# Investigating Fire as a Silvicultural Tool for Regeneration of Mountain Pine Beetle-killed Serotinous Pine of Northern Alberta

by

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# Abstract

Serotinous pine forests in Western Canada are threatened by a record-breaking mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreak - the largest recorded in Western North America. Forest managers are concerned with whether these closed-cone MPB-killed forests will successfully regenerate. The study indicates fire is required for successful regeneration and suggests that of the two limiting factors of serotinous pine regeneration, the differences are likely accounted for by cone opening. It was evident in the data, however, that the objective of duff removal is not as greatly achieved after surface fire and, quite likely linked, MPB-killed stands will likely regenerate most successfully after a continuous crown fire. Due to the variable nature of fire, however, it is difficult to provide a clear recommendation on which type of fire would yield the greatest regeneration.

This study is the first to clearly indicate there is active moisture exchange of serotinous lodgepole pine cones from both live and MPB-killed trees. The moisture exchange rate was similar among cones of live and MPB-killed trees, but it takes more time to open cones from MPB-killed trees. The results suggested that cone moisture is not the sole driving factor determining the time taken to open serotinous cones, but the mortality condition and age also play a role in the process. This indicates that the cones from MPB-killed trees might have wider window of survival after fire.

# Preface

The literature review in Chapter 1; study design, collection and analysis of chapter 2 and concluding analysis in chapter 4 are my original work. Chapter 3 of this thesis has been published as “Sharpe, M. and S.R. Ryu. 2015. The moisture content and opening of serotinous cones from lodgepole pine killed by the mountain pine beetle. The Forestry Chronicle. 91(3): 260-265”. I was responsible for data collection and analysis as well as the manuscript composition. Dr. Soung Ryoul Ryu assisted with the data analysis and contributed to manuscript edits. Dr. Vic Lieffers was involved with the concept formation, data collection and contributed to manuscript edits.

# Dedication

*Dedicated to my late father, David T. Sharpe. A man with incredible spirit and drive.*

*A father, forester, teacher and a loving husband to my mother, Mary Sharpe,*
*who was equally instrumental to my success.*

# Acknowledgments

Thank you to Foothills Research Institute, Alberta Agriculture and Forestry, FPInnovations and the Western Partnership for Wildland Fire Science at the University of Alberta for financial and in kind support. In addition to the financial support, I would also like to take the opportunity to thank my advisors Dr. Soung Ryu and Dr. Victor Leiffers who believed in me and invested a great deal of time in helping see this thesis through to completion.

While Horsecreek and Jaskfish field sites were unable to provide the venue for my research in the end, a great deal of time and effort was spent behind the scenes. Thank you to Mark Handel and Dave Schroder from Alberta Agriculture and Forestry (AAF; formally Environment Sustainable Resource Development; ESRD) for help in organizing logistics for Horescreek and field crew helpers Hyejin Hwang, Rodrigo Campos and Drew McDonald who contributed to data collection. Thank you to Dr. Derek McKenzie and his students who were very helpful in showing me how to process resins and allowed me the use of their lab. Thank you to Forrest Barrett and Kari Matechuk from Grande Prairie AAF for their field support at the Jackfish field site as well as my co-workers Stephanie Koroscil and Devon Barnes.

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I was also fortunate to have a great team of friends and colleagues. Hyejin you were my rock through this and continue to be such a wonderful friend. Thank you to Jon & Chris for supporting me, giving me space and limiting the social temptations on days that I needed to stay on task. A special thanks to Marty Alexander for his support throughout this process. It was an honour to work with you and discuss ideas. I will forever be thankful for your contribution to my work.

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# Chapter 1 - The Roles and Impacts of Mountain Pine Beetle and Fire in the Western Canadian Boreal Forests

## 1.1 Introduction

In the field of Ecology, a disturbance is generally defined as a temporary change in environmental conditions that contribute to a pronounced macroscopic change in the ecosystem (Turner & Dale 1998). A disturbance may result in the removal of large biomass from the system or simply impact ecosystem functions without altering biomass or structure. Western Canadian boreal forests experience both natural disturbances (e.g., flooding, windstorms, fires, and insect outbreaks) and anthropogenic disturbances (e.g., forest harvesting, fire exclusion, and the introduction of exotic species) (Kurz & Apps 1999). In fact, many species that thrive within this forest region rely heavily on various disturbances for their survival and dominancy and the integrity of the boreal forest is believed to be determined by the magnitude, type, and frequency of disturbances. For example, fire may change forest age distribution and structural complexities. Disturbances can have profound immediate effects on ecosystems and may greatly alter its pattern and processes. Moreover, the impacts of a disturbance can persist for an extended time.

The boreal forest has evolved in the presence of disturbance, commonly wildfire, and without it, the natural age range of variability and structure of the forest remain homogeneous. The resilience of the boreal forest is at risk, particularly for forests with little variance in age and composition. This is currently evident with the increasing populations of mountain pine beetle (*Denroctonus ponderosae*, MPB) in forests that have been aided by fire exclusion. This thesis attempts to first highlight the ecological impacts of MPB and fire and examine the interactive effects these two disturbances have on the future of pine dominated areas of the Northern Alberta boreal forest.

### 1.1.0 Serotinous Pine Species in Western Canada

Serotinous cones remain closed and sealed by resin, thereby retaining seeds within the canopy much longer than its non-serotinous counterparts. There are certain species that are characterized as having serotinous cones. These cones release their seed only after exposure of sufficient heat; most commonly by the presence of wildfire and occasionally direct and extended exposure to sunlight (Crossley 1956; Lotan 1964). thought to be adapted to fire (Lotan et al. 1985). These include, but are not limited to jack pine (*Pinus banksiana* Lamb.) and lodgepole pine (*Pinus contorta* var. latifolia). These two species form the basis of my study.

### 1.1.1 Impacts of Mountain Pine Beetle on Regeneration

The MPB has caused economic strife to the forest industry in British Columbia over the past decade. Currently in British Columbia (BC), 14 million hectares of pine forests have been impacted by the MPB (Coops et al., 2012). Moreover, it currently threatens pine species of Alberta and is expected to move into the rest of the lodgepole and jack pine dominated boreal forest regions. Currently in Alberta, 6 million hectares of pine forests are vulnerable (ESRD, 2013). Figure 1-1 illustrates the historic distribution of the MPB in North America as well as the distribution of pine species (i.e. potential for MPB population growth).

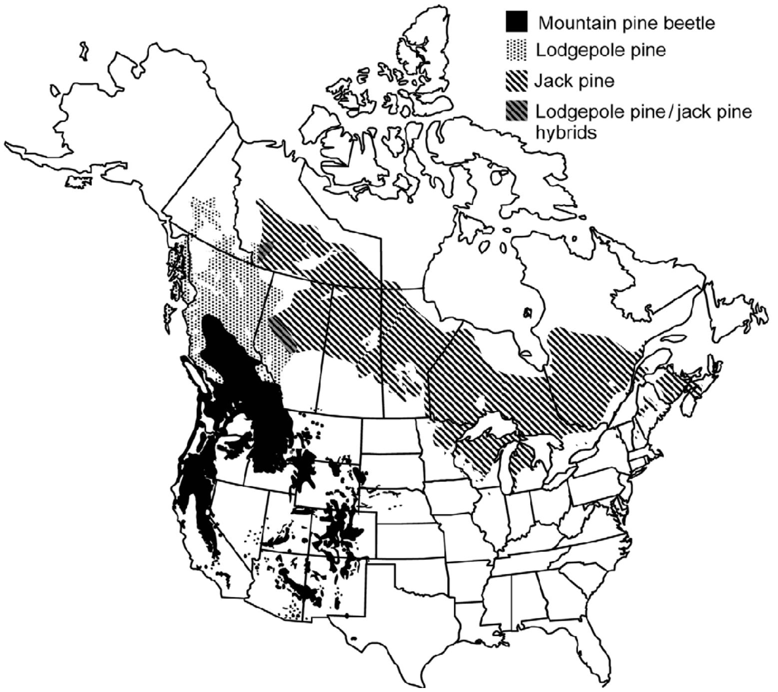

**Figure 1-1:** Historical distribution of mountain pine beetle (*Dendroctonus ponderosae*) lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*). Regions where lodgepole pine and jack pine hybridize are also indicated (adapted from Logan and Powell 2001).

Taylor and Caroll (2004) published a historic perspective of MPB outbreak dynamics in BC. They determined there were two main reasons why the outbreaks have prevailed in recent decades. The first has to do with the increased availability of the MPB host tree, lodgepole pine. In the year 2000, mature lodgepole pine coverage in the Province was three times that of 100 years ago. Increases in mature lodgepole pine are due, in part, to successful fire control over the past century; elevated by the recent commercial utilization of lodgepole pine over the past 40 years.

The second main reason for MPB population increases in Northern and Boreal regions relates to climate conditions. Climatic thresholds for MPB has been well documented by Safranyik and Linton (1998) with -40 degrees Celsius as the lower threshold for larval survival over winter, though contributing most to mortality if sustained over a period of days. Figure 1-2 illustrates spatially, the historical climatic limits as recorded in the literature with observed MPB. As average annual temperatures increase, the distribution of observed MPB will change; moving east towards pine forest of Alberta and Saskatchewan.

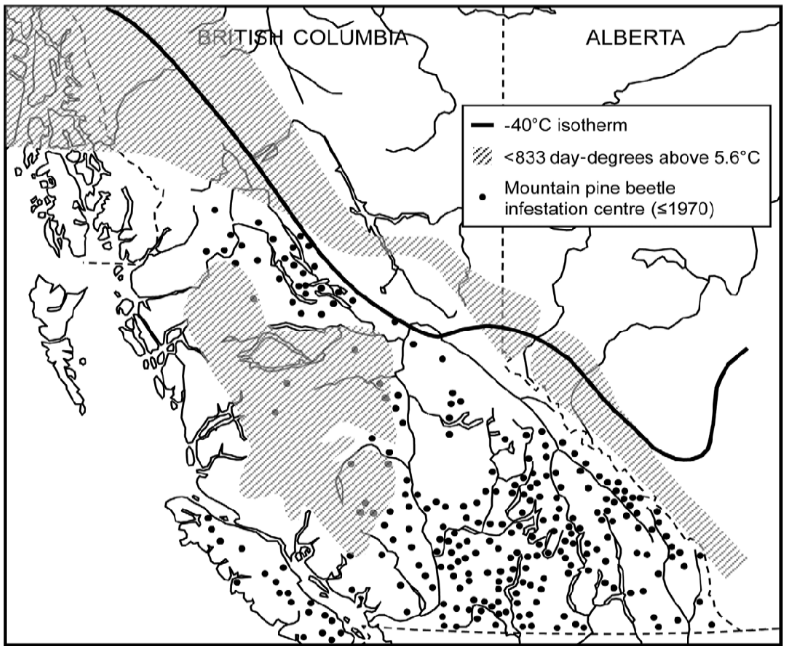

**Figure 1-2:** Historical climatic limits to the northern and eastern distribution of mountain pine beetle (*Dendroctonus ponderosae*). Data points represent the observed distribution of infestations up to and including 1970; shading indicates regions where, on average (1941–1970), there were fewer than 833 day-degrees above 5.6℃ within a growing season, and the heavy line denotes the isotherm where 240℃ occurred, on average (1941–1970), on at least 1 day each winter (data from the Canadian Forest Service Forest Insect and Disease Survey and Environment Canada's Meteorological Service).

There are many possible ecological changes that may occur as a result of the MPB relating to in-stand moisture and structure. Pina (2012) studied the impact of MPB on soil moisture and found that live stands (control) yielded the least moisture at 5cm depth in the mineral soil compared with dead stands. Moreover, stands with 50% mortality had 10% greater moisture than control and stands with 100% mortality had 13% greater moisture than control. This gradient of increasing soil moisture with increasing mortality may influence the recruitment of new seedlings, however it is important to note that seedling recruitment is determined on a much finer scale. The increase in moisture post-MPB will impact decomposition and the rate at which standing pine trees fall.

The MPB can have large impacts to forest structure that trickle down to impacts on many wildlife species. Just as soil moisture will likely be influenced by mortality rates, Lewis and Hartley (2005) found that fall rates increase with increasing mortality. Lewis and Hartley also determined that MPB-killed lodgepole pine trees begin to fall 3-5 years after tree death with 25-50% of the standing trees down within 10 years. Fall rate is highest for standing trees in wet areas (Lewis and Hartley 2005) with soil moisture content indicated as the largest determinant of how long snags remain standing. In addition, Hawkes et al. (2005) projects an increase in surface fuels in severely infested areas. Presence or absence of standing snags and down woody debris has potential for impact on wildlife.

Avian vertebrates benefit from the impacts of MPB using the standing trees as a food source (Koplin 1969) and several studies have documented increase in woodpecker populations (Baldwin 1960; Koplin 1969). Species such as snowshoe hare and blue and spruce grouse consume down needles (Sullivan and Sullivan 1988, Remmington and Hoffman 1996). Other wildlife such as furbearers and ungulates require forested areas for thermal and security cover (Koehler and Aubry 1994). The eventual elimination of cover brought about by the MPB, not only impacts wildlife at a local, forest-stand level, but at a larger landscape level also (Harris 1984). In all cases, a focus towards sustainable forest management with prolific regeneration is beneficial for all wildlife species to provide future forest cover, food and habitat. It is generally understood that fire is required to regenerate serotinous pine stands and this thesis attempts to delve into this idea. The first step to do so it to explore the ecological impacts of fire on plant growth.

### 1.1.2 Ecological Impacts of Fire on Plant Growth

Fire influences seedbed availability and serotinous cone opening, which are currently the two main limitations to serotinous pine regeneration in Western Canada. Additionally, fire can greatly impact regeneration of vegetation by affecting various ecological processes including nutrient availability, microbial activity and decomposition.

#### *Nutrients*

Fire can affect soil chemistry and structure in many ways. After fire, soil temperature can increase due to blackened soil surface and removal of overstory trees (Christensen & Muller 1975). Severe fires also can remove organic matter that would otherwise be slowly made available for use by microbes (Magill & Aber 2000) and convert soil organic nitrogen to inorganic forms. DeBano et al. (1979) reported, however, that low intensity fire had minimal impact on soil organic nitrogen (N).

N is one of the most important limiting factors of many forests and, therefore, it is often the major driver of productivity. N is a component of chlorophyll; the site of carbohydrate formation or photosynthesis and increases the rate of photosynthesis when in sufficient supply (Bonan 2002). Moreover, a plants vigor and ability to grow is a direct function of available N. So, how exactly does wildfire affect the N levels or net primary production of the ecosystem?

During the decomposition of plant matter, organic N is once again converted to inorganic ammonium and released into the soil. The process that converts organic N to ammonium is called mineralization and plays a significant role in the management of N. The substrate, or available coarse woody debris decreases N mineralization. In Boreal lodgepole pine stands, needles decompose slowly (Fahey & Knight 1986), and it is believed that in this type of environment, accumulations of needle litter may slow net N mineralization rates (Stump & Binkley 1993). Fire would provide a level of nutrient cycling that would not otherwise be there in a slow decomposing forest type. Fire exports fixed N from an ecosystem, especially in higher temperatures fires, but as Magill & Aber (2000) state, severe fires may remove organic matter entirely.

Another nutrient that is vital to the growth of a plant by contributing to the conversion of the sun's energy into usable food for plants is phosphorous (P). Fires increase available P within a forest ecosystem; however this increase is short lived (Serrasolsas & Khanna 1995). The decline in P is highly variable depending on the site. A study conducted in a spruce (*Picea spp.*) dominated forest, found that; available P in the upper 30cm of mineral soil had increased by 50%, nine months after slash burning. The beginning stage of decline in P was observed 21 months after the fire event (Macadam 1987). Trees are unable to capture P without the presence of fire, strengthening the argument that fire is an important process to the forest ecosystem.

Fire-induced changes in soil nutrients other than N and P tend to be more variable and depend greatly on the type of nutrients, percentage of burnt organic matter, soil properties and ability for nutrients to leach (Kutiel & Shaviv 1992). Many nutrients like calcium, magnesium and potassium in the soil showed significant rises than their pre-fire levels, dropping back to original content only 3 months after disturbance (Adams & Boyle 1980).

### ***Structure***

Upon the presence of a wildfire within a plant community, the dynamics will change in both structure and components. That is, after a wildfire, the forest experiences an immediate reduction in small wood debris on the ground but an increase in coarse woody debris with time as the dead trees fall to the forest floor; creating structural heterogeneity across the landscape (Ferguson & Elkie 2003; Tinker & Knight 2000). It is generally understood that coarse woody debris within a forest ecosystem may facilitate N fixation (Brunner & Kimmins 2003) and provide a substrate for decomposition and subsequent N mineralization (Busse 1994; Fahey & Knight 1986; Harmon *et al*. 1986).

Previous studies have shown that after fire, litter in frequently burned areas have a higher carbon to nitrogen (C:N) ratio (Hernandez & Hobbie 2008). The C:N ratio represents the ratio of the mass of carbon to the mass of N within a substance and can be used as an indicator of N limitation of plants or organisms. As indicated by Hernandez and Hobbie (2008), an increase C:N ratio could account for a reduction in decomposition rates.

Decomposition is minimized for standing dead trees (Harmon et al 1986). The decomposition rate increases once the standing dead trees reach the forest floor (Busse 1994). What this means from an ecological perspective is that the structure of the stand post fire may have a considerable effect on the stand recovery from a below ground perspective. Vertical and horizontal coarse woody debris will differ in regards to their ability to leach dissolved organic carbon and begin the process of soil formation above the mineral soils (Spears et al. 2003). This suggests that future soil formation should be considered when applying fire on the landscape. It is also very important to consider the impact standing snags may have on fire behavior and post-fire effects by influencing stand temperature and moisture. Impacts of MPB-killed stands will be discussed in further detail in the next section.

### *Microbial Activity and Decomposition*

Some studies were highlighted earlier regarding the effect of fire on structure, particularity of coarse woody debris content. In addition to the coarse woody debris' potential effect on soil formation, some studies suggest that it may also affect microbial community composition and subsequent N availability (Sinsabaugh *et al.* 1993). A common theme within these studies is the notion that changes in enzyme activity by way of fire could affect organic matter decomposition rates.

It is widely accepted that decomposition relates directly to carbon and nutrient cycling through changes in microbial communities or otherwise, however the magnitude and duration of the impact of fire on decomposition remains ambiguous. Following fire, some studies reported an increase in organic matter degradation (Gundale *et al.* 2005), while others suggest a decrease (Monleon & Cromack 1996). Further research is required to understand the relationship between fire and organic matter decomposition rates so that we can better understand the microscopic/belowground changes within the forest stand.

## 1.2 Goals and Structure of Thesis

Overall, my objective is to explore the interactive effects of two boreal forest disturbances; mountain pine beetle and fire on serotinous pine forests. This objective is driven by a series of hypotheses relating to the differences among live and MPB-killed serotinous pine stands with respect to (1) regenerative response to three different types of fire, (2) regenerative obstacles such as seedbed preparation and cone opening; and (3) cone moisture and its relationship to cone opening. In Chapter 2, I will highlight the current literature relating to regenerative limitations within a jack pine stand and evaluate the interactive effects of fire on site preparation and regeneration of live and simulated MPB-killed jack pine stands. Chapter 3 further explores why the differences were evident among treatments; with a focus on cone moisture and opening. Chapter 4 provides management implications and recommendations.

In order to address these goals, the following questions will be asked:

**Chapter 2**

**Q1**: How does live and dead serotinous pine regeneration differ after three different treatments of fire?

**Q2**: Does site preparation vary in live and dead serotinous pine stands after the application of three different treatments of fire?

**Chapter 3**

**Q3**: Does cone moisture differ among live and dead trees?

**Q4**: Does cone age influence cone moisture in both live and dead trees?

**Q5:** How does resin breakage within cones differ among live and dead trees?

**Q6**: Does resin breakage relate to cone moisture?

## 1.3 Literature Cited

**Adams, P.W., and J.R. Boyle. 1980.** Effects of fire on soil nutrients in clearcut and whole-tree harvest sites in central Michigan. Soil Science Society of America Journal. 44(4):847-850.

**AESRD. 2014.** Follow the beetle: crews gear up for another year fighting Alberta's most 'invasive' species. Alberta Environment and Sustainable Resource Development. Blog. September 12, 2014. https://aesrd.wordpress.com/category/forests-and-wildfire/forest-health-and-diseases/

**Baldwin, P.H. 1960.** Overwintering of woodpeckers in bark beetle-infested spruce-fir forests of Colorado. International Ornithological Congress Proceedings. 12:71–84.

**Bonan, G.B. 2002.** Ecosystems. In Ecological climatology: Concepts and Applications. Cambridge, UK: Cambridge University Press. Second Edition. 303-320.

**Brunner, A., and J.P. Kimmins. 2003.** Nitrogen fixation in coarse woody debris of "Thuja plicata" and "Tsuga heterophylla" forests on northern Vancouver Island. Can. J. For. Res. 33:1670-1682. Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Sci. Soc. Am. J. 58: 221– 227.

**Christensen, N.L., and C.H. Muller. 1975.** Effects of fire on factors controlling plant growth in Adenstoma chaparral. Ecological Monographs. 45: 29-55.

**Coops, N. C., Wulder M. A., and R. H. Waring. 2012**. Modeling lodgepole and jack pine vulnerability to mountain pine beetle expansion into the western Canadian boreal forest. Forest Ecology and Management. 274: 161-171.

**Critchfield, W. B. 1957.** Geographic variation in Pinus contorta. Maria Moors Cabot Foundation: Harvard University Publication no.3.

**DeBano, L.F., Rice, R.M., and C.E. Conrad. 1979.** Soil heating in chaparral fires: Effects on soil properties, plant nutrients, erosion, and runoff. USDA Forest Service Research Paper PSW-145. 21p.

**Fahey, T.J., and D.H. Knight. 1986.** Lodgepole pine ecosystems. BioScience. 36: 610-17.

**Ferguson, S.H., and P.C. Elkie. 2003.** Snag abundance 20, 30, and 40 years following fire and harvesting in boreal forests. Forestry Chronicle. 79: 541-549.

**Gundale, M.J. De Luca, T.H., Fiedler, C.E., Ramsey, P.W., Harrington, M.G., and J.E. Gannon. 2005.** Restoration treatments in a Montana ponderosa pine forest: Effects on soil physical, chemical and biological properties. Forest Ecology and Management. 213: 25-38.

**Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr, K., and K.W. Cummins. 1986.** Ecology of coarse woody debris in temperate ecosystems. In Advances in Ecological Research. 15**:** 133-302.

**Harris, L.D. 1984**. The fragmented forest: Island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Ill.

**Hawkes, B., Taylor, S., Stockdale, C., Shore, T., Beukema, S., and D. Robinson. 2005**. Predicting mountain pine beetle impacts on lodgepole pine stands and woody debris characteristics in a mixed severity fire regime using Prognosis (BC) and the Fire and Fuels Extension. Progress report for a study funded by the BC Forest Innovations Investment Research Program, Natural Resources Canada, Canadian Forest Service and the mpb Federal Initiative.

**Hernandez, D.L., and S.E. Hobbie. 2008**. Effects of fire frequency on oak litter decomposition and nitrogen dynamics. Oecologia. 158(3): 535-43.

**Koehler, G.M., and K.B. Aubry. 1994**. Lynx. In The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. L.F. Ruggiero, K.B. Aubrey, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski (editors). U.S. Department of Agriculture Forest Service, Fort Collins, Colo. General Technical Report rm-254. 74–98 pp.

**Koplin, J.R. 1969.** The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. Condor. 71:436–438.

**Kurz, W.A., and M.J. Apps. 1999**. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecol. Applic. 9: 526-547.

**Kutiel, P., and A. Shaviv. 1992.** Effects of soil type, plant composition and leaching on soil nutrients following a simulated forest fire. For.Ecol.Manage. 53: 329-343.

**Lewis, K.J. and I. Hartley. 2005**. Rate of deterioration, degrade and fall of trees killed by mountain pine beetle: A synthesis of the literature and experiential knowledge. University of Northern British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Victoria, B.C. Mountain Pine Beetle Initiative Working Paper 2005-14. url: http://warehouse. pfc.forestry.ca/pfc/25483.pdf

**Logan, J.A., and J.A. Powell. 2001**. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47: 160–173.

**Lotan, J.E., Brown, J.K., Neuenschwander, L.F. 1985**. Role of fire in lodgepole pine forests. Symposium proceedings of lodgepole pine: the species and its management. May 8-10, 1984, Spokane Washington State University, Pullman, WA. 133-152 pp.

**Macadam, A.M. 1987.** Effects of broadcast slash burning on fuels and soil chemical properties in the sub-boreal spruce zone of central British Columbia. Can J For Res. 17:1577–1584.

**Magill, A. H., and J.D. Aber. 2000.** Variation in soil net mineralization rates with dissolved organic carbon additions. Soil Biology and Biochemistry. 32: 597-601

**Monleon, V.J., and K. Cromack, Jr., 1996.** Long-term effects of prescribed underburning on litter decomposition and nutrient release in ponderosa pine stands in central Oregon. For. Ecol. Manage. 81: 143-152.

**Pina, P. 2012.** The impacts of simulated Mountain Pine Beetle attack on the water balance in lodgepole pine forest of the western Alberta foothills. PhD Dissertation, Dept. of Renewable Resources, University of Alberta, Edmonton.

**Remington, T.E. and R.W. Hoffman. 1996**. Food habits and preferences of blue grouse during winter. Journal of Wildlife Management. 60:808–817.

**Safranyik, L., and D. A. Linton. 1998.** Mortality of mountain pine beetle larvae, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in logs of lodgepole pine (*Pinus contorta* var. *latifolia*) at constant low temperatures. Journal of the Entomological Society of British Columbia. 95: 81-87.

**Serrasolsas I., and P.K. Khanna. 1995.** Changes in heated and autoclaved forest soils of S.E. Australia. II. Phosphorus and phosphatase activity. Biogeochemistry. 29:25–41

**Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McClaugherty, C.A., Rayburn, L., Repert, D., and T. Weiland. 1993.** Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. Ecology. 74: 1586–1593.

**Spears, J.D.H., Holub, S.M., Harmon, M.E., and K. Lajtha. 2003.** The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A. Can. J. Forest Res. 33: 2193– 2201.

**Stump, L.M., and D. Binkley. 1993.** Relationship between litter quality and nitrogen availability in Rocky Mountain forests. Can. J. For. Res. 23: 492-502.

**Sullivan, T.P., and D.S. Sullivan. 1988**. Influence of stand thinning on snowshoe hare population dynamics and feeding damage in lodgepole pine forest. Journal of Applied Ecology. 25:791–805.

**Tinker, D.B., and D.H. Knight. 2000.** Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems. 3: 472–483.

**Turner, M. G., and V.H. Dale. 1998.** Comparing large, infrequent disturbances: what have we learned? Ecosystems. 1: 511-523.

# Chapter 2 – Interactive Effects of Fire and MPB -Kill Simulation on Jack Pine Regeneration

## 2.1 Introduction

### 2.1.0 Mountain Pine Beetle

Mild winters and increasing presence of contiguous mature pine forests have resulted in the largest outbreak of mountain pine beetle (*Dendroctonus ponderosae*; MPB) in North American history (Safranyik 1978; Safranyik et al. 2010). To date, over 18 million hectares of Western Canadian coniferous forests have been impacted to some degree, with losses of upwards of 723 million cubic meters (53%) of merchantable pine volume. Much of the infested forests in Canada are dominated by serotinous lodgepole (*Pinus contorta* Dougl.) and jack (*Pinus banksiana* Lamb.) pine resulting in insufficient and often absent regeneration, particularly where the organic layer remains undisturbed (Astrup 2008). The presence of a thick organic layer often limits the growth of small pine seedlings because roots of seedlings cannot reach mineral soil, thereby increasing mortality (Dhar and Hawkins 2011). Therefore, the chance of successful regeneration is low without disturbance to the organic layer and ground vegetation (e.g., feathermoss (*Hylocomium splendens* Hedw.)) through natural disturbances or forest management practices (e.g., prescribed fire and drag scarification). In addition, both the lodgepole and jack pine species develop serotinous cones as a natural strategy to survive after fire disturbances (Critchfield 1957) and without the presence of fire can be considered a limitation to regeneration. Pine regeneration after a fire is relatively well understood in live stands, but little is known whether regeneration limitations change after fire in previously dead stands (e.g., MPB-kill).

How does cone opening change once a stand is dead and does it influence seedbed suitability? It is also not clear how the opening of the serotinous cone is influenced when an additional disturbance is present (e.g., MPB). This is important given the current situation of increasing MPB population in Western Canada. This chapter will explore this dynamic within a jack pine stand.

### 2.1.1 Jack Pine Silvics

Jack pine is a shade intolerant and successful pioneer species after major disturbances (e.g., stand-replacing fire). The major portion of the jack pine range is found in Canada extending its northern boundary eastward from the Mackenzie River in the Northwest territories and across to Cape Breton Island in Nova Scotia (Rudolph and Laidly 1990). The south eastern portion of the range extends through to Maine, New Hampshire, northern New York and it can be found in Michigan, northwest Indiana, northeast Illinois, and northwest through Wisconsin and Minnesota. Due to its adaptation to stand replacing disturbances and hostile environments, it is most common for jack pine to be found in pure, even-aged stands, dominating the stocking over vast areas of Canada and in some sandy areas of northeastern United States (Rudolph and Laidly 1990). Associates to the jack pine are black spruce (*Picea mariana* Mill.), white birch (*Betula papyriferia* Marsh.), and aspen (*Populus tremuloides* Michx.). In the southern parts of its range, it is found intermixed with various hardwood trees (Burns and Honkala 1990).

Jack pine is one of the most shade-intolerant pines within its native range; however it is more tolerant in its seedling stage (Rudolph and Laidly 1990). It is commonly grown on well-drained dry sandy or gravelly soils where other species are unable to compete. On dry sites, jack pine seedlings prefer some shade to reduce surface temperatures and evapotranspiration. Once seedlings are established, they require direct sunlight to assure survival. Jack pine is a pioneer species thriving well on burned or mineral soil-exposed sites, and it is succeeded by more shade tolerant species in the absence of disturbances (Rudolph and Laidly 1990). On nutrient poor and dry sites, it may persist and form an edaphic climax.

### 2.1.2 Limitations to Jack Pine Regeneration

#### ***Cone Opening***

The seeds of jack pine are generally contained in serotinous cones, sealed by a resinous bond (Critchfield 1957). These seeds in the closed cones remain viable for several years and are released after exposed to enough heat; most commonly by the presence of wildfire and occasionally direct and extended exposure to sunlight (Crossley 1956; Lotan 1964). Studies have shown that a temperature of at least 45-60° is required to break the resin bond of closed cones (Cameron 1953). Quantification of heating requirements has been studied using both dry (Beaufait 1960; Hellum 1981) and water bath treatments (Clements 1910; Smith and McMurray 2002) in laboratories. Further studies are needed to test how other environmental factors influence cone opening and seed viability.

#### ***Seedling Establishment***

It is generally accepted that regeneration of coniferous species is limited when there is a thick organic forest floor like those found in boreal and montane regions (Place 1955; Simard et al. 2003); particularly a thick F and H horizon (herein referred to as '*duff*'). Many studies have been conducted to understand the moisture regimes of both the duff and litter layer due to their importance to forest managers. The duff layer, in particular the upper F horizon, tends to dry out more rapidly than mineral soil (Van Wagner 1987) and as a result seedling establishment within the F horizon tends to be more exposed to drought than those established on mineral soil (Coates 2002; Vyse et al. 2009). It is for this reason that post-fire conifer regeneration from seed largely depends on the extent of duff removal and accessibility to mineral soil or decomposed organic matter (Kemball 2006).

Ahlgren and Ahlgren (1960) and DeBano et al. (1998) suggest that duff consumption by fire is favorable to conifer regeneration, but Kembell (2006) suggests that it is not simply the removal of duff. He indicates that in addition to duff consumption, the ash deposits provide for unique thermal and moisture properties within the soil. Ashes dry faster and absorb less water and have higher albedo than unburned organic material (Herr and Duchesne 1995). Kembell (2010) conducted a laboratory experiment to evaluate the effects of ash on the germination of three conifer species, one a serotinous jack pine and found no effect of ash on post-fire pine recruitment. However, additional field experiments are required to confirm these results as there are many factors in the natural condition to alter the interactions among moisture, heat and ash toxicity (Herr and Duchesne 1995). While seedling establishment after fire is widely understood, little is known about how this changes if stands contained dead trees prior to the burn (i.e. mountain pine beetle).

### 2.1.3 Fire as a Silvicultural Tool

In addition to the importance of fire for cone opening and site preparation within pine species in Western Canada, there are also other fire related benefits. Fire aids in the decay of organic matter much faster than other natural processes and releases nutrients much more readily

(Choromanska and DeLuca 2002). Because of this and in addition to opening serotinous cones, fire can be effective in removing the duff layer that acts as the barrier for regeneration by blocking root growth to the much-desired mineral soil. While it is well documented that fire plays an important role in jack pine regeneration, little is known about effects of particular fire behavior on establishment, growth and survival. Therefore, there is limited capability to predict the effect of fire on pine regeneration and post-fire vegetation dynamics.

A great deal of planning is required prior to fire managers implementing a prescribed fire. A prescribed fire plan contains objectives and goals and outlines the conditions required to implement a safe and effective burn. Forest conditions and type of fire required for the burn will depend on the objective. There are many ways to categorize a fire; however for the purposes of this study, the Canadian Fire Behavior Prediction (FBP) System fires types were used as they are the most widely used in Canada. The FBP system provides quantitative estimates of potential head fire spread rate, fuel consumption, and fire intensity, as well as fire descriptions. This system uses the term “type of fire” for a general description of the fire and categorizes fires into three distinct types of fires; surface, intermittent and continuous. These were used as the three treatment types for the purposes of my experiment. Type of fire is a descriptor relating simply to the percentage of crown that has been consumed by the fire; known as crown fraction burned (CFB). A surface fire is represented as an area with less than 0.1 (10%) CFB (Fig. 2-1a). If the CFB is between 10-90%, the fire is an intermittent crown fire (Fig. 2-1b) and if it is greater than 90%, the fire is a continuous crown fire (Fig. 2-1c).

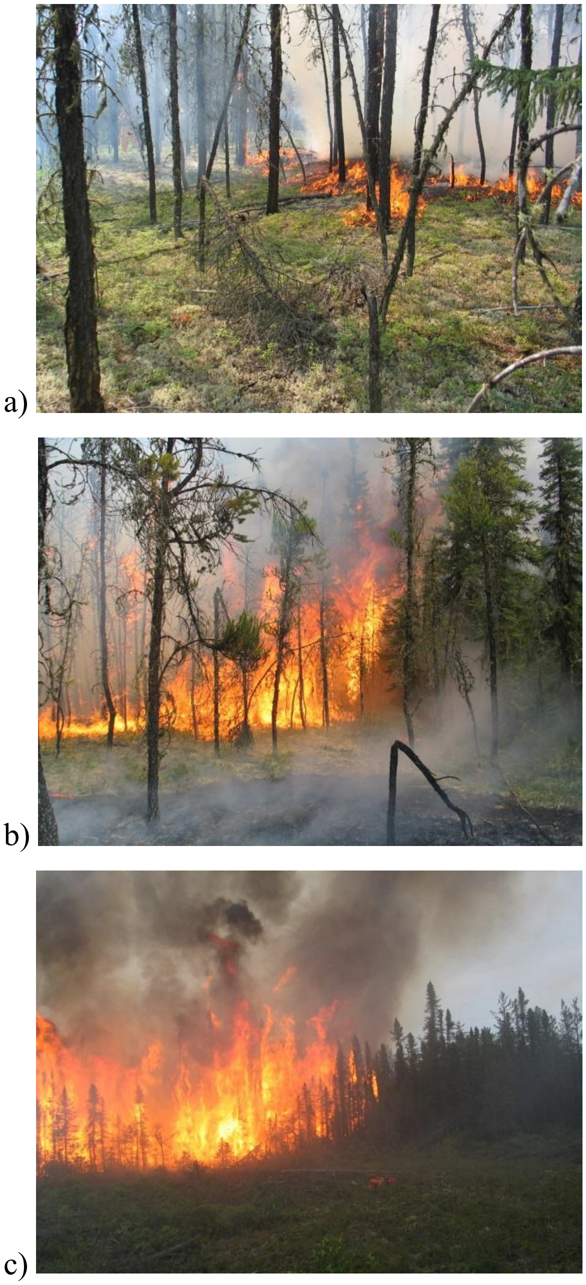

**Figure 2-1:** Illustration of the Canadian Fire Behaviour Prediction System types of fires a) surface fire b) intermittent fire; c) continuous fire (FPInnovations, 2009).

It is important to understand the ideal forest conditions and fire types required to achieve a certain goal when using fire as a tool. Eyre (1938) suggests an intense surface fire alone may not provide enough convective or radiative energy to open cones within the aerial seedbank of pine.

Crown fire interaction with the cones includes both heat generated from the surface fire as well as direct exposure to flames. Fires mostly consume fine fuels such as needles (Despain et al. 1996).

While understory fire has been used in the past as a silvicultural tool, it is unclear how this type of treatment should be used in stands impacted by a mountain pine beetle outbreak. While total available fuels are unchanged, the arrangement is most definitely adding to increased ground fuels form aerial fine fuels falling to the ground. Increased fuel load will increase potential fire intensity (Mitchell and Preisler 1998, Romme et al. 2006, Jenkins et al. 2008; Klutsh et al. 2009 and Simmard et al. 2011), but how much of this is offset by the increase in ground moisture? In general, discussions of differences in fire outcomes between dead and living stands, focus on fire behavior (surface vs continuous; Flannigan and Wotton 1994; deGroot et al. 2004). My intent is to assess how fire behaviour influences regeneration and the factors involved in successful seedling recruitment.

## 2.2 Objective & Hypotheses

The overall objective of this study is to evaluate the interactive effects of fire on site preparation and regeneration of simulated MPB-killed (herein called "dead") jack pine stands. Effects of three varying types of fire were assessed from measurements of seedbed (duff), seedling density and stocking

### *Hypotheses*

The hypotheses include (1) serotinous pine trees that are not treated with fire will not regenerate because heat is required to open serotinous cones in the canopy; (2) surface fire will yield the least amount of jack pine seedlings because while surface fire is capable of providing for increased access to mineral soil (seedbed) through high duff consumption, this type of fire does not provide enough heat to open serotinous cones in the canopy; (3), continuous fire will be more effective at promoting regeneration of previously dead stands than living stands.

## 2.3 Methods

### 2.3.1 Study Area

The study was conducted in a jack pine (*Pinus banksiana* Lamb.) stands located approximately 165 kilometers northeast of Fort McMurray, Alberta (Fig. 2-2; 58°07’ latitude, 110°15’ longitude), in the Central Mixedwood Natural Subregion of Alberta (Natural Regions Committee 2006). The area is characterized by serotinous jack pine forests with ~8% black spruce (*Picea Mariana* (Mill.) BSP.). Overstory density averaged 1700 stems per hectare.

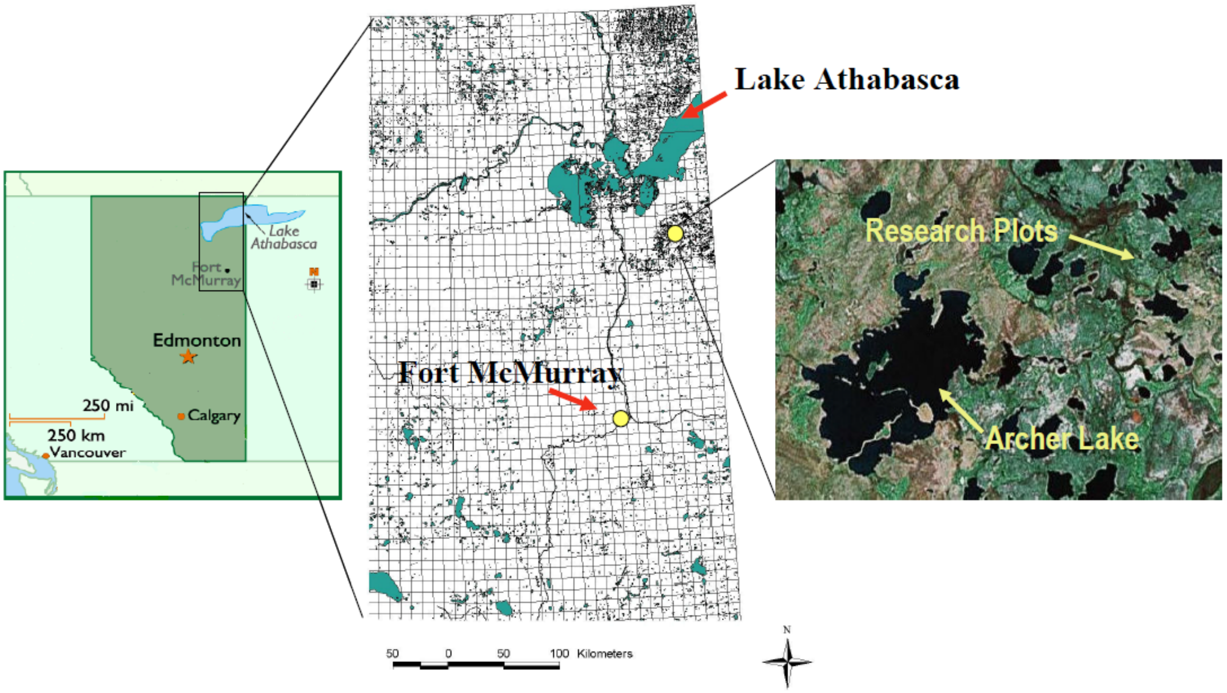

**Figure 2-2:** Map indicating Archer Lake study site location (Schroeder 2012)

The study site has relatively flat topography and featured a homogenous mature jack pine forest representative of the dominant forest cover of the region. Soils were sandy and covered by 8-15 cm of loose organic duff (Schroeder and Mooney 2012). The forest floor consisted of a shallow organic layer with a nearly continuous lichen and feathermoss layer (*Cladonia rangiferina* (L.) Wigg.; *Pleurozium schreberi* (Brid.) Mitt.; 70-80%) with 20-30% coverage of herbs and shrubs, blueberry (*Vaccinium myrtilloides* Michx.) and bearberry (*Arctostaphylos uva-ursi* (L.) Spreng). Fuel load measurements on ignition lines and between live and dead stands were not significantly different ($p<0.05$). In general, study units were uniform in density and fuel load. Please refer to Schroeder (2012) for further details on site characteristics.

### 2.3.2 Emulating Mountain Pine Beetle

In 2007, Alberta Environment and Sustainable Resource Development established an experimental site to study the effects of MPB attacks on crown fire ignition and crown fire rate of spread. The site was first divided into six study units (herein *units*) based on naturally occurring jack pine stands (Fig. 2-3). After the units were identified, they were divided approximately in half; east and west.

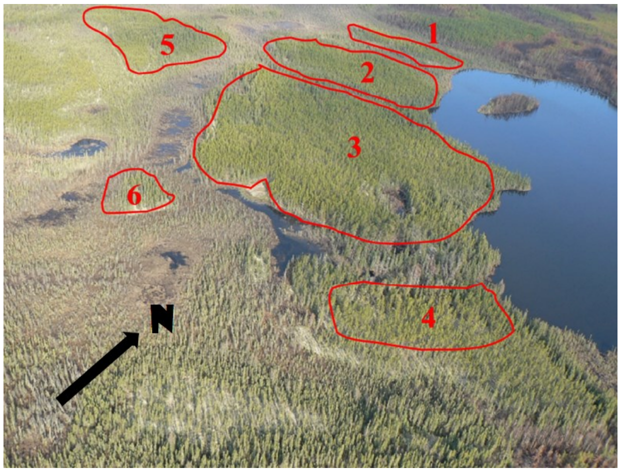

**Figure 2-3.** Study Unit layout by FPInnovations in 2007 at Archer Lake Study area (FPInnovations 2008)

Every tree was girdled at breast height (Fig. 2-4) on the east side of each unit. The bark was removed down to the cambium layer wide enough to prevent the tree from healing.

**Figure 2-4.** Stem of a girdled jack pine tree at Archer Lake study site (FPInnovations 2008).

The intent was to kill a tree in a similar way to that of the MPB and its associated fungus by limiting water and nutrient transport to the crown, but most importantly limiting carbohydrate transport to the roots. The target mortality of the girdling was 90%, similar to that of many MPB disturbances (Fig. 2-5). Trees on the western portion of the units were not girdled.

**Figure 2-5.** Differences in canopy needle retention by 2009 (2 years post treatment) between MPB-killed (right) and living (left) stands (FPInnovations 2009).

Researchers were seeking a mortality condition with red needles retained on the tree. Retained red needles are commonly found 2 years after the presence of MPB and so was the case with the girdling. The burning was done in the summer of 2009.

### 2.3.3 Emulating Wildfire

***Burn Operations and Data Collection***

In 2009, FPInnovations and Alberta Agriculture and Forestry (AAF; formally Alberta Sustainable Resource Development) conducted experimental burns between July 26 -29 in three of the six pre-determined study units; Unit 2 (0.75ha), 3 (4ha) and 4 (2ha). Paired ignition lines in live and dead were deliniated100 m apart and ignited simultaneously from the same direction using drip torches. Ignitions occurred on July 26 (lines 1-4), July 27 (line 5), July 28 (lines 6-7) and July 29 (lines 8-9). A total of 9 paired ignitions were ignited. Each line was 30 m in length (Fig. 2-6).

**Figure 2-6.** Continuous fire in both live (right-west) and dead (left-east) ignited simultaneously to compare fire behavior differences (FPInnovations 2009).

Three different types of fires were ignited (i.e., surface, intermittent and continuous). Table 2-1 identifies the type of fire associated with each of the paired burns by date.

**Table 2-1** Type of fire and date associated with each of the paired burns for jack pine (*Pinus banksiana*) at the Archer Lake Study site.

| Date | Line # (burn) | Tree Condition | Type of fire |
|---|---|---|---|
| July 26, 2009 | 1 | Live | Surface |
| | | Dead | |
| | 2 | Live | Intermittent |
| | | Dead | |
| | 3 | Live | Intermittent |
| | | Dead | |
| | 4 | Live | Surface |
| | | Dead | |
| July 27, 2009 | 5 | Live | Surface |
| | | Dead | |
| July 28, 2009 | 6 | Live | Intermittent |
| | | Dead | |
| | 7 | Live | Intermittent |
| | | Dead | Continuous |

| | | | |
|---|---|---|---|
| July 29, 2009 | 8 | Live | Continuous |
| | | Dead | |
| | 9 | Live | Continuous |
| | | Dead | |

Prior to the burn, instruments were deployed to assess fire behavior and the location of each instrument was recorded in the form of a waypoint. A series of nine instruments were placed in a square sequence in both live and dead stands along the ignition line to collect data on fire weather, fuel moisture as well as fire behavior. In-situ fire behavior data was collected in addition to fire behavior specialist observations. This data, in addition to temperature data loggers were used to evaluate burn condition as well as fire front rate of spread.

### *Fire Weather & Fuel Moisture*

A Remote Automated Weather Station (RAWS) was placed at the site in May 2009 to record hourly weather data; specifically temperature, relative humidity, wind speed, wind direction and precipitation. Average wind speed was 6.3 km/hr, 11.0 km/hr and 8.0 km/hr for surface, intermittent and continuous fires, respectively. The average air temperature during ignition was 22-23 ˚C. Average relative humidity was 37%, 36.5% and 32.3% at time of surface, intermittent and continuous, respectively. The ground surface temperature during the fire was measured using K-type thermocouples (Hobo U12).

Weather data was used to calculate both numeric moisture content of forest floor and fire behavior indices of the Canadian Fire Weather Index System (Van Wagner 1974, 1987; FWI). FWI codes are used by fire managers to help visualize the fire environment. Codes include fine fuel moisture code (FFMC), duff moisture code (DMC), drought code (DC), initial spread index (ISI), build-up index (BUI) and fire weather index (FWI) and were calculated daily for the burn site. Fine fuel moisture (FFMC) is a code calculated as a surrogate for ease of ignition or ability for fire to continue through surface fuels. DMC is an indicator of the moisture content of the loosely compacted organic layer of moderate depth. DC is a measure of moisture deep within the soil profile and an indication of potential for deep burning fires. ISI uses FFMC as well as wind speed to calculate a metric that relates to potential rates of spread (ROS; m/min). BUI is a metric indicating how much fuel is available for combustion and is derived from DMC and DC. FWI takes ISI and BUI to indicate the overall fire potential with respect to spread and severity (depth of burn).

Fuels are another aspect of the fire environment. Fire can behave differently among stands of different species and structure. Expected fire behavior was predicted using the FBP system and fuel types at the site, C3: Mature Jack or Lodgepole Pine. It is important to notethat the site contained lichen, whereas the traditional C3 site contains only feathermoss. The lichen contributes to a more vigorous fire and maybe why observed behavior observed was slightly more intense than anticipated for a C3 fuel type.

FWI values are shown in Table 2-2. Thresholds are used by fire managers to indicate potential for extreme conditions are also shown.

**Table 2-2** Fire weather indices for the four days of burning at the Archer Lake Study site. Red indicates fire weather indices that exceed the trigger for extreme fire behavior.

| Date | FFMC | DMC | DC | ISI | BUI | FWI |
|---|---|---|---|---|---|---|
| June 26, 2009 | 91 | 36 | 317 | 8 | 57 | 20 |
| June 27, 2009 | 91 | 40 | 325 | 7 | 61 | 20 |
| June 28, 2009 | 91 | 43 | 332 | 9 | 65 | 24 |
| June 29, 2009 | 93 | 48 | 340 | 9 | 71 | 25 |
| Trigger for Extreme Fire Behaviour | 90 | 40 | 350 | 10 | 60 | 30 |

The FWI provides a relative rating of moisture levels in different layers of the forest floor and gives relative estimates of potential fire behavior. Actual moisture contents were also measured for each paired ignition line (live and dead).

Forest floor moisture data was collected on the day of the burns along the 30 m ignition line. Single samples were taken every 5 meters along each ignition line over an area of 30 cm x 30 cm to compare fine fuel, duff and crown foliar moisture between live and dead stands. Each sample was divided into 3 categories: 1) fine fuels (litter and 6 classes of dead and down woody debris) and 2) duff (organic layer; mean 2.5 cm deep SD+/-1.7) and 3) crown foliar moisture.

Samples were weighted in the field (wet weight), sealed, transported to the lab and dried in an oven at 100°C for 24 hours and weighed again (dry weight). The following equation was used to calculate gravimetric moisture content of fuel:

Eq. 1 $$\textit{Fuel Moisture Content (\%)} = \frac{\textit{Wet weight (g)} - \textit{Dry weight (g)}}{\textit{Dry weight (g)}} * 100$$

According to moisture sample data from FPInnovations, prior to the burn, dead stands, on average, had higher duff moisture than live stands (Fig. 2-7).

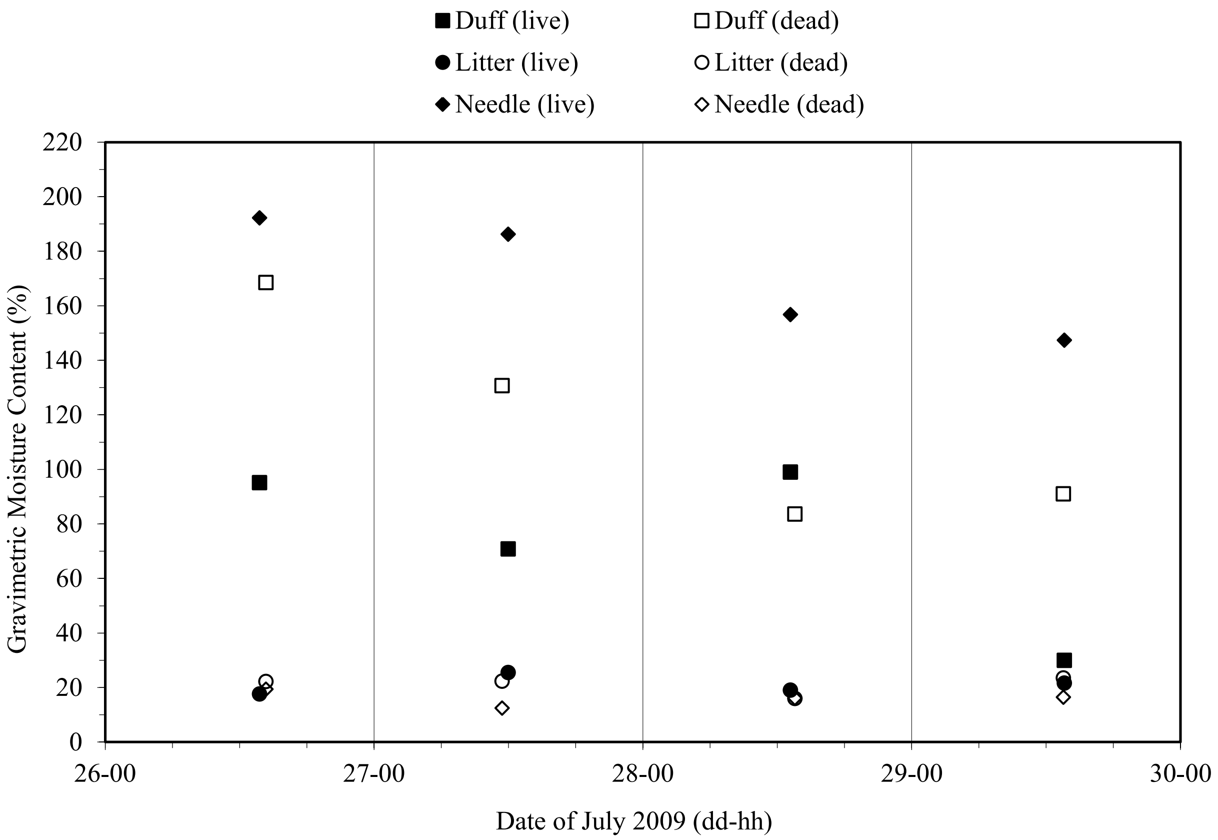

**Figure 2-7.** Moisture content of duff (square), litter (circle) and needles of crown (diamond) from live (solid) and dead (hollow) stands collected prior to fire treatment. Data collection credited to FPInnovations. n=214

FPInnovations noted that the forest floor moisture at the research site was generally higher than the predicted moisture content derived from the standard FFMC model in both live and dead stands. Predictions of fuel moisture using the standard DMC model were generally higher than actual fuel moisture within the living stands. The moisture within the needles of the live crowns was roughly four times higher than that of the dead crowns.

### *Observed Fire Behavior*

Prior to the line ignition, informal test burns using fine fuels (e.g., forest floor needles and small twigs) were conducted in order to understand the differences in potential fire behaviour. During informal testing, the needles from the dead branch appeared to ignite quicker and easier than needles from the live branch (Fig. 2-8).

**Figure 2-8.** Test burn of needles from an un-girdled tree on the left and needles from a girdled tree on the right.

Overall, FPInnovations concluded that there was no difference in fuel load, fuel structure, rate of fire spread and fire behavior among live and dead stands. The main difference was evident in crown moisture (foliar moisture). Dead stands had lower foliar moisture, which likely contributed to the greater crown involvement observed by fire behavior personnel. Refer to Schroeder and Mooney (2012) for more detail on fire behavior comparisons among live and dead stands.

### 2.3.4 Evaluating Regeneration

In August 2012, regeneration surveys were conducted to evaluate the effect of four levels of fire treatment on regeneration: control (no fire), surface, intermittent, and continuous. Three plots were installed at each fire treatment and in both living and dead stands (3 plots x 4 fire treatments x 2 stand conditions = 24 plots) modeled after the pre-fire samples. The waypoint locations for the nine instruments placed on each line during the fire study were used as the locations of the regeneration surveys subplots; consisting of a plot. In each plot, nine 1.78m circular (10 $m^2$) subplots (9 subplots × 3 plots × 4 fire treatments × 2 stand conditions = 216 subplots) were established. Each plot was at least 12 m (~ 1 average tree height) away from the forest edge in order to minimize edge effects and positioned at locations where the fire behavior and weather instrumentation were located during ignition so that future comparisons could be made among the data. While there appears to be limited accuracy with older GPS techniques, linking waypoint locations of regeneration data and fire behavior would provide ability for future researchers to compare fire behavior data and regeneration results. As the locations were not previously selected for the control plots, sets of nine subplots within each of the control plots (representative locations adjacent to treatments with neither girdling or fire treatment) were randomly chosen for regeneration surveys.

At each of the subplots, available seedbed was evaluated by measuring mean residual duff depth (mm) and seedling density by counting the number of seedlings (#/10$m^2$) per plot and stocking – the percentage of subplots with a seedling. More specifically, here is how the three dependent variables were measured:

### ***Seedbed***

Fine fuel and duff consumption data was not available. Post-fire measurements of the depth of duff (mineral soil to upper surface) and fine fuels were recorded in 2009 as a measure of seedbed condition, with the assumption that as the duff layer increases so does the distance between the seed and the mineral soil. Mean duff depth per plot was based upon measurements from three cardinal directions at 0.5 m from the plot center per subplot.

### *Seedling Density*

All seedlings were counted within the subplot and recorded. Seedling density in each treatment unit was determined by averaging the number of seedlings in each subplot (10 $m^2$) and multiplying by 1000 for a per hectare basis to determine a seedling density. The height of a single closest seedling to the duff depth measurement location was also measured (3 heights/subplot) and then averaged per subplot. Though collected, seedling height data was not presented in this chapter. Subplot data was used to determine a mean per plot.

### *Stocking*

Currently, the Alberta Government requires that each stand replacing disturbance on crown land be rectified and planted, where necessary, two years post disturbance and an establishment survey conducted between five to eight years. Regeneration Standards of Alberta (RSA) state that stocking be assessed by either walk-through, aerially by rotor wing or grid based using 10 $m^2$ subplots (1.78 m radii). Our surveys were completed using the grid-based method (Alberta Environment and Sustainable Resource Development 2013).

The measure of stocking used in this study represents the spatial extent to which a site is occupied by trees. The measure of stocking used is similar to that used by the Alberta Government, whereby stocking is the percentage of survey subplots that had at least one acceptable tree. In the present study, a live jack pine seedling was considered an “acceptable tree”. As there were very few one-year old seedlings at time of sampling this was viewed as acceptable.

### 2.3.5 Statistical Design

To evaluate the effect of fire on site preparation and regeneration of dead jack pine stands, the following data was collected: seedbed (duff), seedling density and stocking after three varying types of fire were applied. An analysis of variance (ANOVA) was used as the statistical model to evaluate effects of the treatment (fire) on regeneration.

***Seedbed***

Duff depth was examined as a surrogate for seed preparation for its influence on regeneration ability. Duff depth was analyzed using an ANOVA with duff depth as the dependent variable and tree condition and types of fire as the independent variables. A difference of least square means was conducted for a pairwise comparison of duff depth and types of fire.

***Seedling Density & Stocking***

Seedling density and stocking was analyzed using an ANOVA. In this test, seedling density and stocking are the dependent variables and tree condition and types of fire were the independent variables. An analysis was also conducted to determine whether seedling density and stocking was impacted by seedbed preparation by analyzing duff depth for live and dead stands by types of fire.

## 2.4 Results

### 2.4.1 Seedbed Preparation

#### *Effect of Tree Condition on Duff*

Living and dead plots showed similar trends in duff depth following burning (Fig 2-9); both treatments showed 21-30mm residual duff to be the most frequent among plots.

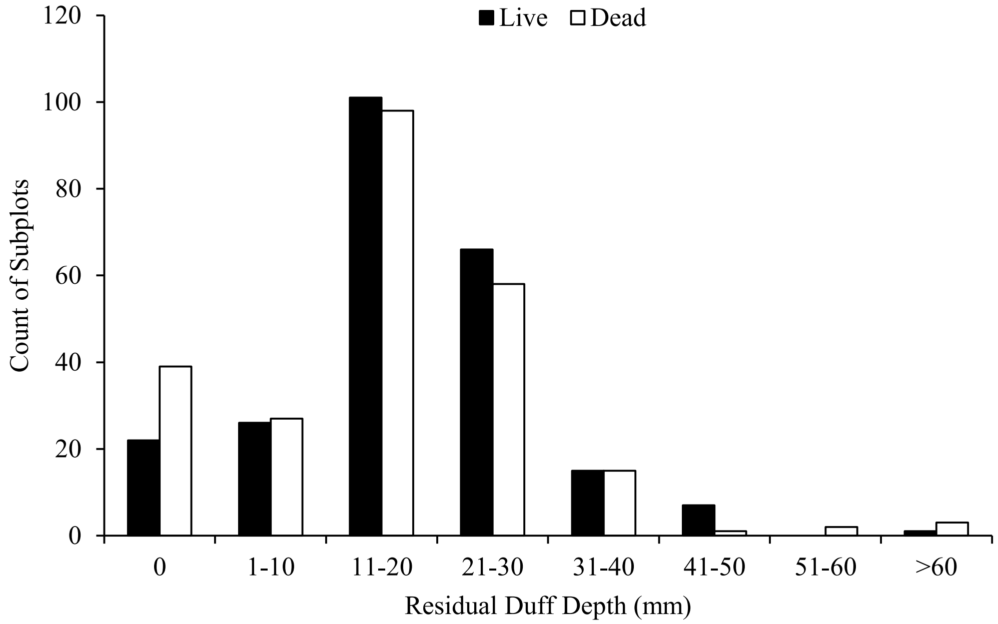

**Figure 2-9.** Frequency residual duff depth in individual subplots (3/sub-plot) for the burned stands at Archer Lake for both live (solid) and dead (hollow) stands. n=481.

#### *Effect of Fire on Duff*

Residual duff depth was deepest in the unburned control plots compared to other types of fires (Fig. 2-10) and similar among living and dead stands. Duff depth after fire treatment was, on average, less than half of that of unburned plots. The remainder of the analyses in the results is conducted without the use of unburned plots.

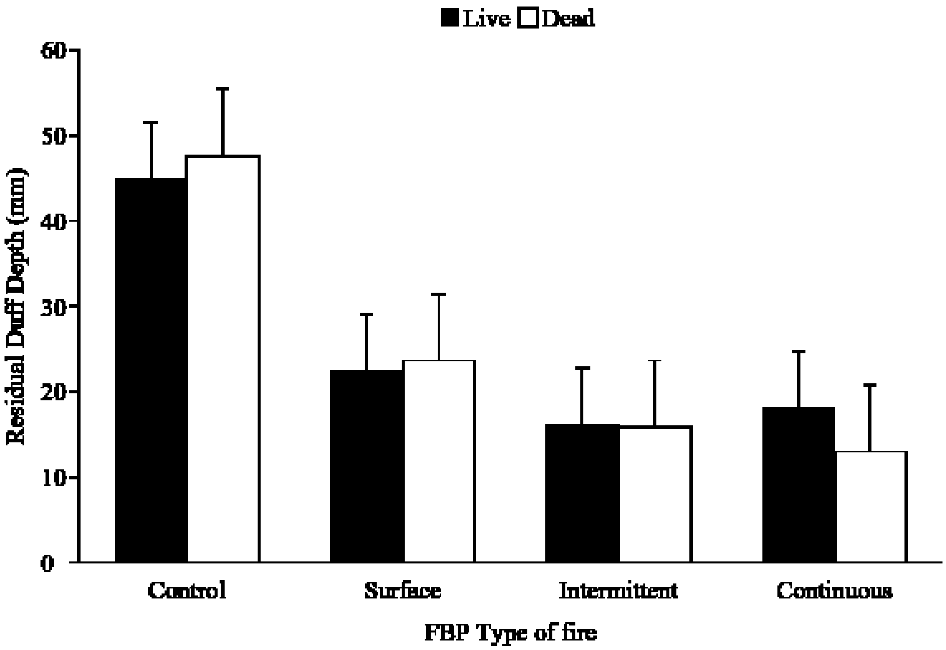

**Figure 2-10.** Mean residual duff depth (error bars indicate S.E.) in relation to FBP types of fire, in stands that were living or dead prior to burning. Sample size for each FBP types of fire and condition: n=215.

Continuous and intermittent fires showed similar residual duff depths. Surface fires had the deepest residual duff. The ANOVA indicated that surface fires resulted in deeper residual duff depth than intermittent and continuous fires. A difference of least square means was conducted for a pairwise comparison. The test indicated that residual duff after surface fire was greater than intermittent (p=0.0321) and continuous (p=0.0754) fires at a threshold of p=0.10. Duff as a function of type of fire was significant at 0.10 (p=0.0695). Duff as a function of tree condition (live/dead) and the interaction of type of fire and tree condition were not. See *Seedling Density* for effect of residual duff on seedling density.

### 2.4.2 Seedling Density and Stocking

***Effect of Fire on Seedling Density and Stocking***

Pine regeneration was absent in the control plots for both live and dead stands. The only near significant ($p<0.05$) effect occurred in the continuous type of fire between live and dead trees ($p=0.0767$; Fig. 2-11). ANOVA of seedling Density as a function of the interaction of type of fire and tree condition was significant at 0.10 ($p=0.0990$).

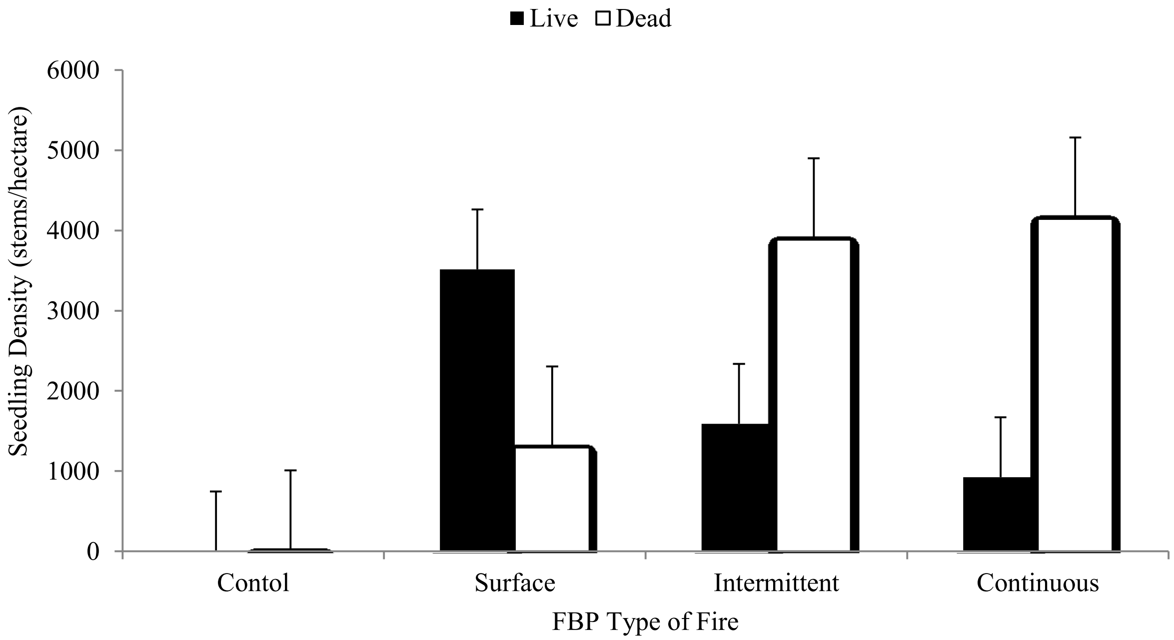

**Figure 2-11**. Mean seedling density (stems/hectare) in relation to type of fire at Archer Lake study site. Errors bar represent the standard error of the mean. n=216

There was variation from location to location as to how a burn responds, however fires that were burned on July 26th had lower regeneration density than those burned on July 27-29th. There was inconsistency in seedling density observations of live vs. dead pairs over the surface and intermediate fires and only the continuous fire were the dead stands had higher seedling recruitment (Fig. 2-12)

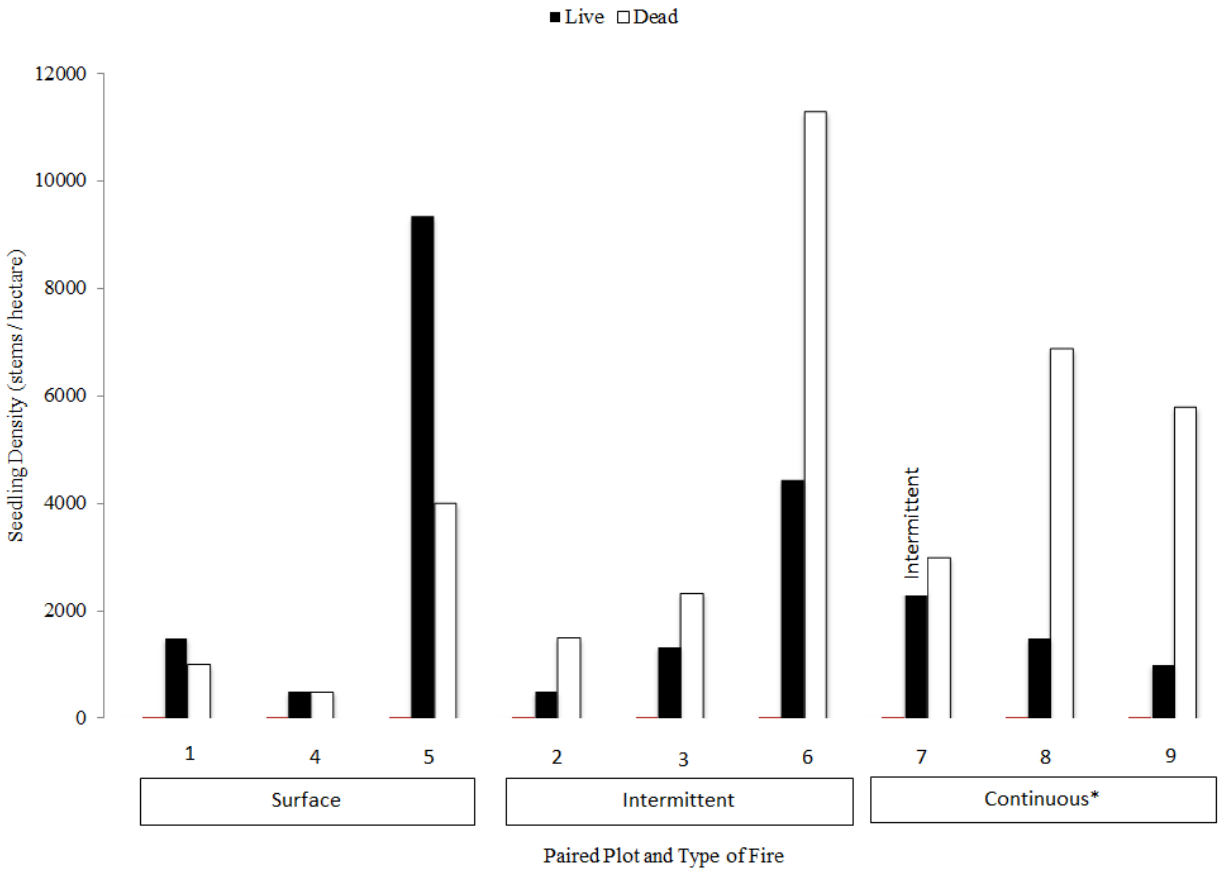

**Figure 2-12** Plot of seedling densities in the 9 paired plots (shown on x axis). Plots 1-4 (July 26), plot 5 (July 27), plot 6-7 (July 28) and plot 8-9 (July 29) organized by type of fire. Exception is *plot 7 which contained both intermittent (live) and continuous (dead) fire. n=216

Similar to seedling density, the only significant ($p<=0.05$) variance occurred in the continuous fire among live and dead stands ($p=0.0355$; Fig. 2-13). ANOVA of stocking as a function of the interaction of type of fire and tree condition was significant at 0.10 ($p=0.0522$).

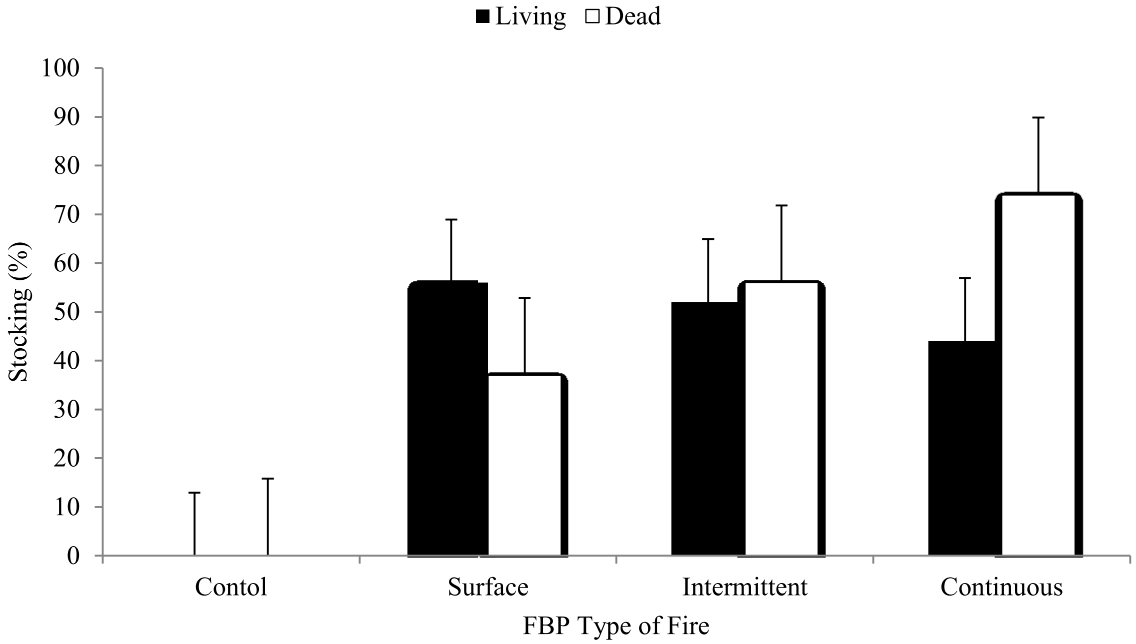

**Figure 2-13.** Comparison of effect of type of fire on stocking (%) for live (solid) and dead (hollow) stands at Archer Lake Study site. n=216.

There was variation from location to location as to how a burn responds, however fires that were burned on July 26th had lower stocking than those burned on July 27-29th. There was inconsistency between live vs. dead pairs over the surface and intermediate type of fire and only in the continuous fire were the dead stands most likely to have higher seedling recruitment (Fig. 2-14)

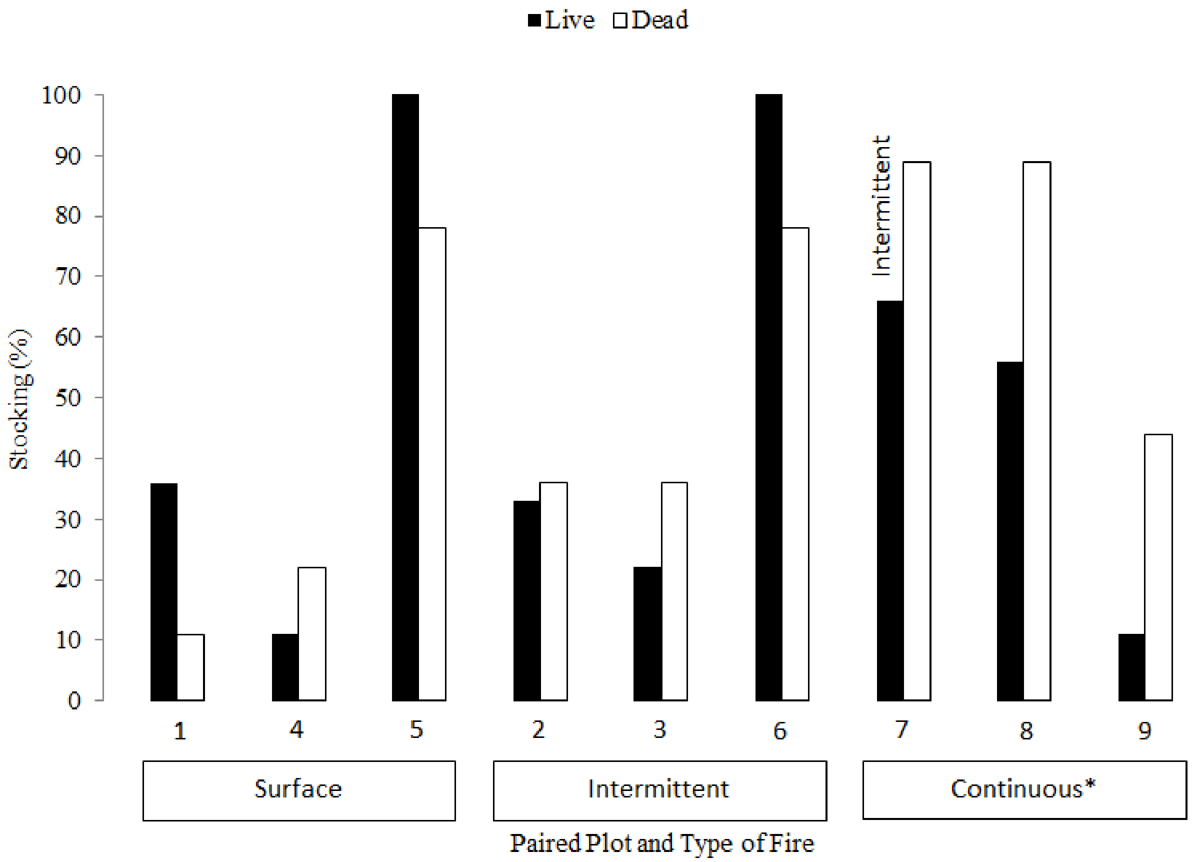

**Figure 2-14.** Plot of stocking in percent within the 9 paired plots (shown on x axis). Plots 1-4 (July 26), plot 5 (July 27), plot 6-7 (July 28) and plot 8-9 (July 29) organized by type of fire. Exception is *plot 7 which contained both intermittent (live) and continuous (dead) fire. n=216.

### *Effect of Duff Depth on Density*

In order to determine the duff depth that was associated with the highest seedling count, a quadratic model was used; resulting in duff depth of 16.6 mm. The data indicates that there might be a weak optimum of density with moderate duff depth, however there is relatively little data at the shallow (<10mm) or deep ends (>25mm) of the data set (Fig. 2-15).

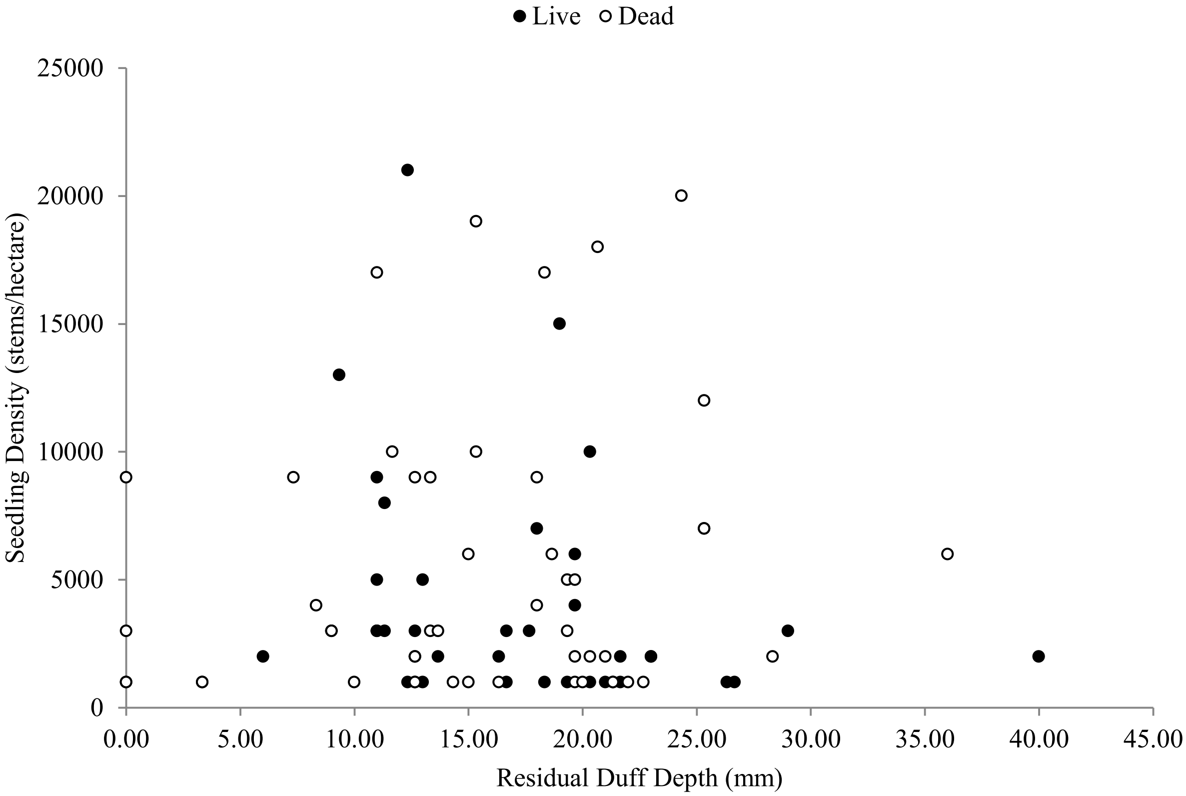

**Fig. 2-15.** Seedling density in relation to duff depth (mm) for both live and dead stands in plots with >=1 seedling present at Archer Lake study site. n=85.

The data was separated into two parts; less than or greater than 16.6 mm residual duff depth in order to reach a greater resolution. While counts tended to increase at ~16 mm and decrease depending on duff depth, the change was not great.

## 2.5 Discussion

This study was unique in that, it is the first to compare regenerative response with or without fire and between both living and dead trees at the same site. Furthermore it has 9 sets of burns with different burning conditions. The results provide forest managers with insight into the potential for regeneration after three types of fire; surface, intermittent and continuous and indicate clearly that without the use of fire, there will be minimal regeneration.

### 2.5.1 Seedbed Preparation

***Absence of Fire on Duff***

In general, my study supported the notion by Cayford (1971), Chrosciewicz (1974) and Charron and Greene (2002) that seedling establishment is greatest on sites with disturbance of the duff above mineral soil. This was indicated in my study by the lack of natural recruitment of seedlings in subplots that were not treated with fire, which indicated recruitment was minimal without a disturbance to the seedbed, coupled with the heating of cones. The findings are consistent with Astrup et al. (2008) who found limited natural regeneration of pine even 10 years after MPB attack in northern BC, which they attributed to the intact feather moss-dominated seedbed. This loosely suggests that seedbed availability is likely a limiting factor for natural regeneration.

***Effect of Tree Condition & Type of fire on Duff***

Without the application of fire to dead stands, duff remained unaffected as it was undisturbed with moss and lichen layers remaining alive. Of the burned stands, moderate residual duff depth was common among subplots. It appears after fire, very few subplots had low or high duff. The distribution was slightly more even within the subplots from the live stands. My study showed similar results to Mohr et al. (2002) who also addressed seedling recruitment by duff depth (in addition to shading) and indicated that among duff treatments, moderate residual duff depth yielded the great density and was also associated with the highest moisture level within the upper mineral soil, particularly in July.

Miyanisi and Johnson (2002) reported that duff consumption in their boreal study area was patchy and ranged from completely burned to scarcely burned in areas throughout the stand. Covington and Sackett (1992) suggest that forest floor depths must be measured at different locations and throughout the stand before and after burning, as duff consumption can vary significantly among points.

Brown and others (1985) found that smoldering combustion was related to the presence of duff moisture and indicated a positive linear relationship among the two variables. Figure 2-7 indicated higher moisture within the duff of dead stands which should indicate a greater chance of smoldering combustion that would result in a deep burn. While not statistically significant, the trend does indicate slightly lower residual duff in dead stands. Interestingly, duff moisture content in dead stands during the first few days of surface burning averaged closer to the burning threshold reported by Van Wagner (1972), that states duff in Eastern Ontario pine forests ceased to burn near 140% moisture content. This threshold may have held for my study area.

With respect to effects of fire on duff, though not statistically significant, surface fire appeared to have retained the most duff with intermittent and continuous fires resulting in relatively similar and less duff than surface (Fig. 2-10). In a study in live stands, presence of large surface fuels increases residence time of fire by drying out underlying duff and increases the likelihood of duff ignition (Harrington 1987). At this study site, little to no large surface fuels were present in either live or dead stands prior to the burn and likely resulted in surface fires that did not penetrate deep into the duff, resulting in minimal duff consumption. This is evident in the results that indicate high residual duff after surface fires in both live and dead stands. I speculate that there was a heavier load of fine fuels in the dead stands, however, given the loss of needles commonly found 2 years after MPB-attack which contributed to potentially higher intensity though would have no impact on rate of spread.

### 2.5.2 Seedling Density

***Type of fire Effect on Seedling Density***

My results suggest that dead stands regenerate best after high intensity continuous fire, and live stands respond best to low intensity surface type fire, however, this relationship was by no means consistent (Fig. 2-11; 2-12; 2-13; 2-14) Within my study, it was shown that dead stands had higher duff moisture content. One can assume this result was related to the likelihood of reduced smoldering combustion and duff consumption rate, therefore requiring a higher intensity continuous fire for site preparation required for seedling establishment. A live stand containing less duff moisture than dead stands would require only a surface fire in order to provide for smoldering combustion contributing to production of nutrients that would promote seedling establishment and growth.

Companies operating on Alberta crown land with superior seedlings on superior seedbeds are seeking a target planting density of 1200-1800 stems/ha (Safranyik and Wilson 2006). Given the relatively high rates of mortality in pines, and the clumped distribution of seedlings, 4000 stems/ha will likely be needed to meet target stocking at maturity. While results were highly variable, it may be fair to suggest density was highest after continuous fire within dead stands, though at least 1 line for each type of fire was represented within the data as meeting 4000 stems/ha target making it hard to discern a prescription that would consistently reach the 4000 seedling threshold.

The results were unexpected because I anticipated a clear relationship among type of fire, tree condition and regeneration, not just within the continuous fire data. I suspect moisture content of the cone may be different among living and dead trees and this would be a factor that would impact regeneration mostly after continuous fire where direct flame contact is made with cones. Moreover, due to the direct contact of the flame with the cone during continuous fire, I suspect it may have influenced the seed viability and or cone opening, generating a difference in regeneration between dead and living after continuous fire.

The RSA requires that companies ensure each block accomplish 80% stocking by eight years post- disturbance. If the required stocking is not accomplished, silvicultural intervention is required and by age 14, to avoid penalty, the stand must be fully stocked as liability is given back to the crown. Using the Province's standards, surveys conducted within both living and dead control subplots (no fire) would not have accomplished the stocking requirements of the Province. In dead stands, surveys within the intermittent and continuous fire treatments would have passed and been re-assed between 10-14 years post-disturbance. In living stands, surveys within the surface fire would have passed and in intermittent and continuous have failed.

The influence of fire on density and stocking is highly variable from location to location as fire response is variable. It is not likely to make strong statements about statistical significance in these data; however data were explored fully. Significant differences were not found. This is not surprising given the variable nature of fire on limiting factors such as seedbed and cone opening. As stated earlier, Covington and Sackett (1992) suggest that duff consumption can vary significantly throughout a stand during a fire. This may also explain some of the variability of results between locations.

### ***Site Preparation Effect on Seedling Density and Stocking***

My study clearly showed that killed jack pine stands (e.g., MPB-attack) are unable to recruit seedlings without the introduction of seedbed disturbance though the cause of differences among success rates between dead and living stands is hard to distinguish because fire is contributes to both seedbed disturbance and cone opening. A layer of forest floor species including lichens and blueberries dominated the plots and potentially contributed to the observed low levels of recruitment. My results concurred with others studies (MacIntosh 2013, Radeloff et al. 2004) which showed low natural regeneration without silvicultural treatment. A study by Nigh et al. (2008) indicated seedling recruitment of lodgepole pine in the absence of fire; however these stands contained an abundance of advanced regeneration that were present before the MPB attack. Sites used in the Nigh et al. (2008) study demonstrated potential to produce reasonably well stocked stands after MPB or at least provide a significant contribution to future stand stocking in regions with shallow duff and partial non-serotinous cones including southern BC and United States (Collins et al. 2011; Kayes and Tinker 2012). A study by Pina (2012) focused on the mineral soil not duff moisture, he saw live stands (control) yielded the least moisture over stands with 50% kill (10% greater moisture than control) and 100% kill (13% greater than control). Perhaps the potential differences in mineral soil moisture influenced results my results. That said, seedling recruitment is determined on a microsite level regardless and will recruit on a suitable seedbed regardless of site moisture mean.

Post burn regeneration in conifer-dominated forests is determined to a large degree to which duff is removed by fire and suitable seedbed is made available (Chrosciewicz 1974, 1976; Zasada et. al. 1983; Thomas and Wein 1985; Weber et. al 1987). A study by Mohr et al. (2002) indicates that successful regeneration of serotinous pine can be achieved through low intensity surface fire; though the study was focused on table mountain pine (*Pinus pungens*) on slope. If this is the case, fire managers would be successful in burning under less risky conditions, reduce risk of erosion and increases the burning window that is often so difficult to achieve.

## 2.6 Conclusion

The results my study in Northeastern Alberta indicated limited natural recruitment of jack pine in both living and dead stands where fire was not applied, which suggested silvicultural intervention is required where regeneration is the goal. Mature MPB-attacked stands have many factors working against them including limited advance regeneration, unsuitable seedbeds and limited access to seed supply in the absence of fire. In addition, Teste et al. (2011) show declining seed rain after nine years post MPB-attack suggesting that even where seedbeds are created through intervention, potential seed supply may decline over time since attack. In this study, the difference in duff remaining in both living and dead subplots was similar, particularly after intermittent and continuous fire and indicates that between the two limiting factors of serotinous pine regeneration (seedbed preparation & cone opening); the differences are likely accounted for by cone opening.

Overall, it is difficult to provide a clear recommendation on which type of fire would yield the greatest regeneration potential due to the variable nature of fire. It was clear in the data, however, that a continuous fire contributes to differences among regeneration between dead and living stands. Cone moisture may have contributed to varied results within the continuous fire among dead and living stands. As such, I went on to study this factor and the results are shown in *Chapter 3*.

## 2.7 Literature Cited

**Ahlgren, I.F., and C.E. Ahlgren. 1960.** Ecological effects of forest fires. Bot. Rev. 26: 483–533.

**Alberta Environment and Sustainable Resource Development. 2013.** Reforestation Standard of Alberta. Government of Alberta, Department of Environment and Sustainable Resource Development, Edmonton, Alberta. 231 p.

**Astrup, R., Coates, K.D., and E. Hall. 2008.** Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. Forest Ecology and Management. 256: 1743 – 1750.

**Brown, J.K., Marsden, M.A., Ryan, K.C., and E.D. Reinhardt. 1985.** Predicting duff and woody fuel consumption in the northern Rocky Mountains. Res. Pap. INT-337. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 23 p.

**Beaufait, W.R. 1960.** Some effects of high temperatures on the cones of seeds of Jack Pine. Forest Science. 6(3): 194-8.

**Burns, R.M., and B.H. Honkala. 1990.** Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. 2: 877.

**Cameron, H. 1953.** Melting point of the bonding material in lodgepole pine and jack pine cones. Can. Dep. Resour. Dev., For. Branch, Div. For. Res., Silvic. Leafl. No. 86.

**Cayford, J.H. 1971.** The role of fire in the ecology and silviculture of jack pine. *In* Proceedings of the Tall Timbers Fire Ecology Conference, Number 10, 20–21 August 1970, Fredericton, New Brunswick. Tall Timbers Research Station, Tallahassee, Fla. pp. 221–244.

**Charron, I., and D.F. Greene. 2002.** Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Can. J. For. Res. 32: 1607–1615.

**Choromanska, U., and T.H. DeLuca. 2002.** Microbial activity and nitrogen mineralization in forest mineral soils following heating: evaluation of post fire effects. Soil Biology and Biochemistry. 34: 263-271.

**Chrosciewicz, Z. 1974.** Evaluation of fire-produced seedbeds for jack pine regeneration in central Ontario. Can. J. For. Res. 4**:** 455–457.

**Chrosciewicz, Z. 1976.** Burning for black spruce regeneration on a lowland cutover site in southeastern Manitoba. Canadian Journal of Forest Research. 6(2): 179-186.

**Clements, F.E. 1910.** The life history of lodgepole pine forests. U.S. Dept. Agric., Forest Serv. Bull. 79. 56. pp.

**Coates, K.D. 2002.** Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. For. Ecol. Manag. 155:387–398.

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

**Covington, W.W., and S.S. Sackett. 1992.** Soil mineral nitrogen changes following prescribed burning in ponderosa pine. Forest Ecology and Management. 54: 175–191.

**Critchfield, W.B. 1957.** Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation: Harvard University Publication no.3.

**Crossley, D.I. 1956.** Effect of crown cover and slash density on the release of seed from slash-borne lodgepole pine cones. Can. Dept. North. Aff. and Natural Resources, Forest Res. Div. Tech. Note 41. 51 pp.

**Dhar, A., and C.D.B. Hawkins. 2011.** Regeneration and growth following mountain pine beetle attack: a synthesis of knowledge. BC J. Ecosyst. Manage. 12**:** 1–16.

**DeBano, L.F., Neary, D.G., and P.F. Folliott. 1998.** Fire's effects on ecosystems. John Wiley & Sons, Inc., New York. Chapter 3. pp. 56.

**de Groot, W.J., Bothwell, P.M., Taylor, S.W., Wotton, B. M., Stocks, B.J., and M.E. Alexander. 2004.** Jack pine regeneration and crown fires. Canadian Journal of Forest Research. 34: 1634-1641.

**Despain, D.G., D.L. Clark, and J.J. Reardon. 1996.** Simulation of crown fire effects on canopy seed bank in lodgepole pine. International Journal of Wildland Fire. 6(1): 45-49.

**Eyre, F. H. 1938.** Can jack pine be regenerated without fire? Journal of Forestry, 36:1067-1072.

**Flannigan, M. D., and B. M. Wotton. 1994.** Fire regime and the abundance of jack pine. In Proceedings of the 2nd International Conference on Forest Fire Research. University of Coimbra, Coimbra, Portugal.

**Harrington M.G. 1987**. Predicting reduction of natural fuels by prescribed burning under ponderosa pine in southwestern Arizona. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Note RM-472. (Fort Collins, CO)

**Hellum, A.K., and N.A. Barker. 1981.** The relationship of lodgepole pine cone age and seed extractability. Forest Sci. 27(1): 62-70.

**Herr, D.G., and L.C. Duchesne. 1995.** Jack pine (*Pinus banksiana*) seedling emergence is affected by organic horizon removal, ashes, soil, water and shade. Water, Air and Soil Pollution. 82: 147-154.

**Jenkins, M.J., Hebertson, E., Page, W., and C.A. Jorgensen. 2008**. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For. Ecol. Manage. 254: 16–34.

**Jolly, W.M., Parsons, R.A., Hadlow, A.M., Cohn, G.M., McAllister, S.S., Popp, J.B., Hubbard, R.M., and J.F. Negron. 2012.** Relationships between moisture, chemistry, and ignition of Pinus contorta needles during the early stages of mountain pine beetle attack. Forest Ecology and Management. 269: 52-59.

**Kayes, L.J., and D.B. Tinker. 2012**. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. Forest ecology and management. 263: 57-66.

**Kemball, K.J. Wang, G.G., and A.R. Westwood. 2006.** Are mineral soils exposed by severe wildfire better seedbeds for conifer regeneration? Can. Jour. of For. Res. 36(8): 1943-1950, 10.1139/x06-073.

**Kemball, K.J., Westwood, R.A., and G.G. Wang. 2010.** Laboratory assessment of the effect of forest floor ash on conifer regeneration. Canadian Journal of Forest Research. 40: 822-826. doi: 10.1139/X10-027

**Klutsch, J.G., Negrón, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., and R. Caissie. 2009.** Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. Forest Ecology and Management 258: 641-649.

**Koch, P. 1996.** Lodgepole Pine in North America. Forest Products Society, Madison, WI. 763 p.

**Lotan, J. E. 1964**. Regeneration of lodgepole pine: a study of slash disposal and cone opening. U.S. Dep. Agric. For. Servo Res. Note INT-16. p. 4.

**MacIntosh, A.C.S., and S.E. Macdonald. 2013**. Potential for lodgepole pine regeneration after mountain pine beetle attack in newly invaded Alberta stands. Forest ecology and management. 295: 11-19.

**Mitchell, R.G., and H.K. Preisler. 1998**. Fall rate of lodgepole pine killed by the mountain pine beetle in Central Oregon. Western Journal of Applied Forestry. 13(1): 23-26.

**Miyanishi, K., and E.A. Johnson. 2002**. Process and patterns of duff consumption in the mixedwood boreal forest. Canadian Journal of Forest Research. 32:1285-1295.

**Mohr H.H., Waldrop, T.A., and V.B. Shelburne. 2002.** Optimal seedbed requirements for the regeneration of Table Mountain pine. In 'Proceedings eleventh biennial southern silvicultural research conference', 20–22 March 2001, Knoxville, TN. (Ed. K. Outcalt) USDA Forest Service, Southern Research Station, General Technical Report SRS-48, pp. 306–309. (Asheville, NC)

**Natural Regions Committee 2006.** Natural Regions and Subregions of Alberta. Compiled by D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. T/852.

**Nigh, G.D., Antos, J.A., and R. Parish. 2008**. Density and distribution of advance regeneration in mountain pine beetle killed lodgepole pine stands of the Montane Spruce zone of southern British Columbia. Can. J. For. Res. 38(11): 2826-2836.

**Place, I.C.M. 1955.** The influence of seed-bed conditions on the regeneration of spruce and balsam fir. Canada Department of Northern Affairs and Natural Resources, Forestry Branch, Forest Research Division, Rep. Bull. 117.

**Pina, P. 2012.** The impacts of simulated Mountain Pine Beetle attack on the water balance in lodgepole pine forest of the western Alberta foothills. PhD Dissertation, Dept. of Renewable Resources, University of Alberta, Edmonton.

**Radeloff, V.C., Mladenoff, D.J., Guries, R.P., and M.S. Boyce. 2004**. Spatial patterns of cone serotiny in Pinus banksiana in relation to fire disturbance. Forest Ecology and Management. 189: 133-141.

**Romme, W.H., Clement, J., Hicke, J., Kulakowski, D., MacDonald, L.H., Shoennagel, T.L., Veblen, T.T. 2006**. Recent Forest Insect Outbreaks and Fire Risk in Colorado Forests: A Brief Synthesis of Relevant Research. Colorado State University, Fort Collins, CO. 24 p.

**Rudolph, T.D., and P.R. Laidly. 1990.** *Pinus banksiana* Lamb. - jack pine. In: R.M. Burns, BH Honkala (eds.) Silvics of North America, vol. 1: Conifers. Agriculture Handbook 654. USDA Forest Service, Washington DC, USA. 280-293 pp.

**Safranyik, L. 1978.** Effects of climate and weather on mountain pine beetle populations. Pages 79-86 in A. Berryman; G. Amman, R. Stark, and D. Kibbee, eds. Symposium proceedings: The theory and practice of mountain pine beetle management in lodgepole pine forests. April 1978, Pullman, WA. University of Idaho – Forest, Wildlife and Range Experiment Station.

**Safranyik L., Carroll A.L., Regniere J., Langor D.W., Reil W.G., Shore T.L. 2010.** Potential for range expansion of mountain pine beetle into the boreal forest of North America. Can Entomol. 142: 415–441.

**Safranyik, L., and B. Wilson. 2006.** The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, Victoria, Canada.

**Schroeder, D., and C. Mooney. 2012.** Fire behaviour in simulated mountain pine beetle-killed stands. Final Report. FP Innovations. Wildfire Operations Research. 17 pp.

**Simard, M.-J., Bergeron, Y., and L. Siros. 2003.** Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. Can. J. For. Res. 33: 672-681.

**Simard, M., Romme, W.H., Griffin, J.M., and M. G. Turner. 2011.** Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs. 81(1): 3-24.

**Smith J.K., and N.E. McMurray. 2002.** FireWorks curriculum featuring ponderosa, lodgepole, and whitebark pine forests. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-65. Fort Collins, CO.

**Teste, F. P., Lieffers V.J., and S.M. Lanhäusser. 2011b**.Viability of forest floor and canopy seed banks in *Pinus contorta* var. latifolia (Pinaceae) forests after a mountain pine beetle outbreak. American Journal of Botany. 98(4): 1-8.

**Thomas, P.A., and R.W. Wein. 1985.** The influence of shelter and the hypothetical effect of fire severity on the postfire establishment of conifers from seed. Can. J. For. Res. 15: 148–155.

**Van Wagner, C. E. 1972.** Duff consumption by fire in eastern pine stands. Can. J. For. Res. 2: 34-39.

**Van Wagner, C. E. 1987**. Development and structure of the Canadian Forest Fire Weather Index System. Canadian Forest Service, Ottawa, ON, Forest Technical Report 35. 37 pp.

**Vyse, A., Ferguson, C., Huggard, D., Roach, J., and B. Zimonick. 2009.** Regeneration beneath lodgepole pine dominated stands at- tacked or threatened by the mountain pine beetle in the south central interior, British Columbia. *For. Ecol. Manage.* 258(Suppl.): S36 –S43.

**Weber, M. G., Hummel, M., and C.E. Van Wagner. 1987.** Selected parameters of fire behavior and *Pinus banksiana* Lamb. regeneration in eastern Ontario. For Chron. 63(5): 340-346.

**Zasada J.C., Norum R.A., van Veldhuizen R.M., and C. Teutsch. 1983.** Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Canadian Journal of Forest Research. 13: 903–913.

# Chapter 3 – The Effects of Mountain Pine Beetle Killed Lodgepole Pine on Moisture Content and Opening of Serotinous Cones

## 3.1 Introduction

The lodgepole pine (*Pinus contorta* Douglas) is a dominant pine species in Canada, composing 20% of Canada's total coniferous growing stock (4 billion $m^3$; https://www.albertacanada.com/files/albertacanada/AIS-BP_LodgepolePine.pdf). Its dominance is mainly owing to its adaptation strategy (e.g., high seed and serotinous cone production) to wildland fire, which is a common disturbance type in Canadian boreal forests (Lotan 1976, Teste et al. 2011a). The scales of the serotinous cone are sealed by resinous bonds which open after exposure to heat from fire or direct sunlight through an open canopy. This often results in high seedling density after a fire event (Tower 1909, Clements 1910, Crossley 1956). Furthermore, serotinous cones significantly improve the longevity of seed viability up to 15 years (Teste et al. 2011b). These large quantities of accumulated seeds increase the regeneration probability after stand-replacing disturbances.

Managed pine forests in Canada are currently composed of older age classes than historically recorded due, in part, to intensive forest protection activities. It is believed that the older age class is a large contributor to the recent record-breaking mountain pine beetle (*Dendroctonus ponderosae*; MPB) outbreak in Canada - the largest in Western North America (Safranyik and Wilson 2006, Raffa et al. 2008, Meddens et al. 2012). Most notably, the beetle is affecting about half of the merchantable lodgepole pine forests of British Columbia and Alberta (Natural Resources Canada 2013) and threatens to expand east into Saskatchewan (Cullingham et al. 2011). This unprecedented MPB outbreak has raised several concerns for forest managers (e.g., Bigler et al. 2005, Negron et al. 2008, Raffa et al. 2008, Simard et al. 2011) namely whether these MPB killed forests will have successful natural regeneration with or without fire.

Cone moisture content is an important factor in determining timing of cone opening (Harlow et al. 1964, Hellum et al. 1980, Johnson and Gutsell 1993) and may potentially affect seed viability (Beaufait 1960). It has not been tested whether, and to what extent, moisture content of cones change once a tree dies or . It is also not known how these stands and their seed availability and survival will be affected by fire. It appears to us that understanding the cone moisture after the presence of MPB is the first step to understanding post-fire regeneration of this serotinous pine stand, because it will begin to help in determining the energy required to open or damage seeds inside of serotinous cones.

## 3.2 Objective & Hypotheses

The objectives of this study were to evaluate the interactive effects of MPB-killed trees (dead) and cone age on the (1) cone moisture content, (2) moisture exchange, and (3) time required to open a cone after exposure to heat.

### ***Hypotheses***

I hypothesized that (1) cones from living trees would have higher moisture content than those from dead, because living trees were likely more vigorous than killed trees with better ability to uptake water*;* (2) moisture content of young cones would be constant and that of older cones vary, due to deterioration of the resin seal; and (3) it would take longer to open cones from living trees because they have higher moisture content.

We believe that results of this study provides further information to our knowledge of cone characteristics on both live and dead lodgepole pine and may lead to further study of the impact of fire on lodgepole pine regeneration after MPB attack.

## 3.3 Methods

### 3.3.1 Study Area & Sample Collection

The study area was located in a pure closed-cone serotinous lodgepole pine forest in the Lower Foothills natural sub-region of Alberta (Natural Regions Committee 2006), approximately 70 kilometers south of Grande Prairie, Alberta (124°54'27" W, 53°36'34" N). The study area was composed of lodgepole pine aged 100-120 years with 60% of the trees killed by mountain pine beetle and the remaining 40% unaffected and living at time of cone collection. The topography was rolling and forest floor consisted of a thick organic layer with nearly 100% coverage of feather moss (*Hylocomium splendens* Hedw. and *Pleurozium schreberi* (Brid.) Mitt.), herbs, or shrubs.

In the study area, we located a site satisfying three criteria; (1) 90% of stems were mature lodgepole pine trees), (2) presence of both living and dead lodgepole trees within a stand, and (3) relatively homogeneous stand age and composition. We chose three sample stands within the site, which were more than 1km and less than 5km away from each other and located in similar topographic condition. At each sample stand, three living lodgepole pine trees (4 trees for one stand due to small cone production) and three MPB-killed lodgepole pine trees of similar size were randomly selected and felled (total 19 trees). The height and diameter of each tree was recorded and a cross section was taken from each tree at breast height (1.3m). The means (standard deviation) of dead and living tree heights were 25.2 (±2.86) m and 23.3 (±2.64) m, respectively, with diameter at breast height 31.2 (±6.03) cm and 25.2 (±2.05) cm, respectively.

All cones on the felled trees were collected and sampled by age cohort. Where cone ages were unable to be identified from the fallen branches, they were not sampled. Aging was completed by first starting at the branch tip and collecting all cones between bud scars (or twig whorls). All cones between a bud scar and a subsequent bud scar were considered to be from the same age cohort. For each tree, cones in the same age cohort were bagged together and each bag marked individually. Cones were transported back to the lab immediately and frozen. For the dead trees, years of cone production (actual age of the cones) were identified in the lab by determining the year of death through a dendrochronological method (Speer 2012). A cross-section was sampled from each dead felled tree at breast height and annual ring growth was measured using a microscope and stage micrometer (Velmex system). We developed a master ring chronology using ring growth measurement from live trees and the annual ring growths of dead trees were cross-dated against the master chronology using the skeleton plot method. The validity of ring data was later confirmed using the COFECHA program (Holmes 1983).

### 3.3.2 Experiment Design

***Effect of tree mortality and cone age on cone moisture content***

We randomly selected 128 cones (78 from living trees and 83 from dead trees) with lengths of 4.0 (±0.2) cm to evaluate if cone moisture content (MC; % wet *weight (w/w)*) was affected by age and mortality condition. Cones aged 4 (live n=21; dead n=22), 6 (live n=20; dead n=22) and 8 (live n=21; dead n=22) years old were evaluated. We restricted the cone size to minimize the potential error caused by different surface areas. Wet weight of each cone (MW) was measured and cones were weighed again after drying them at $105^{\circ}$C for 72 hours to determine the dry weight of the cone (MD). Cone MC was calculated by the weight of water over dry mass (Eq. 1):

Eq. 1
$$\textit{Fuel Moisture Content (\%)} = \frac{\textit{Wet weight (g)} - \textit{Dry weight (g)}}{\textit{Dry weight (g)}} * 100$$

Cone MC were not normally distributed, so the interactive effects of cone age and tree condition (living and dead) on MC were tested using the Kruskal Wallis test. Afterward, the effect of condition on MC was tested for each age class using the Wilcoxon rank sum test.

### *Effect of tree mortality and cone age on cone moisture exchange*

I also examined if cones exchange moisture and whether the moisture exchange pattern differed by tree condition or cone age. Firstly, I randomly selected six cones, 4.0 (±0.2) cm in size, from each age class and tree condition (live and dead). . These cones were taken from the freezer and rested on a table for 24 hours to equilibrate the cone temperature with surrounding temperature. During this procedure, condensation on the surface was removed using a cloth. Each cone was weighed ('*Ambient*'). These cones were then placed in a closed chamber with indicating drierite desiccant for 72 hours preventing direct contact of the desiccant with the cones. Each cone was weighed again immediately after 72 hours incubation ('*Desiccant*'). As a next step, these cones were placed in a closed chamber for 72 hours with a cup of water (preventing direct contact) and weighed afterward ('*Humid*'). Thereafter, cones were dried at $105^0$C for 72 hours to determine dry weight. MC at each step was calculated using Eq. 1. I tested if cones significantly absorbed or released moisture using one way repeated ANOVA followed by the Holm-Sidak pairwise multiple comparison test. Finally, the cone MC was compared between live and dead trees for each age and step using the Wilcoxon rank sum test.

### *Effect of cone moisture content and cone age on time to open*

I randomly selected 30 cones from living trees (10 each for 4, 6 and 8 years old) and 30 cones from dead trees (10 each for 4, 6 and 8 years old) to examine the relationship between cone MC and time taken to open cones. Each cone was weighed and placed individually in a convection oven at $180^0$C (Hellum and Barker 1981) and the time taken to open the cone was recorded. We recorded four measurements for each cone: (1) the time when the first audible popping sound was heard (*First*); (2) the time when popping became indistinguishable from each other (*Start*); (3) the time when the popping were distinguishable again (*Last*); and (4) the time of the final pop (*Finish*). Popping sound of 5 cones was not distinctive and their data was omitted from analysis: 4 from living and 1 from the dead group. The cone was weighed before the experiment and all materials (i.e., seeds, scales, and cone) were collected after the experiment and dried at $105^0$C for 72 hours to determine dry weight for MC calculation. A Pearson correlation analysis was conducted to determine the relationship between four time measurements and cone MC. We also examined if mortality condition (dead and living) influenced time taken to open cones for each cone age class (i.e., 4, 6, and 8 years old) using the t-test. All statistical analyses were conducted using SAS (version 9.2) and all statistical differences were determined at $p<0.05$, unless stated otherwise.

## 3.4 Results

### 3.3.1 Effect of tree mortality and cone age on cone moisture content

Cone MC of dead trees had right skewed distribution and that of living trees showed normal distribution. Consequently, the median value of dead group was always lower than that of living group regardless of age class, while mean MC was always higher in cones from dead trees than those from living trees (Fig. 3-1).

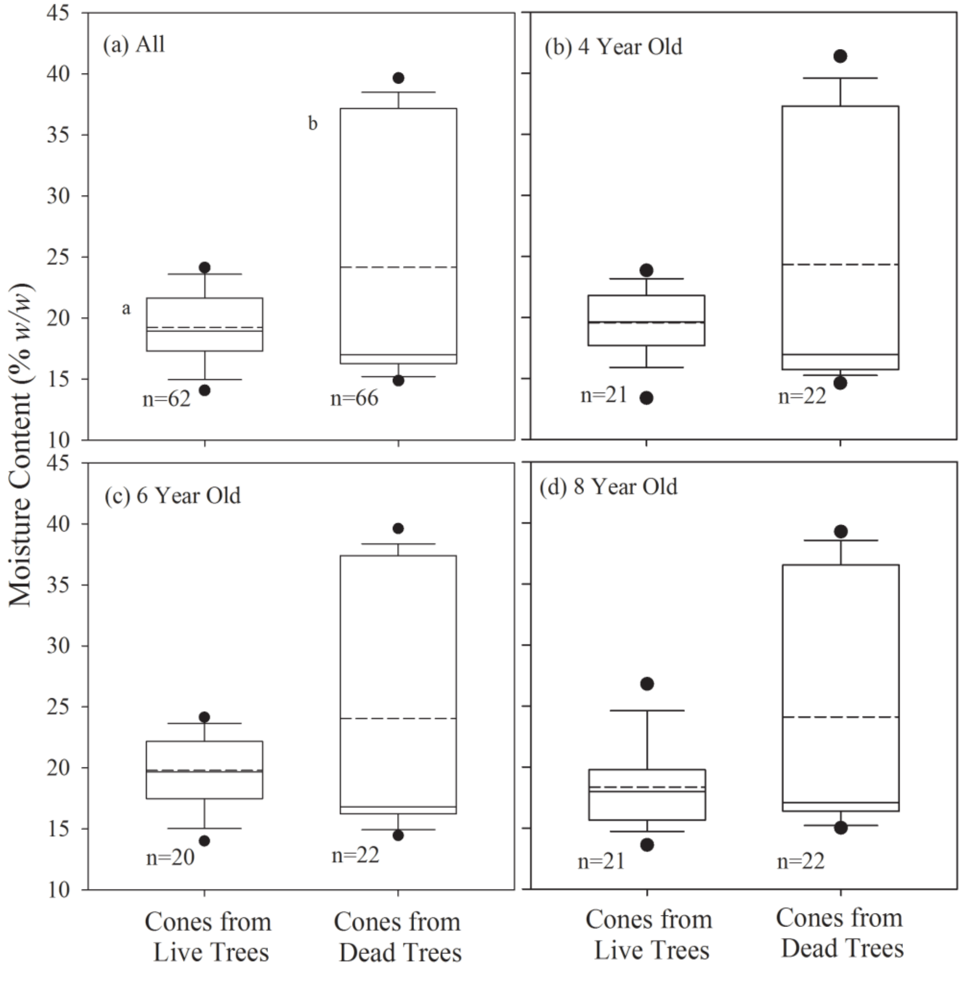

**Figure 3-1**. Moisture content (MC; % w/w) of lodgepole pine closed serotinous cones from living trees and dead trees by: a) all ages pooled, b) 4 year old cones, c) 6 year old cones, and d) 8 year old cones. Dashed bar indicates the mean value, while solid bars represents 10, 25, 50 (median), 75, and 90%. Dots indicate 5 and 95% percentile. Alphabet letters indicate significant (*p*<0.05) statistical difference between live and dead group after Wilcoxon rank sum test.

We found that the pooled cone MC of living group (mean=19.24%; median = 18.93%) was significantly lower than that of dead group (mean=24.17%; median = 17.01%) (Fig. 3-1a). However, the mortality condition did not show any significant influence on cone MC for individual age classes (i.e., 4, 6, and 8 years old; Fig 3-1b-d). We observed that cones from dead trees had higher variation in MC than those from living trees and the mean MC slightly decreased in age 8 compared to other ages.

### 3.3.2 Effect of tree mortality and cone age on cone moisture exchange

In the moisture exchange study, cones regardless of age class lost approximately 3% of moisture during the *Desiccant* process and slightly less amount of moisture was absorbed into the cones during the *Humid* process (Fig. 3-2).

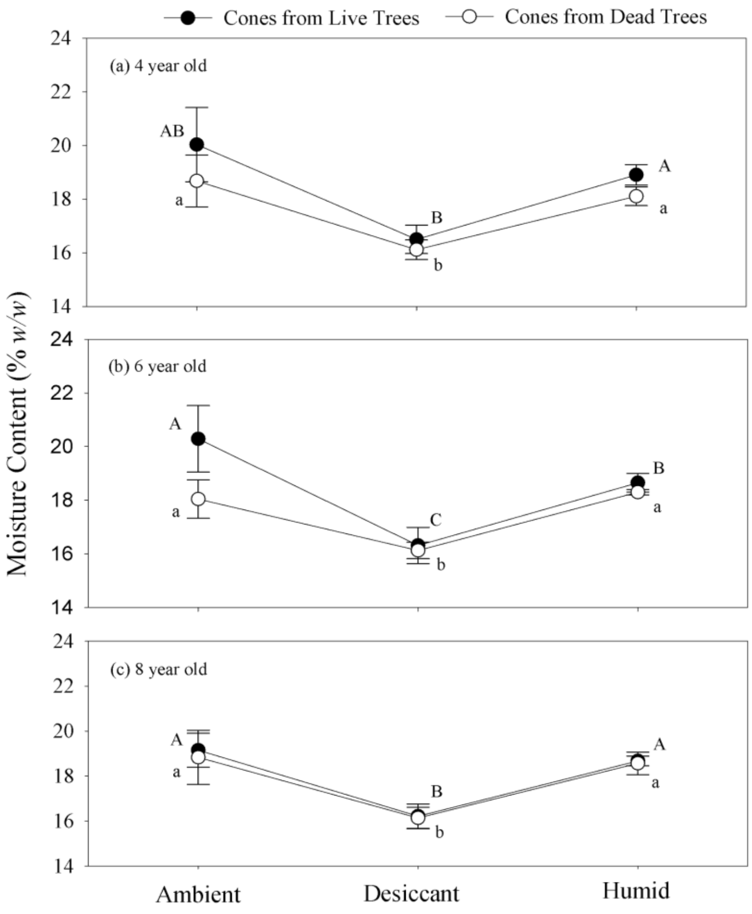

**Figure 3-2**. Exchange of moisture content (MC; % w/w) of cones from live and dead trees at 3 moisture treatments: Ambient, Desiccant and Humid for cones aged a) 4 year old, b) 6 year old and c) 8 year old. Alphabet letters indicate significant (*p*<0.05) statistical difference between 3 treatments (capital for live and lower case for dead) after one way repeated ANOVA test. Error bars indicate one standard error (n=55).

Cones from dead trees generally had higher MC than those from live trees. However sample sizes were much smaller and they were not significantly different. We also observed that cones from living trees absorbed and released moisture more actively than those from dead trees but did not find any statistical difference (Fig. 3-2). Our results clearly showed active moisture exchange of serotinous cones, which was contradictory to our Hypothesis 2 that states resin seal of cones would minimize moisture exchange.

### 3.3.3 Effect of cone moisture content and cone age on time to open

All ‘time to break’ measurements (i.e., *First, Start, Finish, and Last*) were positively correlated with each other (Table 3-1a-b). This means when cone A takes more time to make its First popping sound than cone B, it will also take longer for Start, Finish, and Last pop than cone B.

**Table 3-1.** Results showing the *pearson* correlation analysis results among times (seconds) taken to open lodgepole pine serotinous cones and moisture content (MC; % w/w) from (a) live trees (n= 26) and (b) dead trees (n is indicated in parenthesis). *First, Start, Finish*, and *Last* indicate time takes to hear the ‘first pop’, ‘start of main pop’, ‘finish of main pop’, and ‘last pop’, respectively. *, **, and *** represent significance at the 0.05, 0.01, and 0.001 levels, respectively.

(a)

| Variable | First | Start | Finish | Last | MC |
|---|---|---|---|---|---|
| First | 1.000 | | | | |
| Start | 0.507** | 1.000 | | | |
| Finish | 0.391* | 0.912*** | 1.000 | | |
| Last | 0.468* | 0.820*** | 0.843*** | 1.000 | |
| MC | 0.053 | 0.151 | -0.103 | -0.145 | 1.000 |

(b)

| Variable | First | Start | Finish | Last | MC |
|---|---|---|---|---|---|
| First | 1.000<br>(29) | | | | |
| Start | 0.504**<br>(27) | 1.000<br>(27) | | | |
| Finish | 0.319<br>(27) | 0.831***<br>(27) | 1.000 | | |
| Last | 0.050<br>(29) | 0.800***<br>(27) | 0.902***<br>(27) | 1.000 | |
| MC | -0.491**<br>(29) | 0.118<br>(27) | 0.183<br>(27) | 0.534**<br>(29) | 1.000<br>(29) |

Most of them showed significant correlation with the exception of *First* vs *Finish* and *First* vs *Last* combinations in the dead group (Table 3-1b). MC, however, only showed significant ($p$<0.01) positive correlation with *Last* in cones from dead trees. Surprisingly, MC had significant ($p$<0.01) negative relationship with *First.*

For cones aged 4 and 6 years old, it took more time to open cones from dead trees than those from living trees (Fig. 3-3a-b), but the pattern was reversed for cones aged 8 year old (Fig. 3-3c).

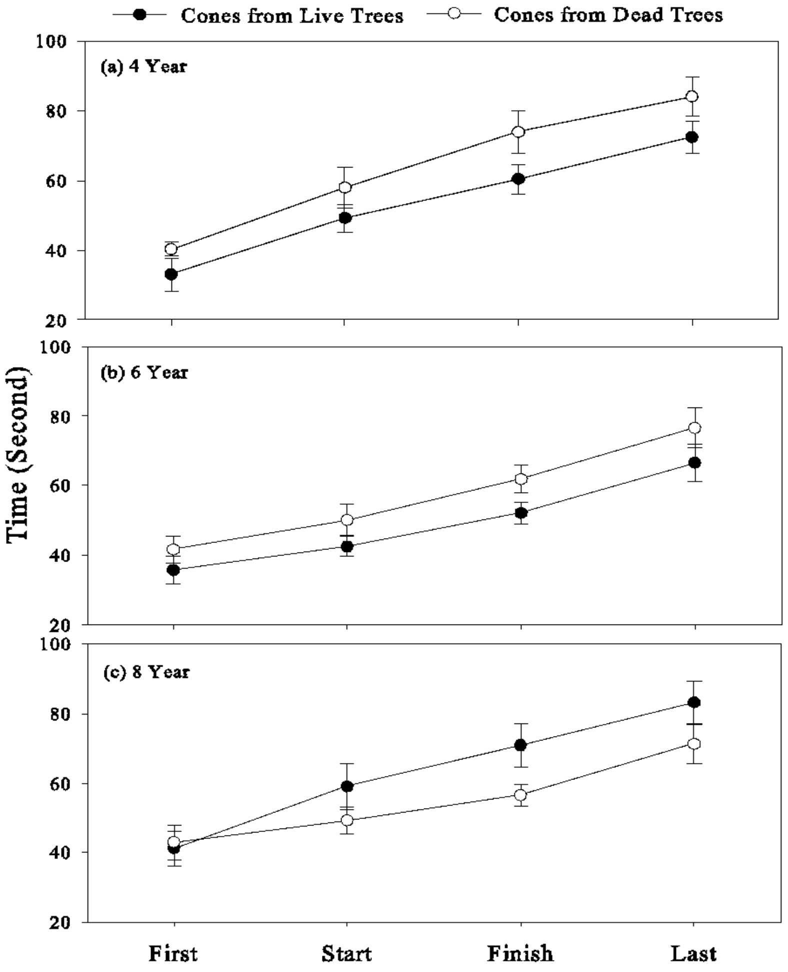

**Figure 3-3.** Time in seconds for the first to last sounds of cone scale opening for cones from live and dead trees (popping) of a) 4 year old cones, b) 6 year old cones and c) 8 year old cones. Error bars indicates one standard error (n=55).

The cone MC was always higher in cones from dead trees than those from living trees. This was the same as the first experiment: 15.87, 16.03, and 16.24% for cones aged 4, 6, and 8 years old sampled from dead trees, respectively, and 17.37, 17.78, and 16.77% for cones aged 4, 6, and 8 years old sampled from living trees, respectively.

## 3.5 Discussion

We observed higher mean MC and MC variation in cones of dead trees compared to those of living trees. Higher crown MC in dead trees could be a result of wetter soil resulting from less transpiration or increased heterogeneity in crown density providing for a larger variability in access to atmospheric moisture. Recent studies in BC also showed that there was higher water table and wetter soil in MPB killed stand (Redding et al. 2008). High MC variation found in dead crown is likely due to higher heterogeneity of canopy structure resulting in heterogeneous light penetration and rain interception.

Hellum (1982) showed that cone moisture content had a positive relationship with time taken to open cones, which made sense because cones with higher moisture would require more energy to increase temperature. Therefore, we expected that it would take more time to open cones from living trees as we had assumed cones from living trees had higher moisture (Hypothesis 3). However, our results indicated cones from dead trees contained higher moisture content and generally required more time to open thus supporting the results of Hellum (1982) (Fig 3). More specifically, it took longer to open cones from dead trees using all four timing methods for 4 and 6 year old cones and *First* for 8 year old cones. We were particularly puzzled, however, that the pattern was reversed in 8 year old cones. It was not clear what influenced this reverse pattern but we suspected that it may be related to the change in cone MC. The cone MC was approximately 1.5% different in 4 and 6 years old cones, but the difference decreased to 0.5% in 8 years old cones.

Our results imply that the seeds contained within a MPB killed lodgepole pine stand may have a better chance to survive a longer residing fire, since it takes more time to open the cones – decreasing the opportunity for scorching. Furthermore, if moisture content has influence on the cone opening timing and heat tolerance, as suggested by previous works, the higher moisture variation of cones from dead trees may provide a wider window of survival against various fire intensity and fire residence time.

We only observed significant positive relationship between *Last* and cone MC of dead trees, although our time to resin break measurements were correlated to each other (Table 3-1a-b). It was not clear why we did not find significant influence of cone moisture to resin break, which indicated that cone MC was not a dominant driver determining cone opening timing and there are other factors associated with this process.  Perry and Lotan (1977) showed that temperature required for cone opening differs among serotinous cones of lodgepole pine. Neumann et al (1964) also reported that both epidermal hairs and resin may play role in keeping serotinous cones closed. Further studies are needed to clearly understand how quality and quantity of resin seal influence cone opening mechanism and role of epidermal hairs in the mechanism.

## 3.6 Conclusion

This study is the first to clearly indicate there is active moisture exchange of serotinous lodgepole pine cones from both live and dead trees. The moisture exchange rate was similar among cones of live and dead trees, but it takes more time to open cones from dead trees. Our results suggested that cone moisture is not the sole driving factor determining the time taken to open serotinous cones, but the mortality condition and age also play a role in the process. Our results indicated that the cones from dead trees might have wider window of survival after fire.

## 3.7 Literature Cited

**Beaufait, W.R. 1960.** Some effects of high temperatures on the cones of seeds of jack pine. For. Sci. 6(3): 194-8.

**Bigler, C., D. Kulakoswki and T.T. Veblen. 2005.** Multiple disturbance interactions and drought interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecol. 86: 3018-3029.

**Clements, F.E. 1910.** The life history of lodgepole burn forests. USDA For. Ser. Bulletin 79. Washington, D.C.

**Crossley, D. I. 1956.** Fruiting habits of lodgepole pine. Canada Dept. North. Affairs and Nat. Resources Forest Res. Div. Tech. Note 35.

**Cullingham, C.I., J.E. Cooke, S. Dang, C.S. Davis, B.J. Cooke and D.W. Coltman. 2011.** Mountain pine beetle host-range expansion threatens the boreal forest. Mol. Ecol. 20: 2157-2171.

**Harlow, W.M., W.A. Jr. Cote and A.C. Day. 1964.** The opening mechanism of pine cone scales. J. For. 62: 538-540.

**Hellum, A.K. 1982.** Cone moisture and relative humidity effects on seed release from lodgepole pine cones from Alberta. Can. J. For. Res. 12: 102-105.

**Hellum, A.K. and N.A. Barker. 1980.** Cone moisture content influences seed release in lodgepole pine. Can. J. For. Res. 10(3): 239-244.

**Hellum, A.K. and N.A. Barker. 1981.** The relationship of lodgepole pine cone age and seed extractability. Forest Sci. 27(1): 62-70.

**Holmes, R. 1983.** Computer-assisted quality control in tree-ring dating and measurement. Tree Ring Bull. 43: 69-75.

**Johnson, E.A. and S.L. Gutsell. 1993.** Heat budget and fire behavior associated with the opening of serotinous cones in two pinus species. J Veg. Sci. 4: 745-750.

**Lotan, J. 1976.** Cone serotiny-fire relationships in lodgepole pine. Proceedings of the 14th Annual Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium. Tall Timbers Research Station. Tallahassee, Florida. 267-278 pp.

**Meddens, A.J.H., J.A. Hicke and C.A. Ferguson. 2012.** Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecol. Appl. 22: 1876-1891.

**Natural Regions Committee. 2006.** Natural Regions and Subregions of Alberta. Compiled by D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. T/852.

**Natural Resources Canada. 2013.** Mountain pine beetle (factsheet). Available from http://www.nrcan.gc.ca/forests/insects-diseases/13397 [accessed 20 October 2013].

**Negron, J. F., B. J. Bentz, C. J. Fettig, N. Gillette, E. M. Hansen, J. L. Hays, R. G. Kelsey, J. E. Lundquist, A. M. Lynch, R. A. Progar and S. J. Seybold. 2008.** U.S. Forest Service bark beetle research in the western United States: Looking toward the future. J. For. 106: 325–331.

**Neumann, F.P, T. Schantz-Hansen and L.W. Rees. 1964.** Cone scale movements of jack pine (*Pinus banksiana* Lamb.). Minnesota Forestry Notes #142.

**Perry, D.A. and J.E. Lotan. 1977.** Opening temperatures in serotinous cones in lodgepole pine. USDA FSRN INT-228.

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

**Redding, T., R. Winkler, P. Teti, D. Spittlehouse, S. Boon, J. Rex, S.Dubé, R.D. Moore, A. Wei, M. Carver, M. Schnorbus, L. Reese-Hansen, and S. Chatwin. 2008.** Mountain pine beetle and watershed hydrology. In Mountain Pine Beetle: From Lessons Learned to Community-based Solutions Conference Proceedings, June 10–11, 2008. BC Journal of Ecosystems and Management. 9(3): 33–50.

**Safranyik, L. and B. Wilson. 2006.** The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, Victoria, Canada.

**Simard, M., W.H. Romme, J.M. Griffin and M.G. Turner. 2011.** Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol. Monogr. 81: 3-24.

**Speer, J.H. 2012**. Fundamentals of Tree Ring Research. The University of Arizona Press. 324pp.

**Teste, F.P., V.J. Lieffers and S.M. Landhausser. 2011a.** Seed release in serotinous Lodgepole pine forests after mountain pine beetle outbreak. Ecol. appl. 21(1): 150-162.

**Teste, F.P., V.J. Lieffers and S.M. Landhausser. 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): 1-8.

**Tower, G.E. 1909.** A study of the reproductive characteristics of lodgepole pine. Proc. Soc. Am. For. 4: 84-106.

# Chapter 4 - Management Implications

My study on the interactive effects of fire and MPB in serotinous jack pine stands is novel in that it is the first of its kind to examine regeneration for both live and dead trees after the application of three different FBP types of fire; surface, intermittent and continuous. Prescribed fire research can be challenging, in that, conditions associated with achieving a certain research related goal often exceed a range of conditions that are deemed safe to do so and/or able to do in a controlled fashion. In addition to the risks associated with applying fire to the landscape for a particular ecological objective, researchers must be prepared to work with a wide range of variability in their results.

It is clear from my research that serotinous pine is unable to regenerate within the Western boreal systems without fire, requiring forest managers to consider silviculture intervention post MPB. Limitation to regeneration is largely attributed to the presence of a thick organic layer associated with these types of stands that is unable to regulate moisture and acts as a barrier between seed and required access to mineral soil. At this site, the duff remaining after fire was highest after the surface fire treatment among the 3 types of fire. This indicates both intermittent and continuous fire may be a more successful fire treatment under the fire weather conditions for the day of the burn with respect to the ability to prepare the site. Overall though, variability within the results was very high within all three of the types of fire.

Of all types of fire, a continuous fire appeared to best achieve sustainable forest management goals in jack pine stands; though further research is required to definitively provide that recommendation. The research clearly indicates that an increase in fire intensity, assuming intensity is linked to type of fire, equates to an increase in seedling density and stocking. This is likely attributed to the increasing ability for a higher intensity fire to remove the organic layer and expose mineral soil as well as provide enough heat to open cones. A study was conducted by a fellow Masters student, Hyejin Hwang (Hwang 2013) at the same research site and indicated that there was greater seed release under the continuous type of fire, again suggesting that continuous fire may be the optimal type of fire for successful regeneration. Cone opening is a secondary, yet equally influential limitation. Without the presence of heat, cones are unable to open and provide seed for a suitable seed crop.

While studies have been conducted on cone opening since the early 1900's, my study is the first to indicate there is active moisture exchange of serotinous lodgepole pine cones from both live and dead trees. The moisture exchange rate was similar among cones of live and dead trees, but it takes more time to open cones from dead trees. My results suggested that cone moisture is not the sole driving factor determining the time taken to open serotinous cones, but the mortality condition and age also play a role in the process. Given the variability within the cone moisture data from the dead trees and the fact that it took longer to open cones, one can surmise that the cones from dead trees might have wider window of survival after fire. I believe that the results provide fundamental information to improve understanding of serotinous pine regeneration after MBP attack, however further research is required to between understand the relationship between cone moisture and fire within MPB-killed stands. Dead stands contained cones that took longer to open, however this was not linked to cone moisture. Cone moisture may be a factor, however in the protection of seed.

This information provides forest managers additional insight into their potential future forest post MPB. Given the economic impact of the MPB and the inability for these stands to regenerate naturally, it is clear that future work is required in fire ecology in dead stands. Having a clear idea of how these stands will contribute to our future forests is important and moreover, how we can optimize forests moving forward. While my study helps to move the research further towards an understanding of disturbance dynamics and its impact on future forests, the following additional questions should be addressed:

- Compare seedling establishment in dead stands after the use of various site preparation techniques (i.e. mechanical site preparation vs. fire, etc.)?
- What is the long term survivorship of seedlings post fire?
- Is there a relationship of regeneration post fire to volume and arrangement of residual woody debris?
- Does the moisture within a cone provide cooling to the seed and enhance viability through a moisture barrier in the event of a continuous fire?
- What aspects of the cone is influencing success or failure of regeneration of future forests?
- Is there a relationship between fire intensity and cone opening in dead stands?
- Is there a relationship between cone moisture and seed viability after application of heat energy in dead stands?

# Literature Cited in Thesis

**Adams, P.W., and J.R. Boyle. 1980.** Effects of fire on soil nutrients in clearcut and whole-tree harvest sites in central Michigan. Soil Science Society of America Journal. 44(4):847-850.

**AESRD. 2014.** Follow the beetle: crews gear up for another year fighting Alberta's most 'invasive' species. Alberta Environment and Sustainable Resource Development. Blog. September 12, 2014. https://aesrd.wordpress.com/category/forests-and-wildfire/forest-health-and-diseases/

**Ahlgren, I.F., and C.E. Ahlgren. 1960.** Ecological effects of forest fires. Bot. Rev. 26: 483–533.

**Alberta Environment and Sustainable Resource Development. 2013.** Reforestation Standard of Alberta. Government of Alberta, Department of Environment and Sustainable Resource Development, Edmonton, Alberta. 231 p.

**Astrup, R., Coates, K.D., and E. Hall. 2008.** Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. Forest Ecology and Management. 256: 1743 – 1750.

**Baldwin, P.H. 1960.** Overwintering of woodpeckers in bark beetle-infested spruce-fir forests of Colorado. International Ornithological Congress Proceedings. 12:71–84.

**Beaufait, W.R. 1960.** Some effects of high temperatures on the cones of seeds of jack pine. For. Sci. 6(3): 194-8.

**Bigler, C., D. Kulakoswki and T.T. Veblen. 2005.** Multiple disturbance interactions and drought interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecol. 86: 3018-3029.

**Bonan, G.B. 2002.** Ecosystems. In Ecological climatology: Concepts and Applications. Cambridge, UK: Cambridge University Press. Second Edition. 303-320.

**Brown, J.K., Marsden, M.A., Ryan, K.C., and E.D. Reinhardt. 1985.** Predicting duff and woody fuel consumption in the northern Rocky Mountains. Res. Pap. INT-337. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 23 p.

**Brunner, A., and J.P. Kimmins. 2003.** Nitrogen fixation in coarse woody debris of "Thuja plicata" and "Tsuga heterophylla" forests on northern Vancouver Island. Can. J. For. Res. 33:1670-1682. Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Sci. Soc. Am. J. 58: 221– 227.

**Burns, R.M., and B.H. Honkala. 1990.** Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. 2: 877.

**Cameron, H. 1953.** Melting point of the bonding material in lodgepole pine and jack pine cones. Can. Dep. Resour. Dev., For. Branch, Div. For. Res., Silvic. Leafl. No. 86.

**Cayford, J.H. 1971.** The role of fire in the ecology and silviculture of jack pine. In Proceedings of the Tall Timbers Fire Ecology Conference, Number 10, 20–21 August 1970, Fredericton, New Brunswick. Tall Timbers Research Station, Tallahassee, Fla. pp. 221–244.

**Charron, I., and D.F. Greene. 2002.** Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Can. J. For. Res. 32: 1607–1615.

**Choromanska, U., and T.H. DeLuca. 2002.** Microbial activity and nitrogen mineralization in forest mineral soils following heating: evaluation of post fire effects. Soil Biology and Biochemistry. 34: 263-271.

**Christensen, N.L., and C.H. Muller. 1975.** Effects of fire on factors controlling plant growth in Adenstoma chaparral. Ecological Monographs. 45: 29-55.

**Chrosciewicz, Z. 1974.** Evaluation of fire-produced seedbeds for jack pine regeneration in central Ontario. Can. J. For. Res. 4**:** 455–457.

**Chrosciewicz, Z. 1976.** Burning for black spruce regeneration on a lowland cutover site in southeastern Manitoba. Canadian Journal of Forest Research. 6(2): 179-186.

**Clements, F.E. 1910.** The life history of lodgepole burn forests. USDA For. Ser. Bulletin 79. Washington, D.C.

**Coates, K.D. 2002.** Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. For. Ecol. Manag. 155:387–398.

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

**Coops, N. C., Wulder M. A., and R. H. Waring. 2012**. Modeling lodgepole and jack pine vulnerability to mountain pine beetle expansion into the western Canadian boreal forest. Forest Ecology and Management. 274: 161-171.

**Covington, W.W., and S.S. Sackett. 1992.** Soil mineral nitrogen changes following prescribed burning in ponderosa pine. Forest Ecology and Management. 54: 175–191.

**Critchfield, W.B. 1957.** Geographic variation in Pinus contorta. Maria Moors Cabot Foundation: Harvard University Publication no.3.

**Crossley, D. I. 1956.** Fruiting habits of lodgepole pine. Canada Dept. North. Affairs and Nat. Resources Forest Res. Div. Tech. Note 35.

**Crossley, D.I. 1956.** Effect of crown cover and slash density on the release of seed from slash-borne lodgepole pine cones. Can. Dept. North. Aff. and Natural Resources, Forest Res. Div. Tech. Note 41. 51 pp.

**Cullingham, C.I., J.E. Cooke, S. Dang, C.S. Davis, B.J. Cooke and D.W. Coltman. 2011.** Mountain pine beetle host-range expansion threatens the boreal forest. Mol. Ecol. 20: 2157-2171.

**Dhar, A., and C.D.B. Hawkins. 2011.** Regeneration and growth following mountain pine beetle attack: a synthesis of knowledge. BC J. Ecosyst. Manage. 12**:** 1–16.

**DeBano, L.F., Rice, R.M., and C.E. Conrad. 1979.** Soil heating in chaparral fires: Effects on soil properties, plant nutrients, erosion, and runoff. USDA Forest Service Research Paper PSW-145. 21p.

**DeBano, L.F., Neary, D.G., and P.F. Folliott. 1998.** Fire's effects on ecosystems. John Wiley & Sons, Inc., New York. Chapter 3. pp. 56.

**de Groot, W.J., Bothwell, P.M., Taylor, S.W., Wotton, B. M., Stocks, B.J., and M.E. Alexander. 2004.** Jack pine regeneration and crown fires. Canadian Journal of Forest Research. 34: 1634-1641.

**Despain, D.G., D.L. Clark, and J.J. Reardon. 1996.** Simulation of crown fire effects on canopy seed bank in lodgepole pine. International Journal of Wildland Fire. 6(1): 45-49.

**Eyre, F. H. 1938.** Can jack pine be regenerated without fire? Journal of Forestry, 36:1067-1072.

**Fahey, T.J., and D.H. Knight. 1986.** Lodgepole pine ecosystems. BioScience. 36: 610-17.

**Ferguson, S.H., and P.C. Elkie. 2003.** Snag abundance 20, 30, and 40 years following fire and harvesting in boreal forests. Forestry Chronicle. 79: 541-549.

**Flannigan, M. D., and B. M. Wotton. 1994.** Fire regime and the abundance of jack pine. In Proceedings of the 2nd International Conference on Forest Fire Research. University of Coimbra, Coimbra, Portugal.

**Gundale, M.J. De Luca, T.H., Fiedler, C.E., Ramsey, P.W., Harrington, M.G., and J.E. Gannon. 2005.** Restoration treatments in a Montana ponderosa pine forest: Effects on soil physical, chemical and biological properties. Forest Ecology and Management. 213: 25-38.

**Harlow, W.M., W.A. Jr. Cote and A.C. Day. 1964.** The opening mechanism of pine cone scales. J. For. 62: 538-540.

**Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr, K., and K.W. Cummins. 1986.** Ecology of coarse woody debris in temperate ecosystems. In Advances in Ecological Research. 15**:** 133-302.

**Harrington M.G. 1987**. Predicting reduction of natural fuels by prescribed burning under ponderosa pine in southwestern Arizona. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Note RM-472. (Fort Collins, CO)

**Harris, L.D. 1984**. The fragmented forest: Island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Ill.

**Hawkes, B., Taylor, S., Stockdale, C., Shore, T., Beukema, S., and D. Robinson. 2005**. Predicting mountain pine beetle impacts on lodgepole pine stands and woody debris characteristics in a mixed severity fire regime using Prognosis (BC) and the Fire and Fuels

Extension. Progress report for a study funded by the BC Forest Innovations Investment Research Program, Natural Resources Canada, Canadian Forest Service and the mpb Federal Initiative.

**Hellum, A.K. and N.A. Barker. 1980.** Cone moisture content influences seed release in lodgepole pine. Can. J. For. Res. 10(3): 239-244.

**Hellum, A.K., and N.A. Barker. 1981.** The relationship of lodgepole pine cone age and seed extractability. Forest Sci. 27(1): 62-70.

**Hellum, A.K. 1982.** Cone moisture and relative humidity effects on seed release from lodgepole pine cones from Alberta. Can. J. For. Res. 12: 102-105.

**Hernandez, D.L., and S.E. Hobbie. 2008**. Effects of fire frequency on oak litter decomposition and nitrogen dynamics. Oecologia. 158(3): 535-43.

**Herr, D.G., and L.C. Duchesne. 1995.** Jack pine (*Pinus banksiana*) seedling emergence is affected by organic horizon removal, ashes, soil, water and shade. Water, Air and Soil Pollution. 82: 147-154.

**Holmes, R. 1983.** Computer-assisted quality control in tree-ring dating and measurement. Tree Ring Bull. 43: 69-75.

**Hwang, H. 2013.** Using fire to trigger cone opening in aerial seedbanks in healthy or recently dead jack pine stands. Unpublished dissertation. University of Alberta.

**Jenkins, M.J., Hebertson, E., Page, W., and C.A. Jorgensen. 2008**. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For. Ecol. Manage. 254: 16–34.

**Johnson, E.A. and S.L. Gutsell. 1993.** Heat budget and fire behavior associated with the opening of serotinous cones in two pinus species. J Veg. Sci. 4: 745-750.

**Jolly, W.M., Parsons, R.A., Hadlow, A.M., Cohn, G.M., McAllister, S.S., Popp, J.B., Hubbard, R.M., and J.F. Negron. 2012.** Relationships between moisture, chemistry, and ignition of Pinus contorta needles during the early stages of mountain pine beetle attack. Forest Ecology and Management. 269: 52-59.

**Kayes, L.J., and D.B. Tinker. 2012**. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. Forest ecology and management. 263: 57-66.

**Kemball, K.J. Wang, G.G., and A.R. Westwood. 2006.** Are mineral soils exposed by severe wildfire better seedbeds for conifer regeneration? Can. Jour. of For. Res. 36(8): 1943-1950, 10.1139/x06-073.

**Kemball, K.J., Westwood, R.A., and G.G. Wang. 2010.** Laboratory assessment of the effect of forest floor ash on conifer regeneration. Canadian Journal of Forest Research. 40: 822-826. doi: 10.1139/X10-027

**Klutsch, J.G., Negrón, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J., and R. Caissie. 2009.** Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. Forest Ecology and Management 258: 641-649.

**Koch, P. 1996.** Lodgepole Pine in North America. Forest Products Society, Madison, WI. 763 p.

**Koehler, G.M., and K.B. Aubry. 1994**. Lynx. In The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. L.F. Ruggiero, K.B. Aubrey, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski (editors). U.S.

Department of Agriculture Forest Service, Fort Collins, Colo. General Technical Report rm-254. 74–98 pp.

**Koplin, J.R. 1969.** The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. Condor. 71:436–438.

**Kurz, W.A., and M.J. Apps. 1999**. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecol. Applic. 9: 526-547.

**Kutiel, P., and A. Shaviv. 1992.** Effects of soil type, plant composition and leaching on soil nutrients following a simulated forest fire. For.Ecol.Manage. 53: 329-343.

**Lewis, K.J. and I. Hartley. 2005**. Rate of deterioration, degrade and fall of trees killed by mountain pine beetle: A synthesis of the literature and experiential knowledge. University of Northern British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Victoria, B.C. Mountain Pine Beetle Initiative Working Paper 2005-14. url: http://warehouse. pfc.forestry.ca/pfc/25483.pdf

**Logan, J.A., and J.A. Powell. 2001**. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47: 160–173.

**Lotan, J. E. 1964**. Regeneration of lodgepole pine: a study of slash disposal and cone opening. U.S. Dep. Agric. For. Servo Res. Note INT-16. p. 4.

**Lotan, J. 1976.** Cone serotiny-fire relationships in lodgepole pine. Proceedings of the 14th Annual Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium. Tall Timbers Research Station. Tallahassee, Florida. 267-278 pp.

**Lotan, J.E., Brown, J.K., Neuenschwander, L.F. 1985**. Role of fire in lodgepole pine forests. Symposium proceedings of lodgepole pine: the species and its management. May 8-10, 1984, Spokane Washington State University, Pullman, WA. 133-152 pp.

**Macadam, A.M. 1987.** Effects of broadcast slash burning on fuels and soil chemical properties in the sub-boreal spruce zone of central British Columbia. Can J For Res. 17:1577–1584.

**MacIntosh, A.C.S., and S.E. Macdonald. 2013**. Potential for lodgepole pine regeneration after mountain pine beetle attack in newly invaded Alberta stands. Forest ecology and management. 295: 11-19.

**Magill, A. H., and J.D. Aber. 2000.** Variation in soil net mineralization rates with dissolved organic carbon additions. Soil Biology and Biochemistry. 32: 597-601

**Meddens, A.J.H., J.A. Hicke and C.A. Ferguson. 2012.** Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecol. Appl. 22: 1876-1891.

**Mitchell, R.G., and H.K. Preisler. 1998**. Fall rate of lodgepole pine killed by the mountain pine beetle in Central Oregon. Western Journal of Applied Forestry. 13(1): 23-26.

**Miyanishi, K., and E.A. Johnson. 2002**. Process and patterns of duff consumption in the mixedwood boreal forest. Canadian Journal of Forest Research. 32:1285-1295.

**Mohr H.H., Waldrop, T.A., and V.B. Shelburne. 2002.** Optimal seedbed requirements for the regeneration of Table Mountain pine. In 'Proceedings eleventh biennial southern silvicultural research conference', 20–22 March 2001, Knoxville, TN. (Ed. K. Outcalt) USDA Forest Service, Southern Research Station, General Technical Report SRS-48, pp. 306–309. (Asheville, NC)

**Monleon, V.J., and K. Cromack, Jr., 1996.** Long-term effects of prescribed underburning on litter decomposition and nutrient release in ponderosa pine stands in central Oregon. For. Ecol. Manage. 81: 143-152.

**Natural Regions Committee 2006.** Natural Regions and Subregions of Alberta. Compiled by D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. T/852.

**Natural Resources Canada. 2013.** Mountain pine beetle (factsheet). Available from http://www.nrcan.gc.ca/forests/insects-diseases/13397 [accessed 20 October 2013].

**Negron, J. F., B. J. Bentz, C. J. Fettig, N. Gillette, E. M. Hansen, J. L. Hays, R. G. Kelsey, J. E. Lundquist, A. M. Lynch, R. A. Progar and S. J. Seybold. 2008.** U.S. Forest Service bark beetle research in the western United States: Looking toward the future. J. For. 106: 325–331.

**Neumann, F.P, T. Schantz-Hansen and L.W. Rees. 1964.** Cone scale movements of jack pine (*Pinus banksiana* Lamb.). Minnesota Forestry Notes #142.

**Nigh, G.D., Antos, J.A., and R. Parish. 2008**. Density and distribution of advance regeneration in mountain pine beetle killed lodgepole pine stands of the Montane Spruce zone of southern British Columbia. Can. J. For. Res. 38(11): 2826-2836.

**Perry, D.A. and J.E. Lotan. 1977.** Opening temperatures in serotinous cones in lodgepole pine. USDA FSRN INT-228.

**Place, I.C.M. 1955.** The influence of seed-bed conditions on the regeneration of spruce and balsam fir. Canada Department of Northern Affairs and Natural Resources, Forestry Branch, Forest Research Division, Rep. Bull. 117.

**Pina, P. 2012.** The impacts of simulated Mountain Pine Beetle attack on the water balance in lodgepole pine forest of the western Alberta foothills. PhD Dissertation, Dept. of Renewable Resources, University of Alberta, Edmonton.

**Raffa, K.F., B.H. Aukema, B.J. Bentz, A.L. Carroll, J.A. Hicke, M.G. Turner and W.H.**

**Romme. 2008.** Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. BioScience. 58(6): 501-517.

**Radeloff, V.C., Mladenoff, D.J., Guries, R.P., and M.S. Boyce. 2004**. Spatial patterns of cone serotiny in Pinus banksiana in relation to fire disturbance. Forest Ecology and Management. 189: 133-141.

**Redding, T., R. Winkler, P. Teti, D. Spittlehouse, S. Boon, J. Rex, S.Dubé, R.D. Moore, A. Wei, M. Carver, M. Schnorbus, L. Reese-Hansen, and S. Chatwin. 2008.** Mountain pine beetle and watershed hydrology. In Mountain Pine Beetle: From Lessons Learned to Community-based Solutions Conference Proceedings, June 10–11, 2008. BC Journal of Ecosystems and Management. 9(3): 33–50.

**Remington, T.E. and R.W. Hoffman. 1996**. Food habits and preferences of blue grouse during winter. Journal of Wildlife Management. 60:808–817.

**Romme, W.H., Clement, J., Hicke, J., Kulakowski, D., MacDonald, L.H., Shoennagel, T.L., Veblen, T.T. 2006**. Recent Forest Insect Outbreaks and Fire Risk in Colorado Forests: A Brief Synthesis of Relevant Research. Colorado State University, Fort Collins, CO. 24 p.

**Rudolph, T.D., and P.R. Laidly. 1990.** *Pinus banksiana* Lamb. - jack pine. In: R.M. Burns, BH Honkala (eds.) Silvics of North America, vol. 1: Conifers. Agriculture Handbook 654. USDA Forest Service, Washington DC, USA. 280-293 pp.

**Schroeder, D., and C. Mooney. 2012.** Fire behaviour in simulated mountain pine beetle-killed stands. Final Report. FP Innovations. Wildfire Operations Research. 17 pp.

**Safranyik, L. 1978.** Effects of climate and weather on mountain pine beetle populations. Pages 79-86 in A. Berryman; G. Amman, R. Stark, and D. Kibbee, eds. Symposium proceedings: The theory and practice of mountain pine beetle management in lodgepole pine forests. April 1978, Pullman, WA. University of Idaho – Forest, Wildlife and Range Experiment Station.

**Safranyik, L., and D. A. Linton. 1998.** Mortality of mountain pine beetle larvae, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in logs of lodgepole pine (*Pinus contorta* var. *latifolia*) at constant low temperatures. Journal of the Entomological Society of British Columbia. 95: 81-87.

**Safranyik, L., and B. Wilson. 2006.** The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, Victoria, Canada.

**Safranyik L., Carroll A.L., Regniere J., Langor D.W., Reil W.G., and T.L. Shore. 2010.** Potential for range expansion of mountain pine beetle into the boreal forest of North America. Can Entomol. 142: 415–441.

**Serrasolsas I., and P.K. Khanna. 1995.** Changes in heated and autoclaved forest soils of S.E. Australia. II. Phosphorus and phosphatase activity. Biogeochemistry. 29:25–41

**Simard, M.-J., Bergeron, Y., and L. Siros. 2003.** Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. Can. J. For. Res. 33: 672-681.

**Simard, M., Romme, W.H., Griffin, J.M., and M. G. Turner. 2011.** Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs. 81(1): 3-24.

**Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McClaugherty, C.A., Rayburn, L., Repert, D., and T. Weiland. 1993.** Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. Ecology. 74: 1586–1593.

**Smith J.K., and N.E. McMurray. 2002.** FireWorks curriculum featuring ponderosa, lodgepole, and whitebark pine forests. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-65. Fort Collins, CO.

**Spears, J.D.H., Holub, S.M., Harmon, M.E., and K. Lajtha. 2003.** The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A. Can. J. Forest Res. 33: 2193– 2201.

**Speer, J.H. 2012**. Fundamentals of Tree Ring Research. The University of Arizona Press. 324pp.

**Stump, L.M., and D. Binkley. 1993.** Relationship between litter quality and nitrogen availability in Rocky Mountain forests. Can. J. For. Res. 23: 492-502.

**Sullivan, T.P., and D.S. Sullivan. 1988**. Influence of stand thinning on snowshoe hare population dynamics and feeding damage in lodgepole pine forest. Journal of Applied Ecology. 25:791–805.

**Teste, F.P., V.J. Lieffers and S.M. Landhausser. 2011a.** Seed release in serotinous Lodgepole pine forests after mountain pine beetle outbreak. Ecol. appl. 21(1): 150-162.

**Teste, F. P., Lieffers V.J., and S.M. Lanhäusser. 2011b**.Viability of forest floor and canopy seed banks in *Pinus contorta* var. *latifolia* (*Pinaceae*) forests after a mountain pine beetle outbreak. American Journal of Botany. 98(4): 1-8.

**Thomas, P.A., and R.W. Wein. 1985.** The influence of shelter and the hypothetical effect of fire severity on the postfire establishment of conifers from seed. Can. J. For. Res. 15: 148–155.

**Tinker, D.B., and D.H. Knight. 2000.** Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems. 3: 472–483.

**Tower, G.E. 1909.** A study of the reproductive characteristics of lodgepole pine. Proc. Soc. Am. For. 4: 84-106.

**Turner, M. G., and V.H. Dale. 1998.** Comparing large, infrequent disturbances: what have we learned? Ecosystems. 1: 511-523.

**Van Wagner, C. E. 1972.** Duff consumption by fire in eastern pine stands. Can. J. For. Res. 2: 34-39.

**Van Wagner, C. E. 1987**. Development and structure of the Canadian Forest Fire Weather Index System. Canadian Forest Service, Ottawa, ON, Forest Technical Report 35. 37 pp.

**Vyse, A., Ferguson, C., Huggard, D., Roach, J., and B. Zimonick. 2009.** Regeneration beneath lodgepole pine dominated stands at- tacked or threatened by the mountain pine beetle in the south central interior, British Columbia. For. Ecol. Manage. 258(Suppl.): S36 –S43.

**Weber, M. G., Hummel, M., and C.E. Van Wagner. 1987.** Selected parameters of fire behavior and *Pinus banksiana* Lamb. regeneration in eastern Ontario. For Chron. 63(5): 340-346.

**Zasada J.C., Norum R.A., van Veldhuizen R.M., and C. Teutsch. 1983.** Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Canadian Journal of Forest Research. 13: 903–913.