik, L. 2004. The bionomics of the mountain pine beetle in lodgepole pine forests: establishing a context. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 21–32.

Chapin, F.S., Callaghan, T.V, Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G., and Zimov, S.A. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? Ambio **33**(6): 361–365. doi:10.1579/0044-7447-33.6.361.

Cigan, P.W., Karst, J., Cahill, J.F., Sywenky, A.N., Pec, G.J., and Erbilgin, N. 2015. Influence of bark beetle outbreaks on nutrient cycling in native pine stands in western Canada. Plant Soil **390**: 29–47. doi:10.1007/s11104-014-2378-0.

Clason, A.J., Macdonald, S.E., and Haeussler, S. 2014. Forest response to cumulative disturbance and stress: Two decades of change in whitebark pine ecosystems of west-central British Columbia. Écoscience **21**(2): 174–185. doi:10.2980/21-2-3686.

Cole, W.E., and Amman, G.D. 1980. Mountain pine beetle dynamics in lodgepole pine forests, Part 1: course of an infectation. USDA For. Serv. Intermountain Research Station. Research Paper **INT-89**. 56 pp.

Collins, B.J., Rhoades, C.C., Hubbard, R.M., and Battaglia, M.A. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. For. Ecol. Manage. **261**(11): 2168–2175. doi:10.1016/j.foreco.2011.03.016.

Cullingham, C.I., Cooke, J.E.K., Dang, S., Davis, C.S., Cooke, B.J., and Coltman, D.W. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. Mol. Ecol. **20**(10): 2157–2171. doi:10.1111/j.1365-294X.2011.05086.x.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., and Wotton, M.B. 2001. Climate change and forest disturbances. Bioscience **51**(9): 723–734. doi:10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2.

Delisle, G., and Woodard, P. 1988. Constants for calculating fuel loads in Alberta. Canadian Forestry Service, Northern Forestry Centre. Note No. **45**: 3 pp. Available from http://www.cabdirect.org/abstracts/19920662847.html.

Despain, D.G. 1983. Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. Ecology **64**(2): 231–234. Available from https://www.jstor.org/stable/1937070.

Dhar, A., and Hawkins, C.D.B. 2011. Regeneration and growth following mountain pine beetle attack: A synthesis of knowledge. BC J. Ecosyst. Manag. **12**(2): 1–16. Available from http://jem.forrex.org/index.php/jem/article/ view/22/84.

Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. **67**: 345-366.

Dykstra, P.R., and Braumandl, T.F. 2006. Historic influence of the mountain pine beetle on stand dynamics in Canada's Rocky Mountain parks. Canadian Forest Service, Pacific Forestry Centre. MPB Initiative Working Paper **2006-15**: 75 pp.

Edburg, S.L., Hicke, J.A., Brooks, P.D., Pendall, E.G., Ewers, B.E., Norton, U., Gochis, D., Gutmann, E.D., and Meddens, A.J.H. 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. Front. Ecol. Environ. **10**(8): 416–424. doi:10.1890/110173.

Edwards, M., Krawchuk, M.A., and Burton, P.J. 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: Understory and overstory response to mountain pine beetle and fire. For. Ecol. Manage. **338**: 163–175. doi:10.1016/j.foreco.2014.11.011.

Ehrenfeld, J. 1980. Understory response to canopy gaps of varying size in a mature oak forest. Bull. Torrey Bot. Club **107**(1): 29–41.

Environment Canada. 2018. Canadian Climate Normals 1981-2010 Station Data. Available from http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=2718&autofwd=1 [accessed 28 February 2018].

Gärtner, S.M., Bokalo, M., Macdonald, S.E., and Stadt, K. 2014. Variation in post-wildfire regeneration of boreal mixedwood forests: Underlying factors and implications for natural disturbance-based management. New For. **45**(2): 215–234. doi:10.1007/s11056-013-9404-6.

Gendreau-Berthiaume, B., Macdonald, S.E., and Stadt, J.J. 2018. Importance of the canopy in determining on-going regeneration and stand successional development in lodgepole pine forests. J. Veg. Sci. **29**(2): 213–225. doi:10.1111/jvs.12622.

Goodsman, D.W., Erbilgin, N., and Lieffers, V.J. 2012. The impact of phloem nutrients on overwintering mountain pine beetles and their fungal symbionts. Environ. Entomol. **41**(3): 478–486. doi:10.1603/EN11205.

Goslee, S.C., and Urban, D.L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. J. Stat. Softw. **22**(7): 1–19.

Griffin, J.M., Simard, M., and Turner, M.G. 2013. Salvage harvest effects on advance tree regeneration, soil nitrogen, and fuels following mountain pine beetle outbreak in lodgepole pine. For. Ecol. Manage. **291**: 228–239. doi:10.1016/j.foreco.2012.11.029.

Griffin, J.M., Turner, M.G., and Simard, M. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. For. Ecol. Manage. **261**(6): 1077–1089. doi:10.1016/j.foreco.2010.12.031.

Hart, S.A., and Chen, H.Y.H. 2006. Understory vegetation dynamics of North American boreal forests. CRC. Crit. Rev. Plant Sci. **25**(4): 381–397. doi:10.1080/07352680600819286.

Hart, S.A., and Chen, H.Y.H. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol. Monogr. **78**(1): 123–140. doi:10.1890/06-2140.1.

Hawkes, B., Taylor, S., Stockdale, C., Shore, T., Alfaro, R., Campbell, R., and Vera, P. 2004. Impact of mountain pine beetle on stand dynamics in British Columbia. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 177–199.

Heath, R., and Alfaro, R.I. 1990. Growth response in a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle: A case study. J. Entomol. Soc. Br. Columbia **87**: 16–21. Available from http://cfs.nrcan.gc.ca/publications?id=3074.

Hicke, J.A., Johnson, M.C., Hayes, J.L., and Preisler, H.K. 2012. Effects of bark beetle-caused tree mortality wildfire. For. Ecol. Manage. **271**: 81–90. doi:10.1002/jgrg.20078.

Hubbard, R.M., Rhoades, C.C., Elder, K., and Negron, J. 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. For. Ecol. Manage. **289**: 312–317. doi:10.1016/j.foreco.2012.09.028.

Johnson, E.A. 1992. Fire and vegetation dynamics: Studies from the North American boreal forest. *Edited by* R.S. Barnes, H.J. Birks, E.F. Connor, and R.T. Paine. Cambridge University Press. 129 pp.

Kayes, L.J., and Tinker, D.B. 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. For. Ecol. Manage. **263**: 57–66. doi:10.1016/j.foreco.2011.09.035.

Klutsch, J.G., Negrón, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., and Caissie, R. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (Dendroctonus ponderosae Hopkins) outbreak in Colorado. For. Ecol. Manage. **258**(5): 641–649. doi:10.1016/j.foreco.2009.04.034.

Kovacic, D.A., Dyer, M.I., and Cringan, A.T. 1985. Understory biomass in ponderosa pine following mountain pine beetle infestation. For. Ecol. Manage. **13**(1–2): 53–67. doi:10.1016/0378-1127(85)90005-2.

Lenth, R.V. 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Softw. **69**(1): 1–33. doi:10.18637/jss.v069.i01.

Lieffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for Calamagrostis canadensis in boreal forest sites. Can. J. For. Res. **23**: 2070–2077.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A., and Perry, D. 2004. Salvage harvesting policies after natural disturbance. Science **303**: 1303.

Logan, J.A., Régnière, J., and Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. **1**(3): 130–137. doi:10.1890/1540-9295(2003)001[0130:ATIOGW]2.0.CO;2.

Lotan, J.E. 1964. Initial germination and survival of lodgepole pine on prepared seedbeds. USDA For. Serv. Intermountain Research Station. Research Paper **INT-29**: 1–8.

Lotan, J.E., Brown, J.K., and Neuenschwander, L.F. 1985. Role of fire in lodgepole pine forests. *In* Lodgepole pine, the species and it management Symposium proceedings. *Edited by* D. Baumgartner et al. Washington State University, Pullman. pp. 133–152.

Lotan, J.E., and Critchfield, W.B. 1990. Pinus contorta Dougl. ex. Loud. *In* Silvics of North America, Agricultur. *Edited by* R.M. Burns and B.H. Honkala. Washington, DC. pp. 302–315. doi:10.1094/PHYTO-95-0284.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

McCambridge, W.F., Edminster, C.B., and Morris, M.J. 1982. Herbage production under ponderosa pine killed by the mountain pine beetle in Colorado. USDA For. Serv. Rocky Mountain Forest and Range Experiment Station. Research Note **RM-416**: 1-3.

McCune, B. 2007. Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. J. Veg. Sci. **18**(2002): 751–754. doi:10.1658/1100-9233(2007)18%5B751:IEOIRA%5D2.0.CO;2.

McCune, B., and Keon, D. 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. **13**(4): 603–606. doi:10.1111/j.1654-1103.2002.tb02087.x.

McCune, B., and Mefford, M.J. 2006. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach, Oregon, USA.

McIntosh, A.C.S., and Macdonald, S.E. 2013. Short-term resistance of ecosystem properties and processes to simulated mountain pine beetle attack in a novel region. Ecosphere **4**(6): 68. doi:10.1890/ES12-00344.1.

McIntosh, A.C.S., and Macdonald, S.E. 2013. Potential for lodgepole pine regeneration after mountain pine beetle attack in newly invaded Alberta stands. For. Ecol. Manage. **295**: 11–19. doi:10.1016/j.foreco.2012.12.050.

McRae, D.J., Alexander, M.E., and Stocks, B.J. 1979. Measurement and description of fuels and fire behaviours on prescribed burns: A handbook. Canadian Forestry Service, Great Lakes Forest Research Centre. Information Report **O-X-287**: 44 pp.

Mitchell, R.G., and Preisler, H.K. 1998. Fall rate of lodgepole pine killed by the mountain pine beetle in Central Oregon. West. J. Appl. For. **13**(1): 23–26.

Moisey, D., Young, J., Lawrence, D., Stone, C., and Willoughby, M.G. 2012. Guide to range plant community types and carrying capacity for the dry and central mixedwood subregions in Alberta. 7th edition. Alberta Environment and Sustainable Resource Development, Lands Division. Pub. No. **T/276**.

Morehouse, K., Johns, T., Kaye, J., and Kaye, M. 2008. Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests. For. Ecol. Manage. **255**(7): 2698–2708. doi:10.1016/j.foreco.2008.01.050.

Morris, J.L., Mustaphi, C.J.C., Carter, V.A., Watt, J., Derr, K., Pisaric, M.F.J., Anderson, R.S., and Brunelle, A.R. 2015. Do bark beetle remains in lake sediments correspond to severe outbreaks? A review of published and ongoing research. Quat. Int. **387**: 72–86. doi:10.1016/j.quaint.2014.03.022.

Muir, P. 1993. Disturbance Effects on Structure and Tree Species Composition of Pinus Contorta in Western Montana. Can. J. For. Res. **23**: 1617–1625.

Muir, P.S., and Lotan, J.E. 1985. History and serotiny of Pinus contorta in Western Montana. Ecology **66**(5): 1658–1668.

Nalder, I.A, Wein, R.W., Alexander, M.E., and de Groot, W.J. 1997. Physical properties of dead and downed round-wood fuels in the boreal forests of Alberta and Northwest Territories. Int. J. Wildl. Fire **27**(9): 1513–1517. doi:10.1139/x97-083.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. *Compiled by* D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. **1/005**.

Natural Resources Canada. 2017. Mountain pine beetle (factsheet). Available from http://www.nrcan.gc.ca/forests/fire-insects-disturbances/top-insects/13397 [accessed 25 August 2018].

Nealis, V.G., and Peter, B. 2008. Risk assessment of the threat of mountain pine beetle to Canada’s boreal and eastern pine forests. Canadian Forest Service, Pacific Forestry Centre, Information Report **BC-X-417**: 31 pp.

Oboite, F.O. 2018. Growth of understory spruce following mountain pine beetle attack and recalibration and validation of the Mixedwood Growth Model for black spruce. PhD thesis, Dept. of Renewable Resources, University of Alberta.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., and Wagner, H. 2017. Vegan: Community Ecology Package. R package version 2.4-2. Available from http://cran.r-project.org/package=vegan.

Ono, H. 2004. The mountain pine beetle: Scope of the problem and key issues in Alberta. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 62–66.

Page, W.G., and Jenkins, M.J. 2007. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. For. Sci. **53**(4): 507–518.

Paradis, E., Claude, J., and Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics **20**: 289–290.

Parker, A.J. 1986. Persistence of lodgepole pine forests in the Central Sierra Nevada. Ecology **67**(6): 1560–1567. Available from http://www.jstor.org/stable/1939086 .

Pec, G.J., Karst, J., Sywenky, A.N., Cigan, P.W., Erbilgin, N., Simard, S.W., and Cahill, J.F. 2015. Rapid increases in forest understory diversity and productivity following a mountain pine beetle (Dendroctonus ponderosae) outbreak in pine forests. PLoS One **10**(4): 1–16. doi:10.1371/journal.pone.0124691.

Piña, P.C.P. 2013. Impact of mountain pine beetle attack on water balance of lodgepole pine forests in Alberta. PhD thesis, Dept. of Renewable Resources, University of Alberta.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team. 2016. _nlme: Linear and Nonlinear Mixed Effects Models_. Available from http://cran.r-project.org/package=nlme.

Pykälä, J. 2004. Immediate increase in plant species richness after clear-cutting of boreal herb-rich forests. Appl. Veg. Sci. **7**: 29–34. doi:10.1111/j.1654-109X.2004.tb00592.x.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. Bioscience **58**(6): 501–517. doi:10.1641/B580607.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Rees, D.C., and Juday, G.P. 2002. Plant species diversity on logged versus burned sites in central Alaska. For. Ecol. Manage. **155**: 291–302. doi:10.1016/S0378-1127(01)00566-7.

Rhoades, C.C., McCutchan, J.H., Cooper, L.A., Clow, D., Detmer, T.M., Briggs, J.S., Stednick, J.D., Veblen, T.T., Ertz, R.M., Likens, G.E., and Lewis, W.M. 2013. Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response. Proc. Natl. Acad. Sci. **110**(5): 1756–1760. doi:10.1073/pnas.1221029110.

Rice, A.V., Thormann, M.N., and Langor, D.W. 2008. Mountain pine beetle-associated blue-stain fungi are differentially adapted to boreal temperatures. For. Pathol. **38**(2): 113–123. doi:10.1111/j.1439-0329.2007.00525.x.

Roe, A.L., and Amman, G.D. 1970. The mountain pine beetle in lodgepole pine forests. USDA For. Serv. Intermountain Research Station. Research Paper **INT-71**: 26 pp. doi:10.5962/bhl.title.68786.

Royo, A.A., and Carson, W.P. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. **36**(6): 1345–1362. doi:10.1139/x06-025.

Rydgren, K., Hestmark, G., and Økland, R.H. 1998. Revegetation following experimental disturbance in a boreal old-growth Picea abies forest. J. Veg. Sci. **9**(3): 763–776. doi:10.2307/3237042.

Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., and Taylor, S.W. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. Can. Entomol. **142**(5): 415–442. doi:10.4039/n08-CPA01.

Safranyik, L., Shrimpton, D., and Whitney, H. 2002. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service, Pacific Forestry Centre. Forestry Technical Report **1**: 23 pp.

Sharpe, M., Hwang, H., Schroeder, D., Ryu, S.R., and Lieffers, V.J. 2017. Prescribed fire as a tool to regenerate live and dead serotinous jack pine (Pinus banksiana) stands. Int. J. Wildl. Fire **26**(6): 478–484. doi:10.1071/WF17046.

Sibold, J.S., Veblen, T.T., Chipko, K., Lawson, L., Mathis, E., and Scott, J. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. Ecol. Appl. **17**(6): 1638–1655.

Simberloff, D. 2011. Native Invaders. *In* Encyclopedia of biological invasions. *Edited by* D. Simberloff and R. Rejmanek. University of California Press, Berkeley, CA. pp. 472–475.

Stone, W.E., and Wolfe, M.L. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. Vegetation **122**(1): 1–12. doi:10.1007/BF00052811.

Stretch, V., Gedalof, Z., Cockburn, J., and Pisaric, M.F.J. 2016. Sensitivity of reconstructed fire histories to detection criteria in mixed-severity landscapes. For. Ecol. Manage. **379**: 61–69. doi:10.1016/j.foreco.2016.08.009.

Stuart, J., Agee, J., and Gara, R. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. Can. J. For. Res. **19**: 1096–1104.

Taylor, S.W., and Carroll, A.L. 2004. Disturbance, forest age, and mountain pine beetle outbreak in BC: A historical perspective. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 41–51.

Teste, F.P., Lieffers, V.J., and Landhäuser, S.M. 2011a. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. Ecol. Appl. **21**(1): 150–162. doi:10.1890/09-1881.1.

Teste, F.P., Lieffers, V.J., and Landhäusser, S.M. 2011b. Viability of forest floor and canopy seed banks in pinus contorta var. latifolia (pinaceae) forests after a mountain pine beetle outbreak. Am. J. Bot. **98**(4): 630–637. doi:10.3732/ajb.1000252.

de Ville, N. 2013. Forest light and structure in relation to disturbances: comparing mountain pine beetle, wildfire and salvage logging. MRM thesis, School of Resource and Environmental Management, Simon Fraser University.

VRI. 2007. Vegetation resources inventory: Ground sampling procedures. The Province of British Columbia Ministry of Forests and Range Forest Analysis and Inventory Branch for the Terrestrial Ecosystems Task Force Resources Information Standards Committee. 236 pp.

Vyse, A., and Navratil, S. 1985. Advances in lodgepole pine regeneration. *In* Lodgepole pine, the species and its management. *Edited by* D. Baumgartner, R. Krebill, J. Arnott, and G. Weetman. Washington State University, Spokane. pp. 173–186.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. For. Sci. **14**: 20–27.

Van Wagner, C.E. 1982. Practical aspects of the line intersect method. Canadian Forestry Service, Petawawa National Forestry Institute. Information Report **PI-X-12**: 11 pp. Available from http://www.floresta.ufpr.br/firelab/artigos/artigo389.pdf.

Waring, R.H., and Pitman, G.B. 1985. Modifying Lodgepole Pine Stands to Change Susceptibility to Mountain Pine Beetle Attack. Ecology **66**(3): 889–897. Available from http://www.jstor.org/stable/1940551.

Whitehead, R.J., Russo, G.L., Hawkes, B.C., and Armitage, O.B. 2007. A silvicultural assessment of 10 lodgepole pine stands after partial cutting to reduce susceptibility to mountain pine beetle. Natural Resources Canada, Canadian Forest Service, Canadian Wood Fibre Centre, Victoria, BC. 48 pp.

Whitehead, R.J., Safranyik, L., Russo, G.L., Shore, T.L., and Carroll, A. 2004. Silviculture to reduce landscape and stand susceptibility to the mountain pine beetle. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 233–244.

Wilson, B. 2004. An overview of the mountain pine beetle initiative. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E. Stone. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. pp. 3–9.