

University of Alberta

**Using Fire To Trigger Cone Opening In Aerial Seedbanks
In Healthy or Recently Dead Jack Pine Stands**

by

Hyejin Hwang

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science

in

Forest Biology and Management

Department of Renewable Resources

© Hyejin Hwang

Fall 2013

Edmonton, Alberta

Permission is hereby granted to the University of Alberta Libraries to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only. Where the thesis is converted to, or otherwise made available in digital form, the University of Alberta will advise potential users of the thesis of these terms.

The author reserves all other publication and other rights in association with the copyright in the thesis and, except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatsoever without the author's prior written permission.

Abstract

Mountain pine beetle (*Dendroctonus ponderosae*; MPB) is a natural disturbance agent in western North America. Recently, MPB has been found beyond its historical habitats and threatening jack pine (*Pinus banksiana*) in western Canadian boreal forests. Jack pine is a fire-dependent species that relies on periodic fires for seed release of serotinous cones and stand regeneration. In this study, we examined cone opening in both living and MPB-simulated jack pine stands occurred by prescribed fires of different intensities. Fire-induced cone opening was related to char height, a proxy for fire intensity. In living trees, moderate fires could only open cones at the bottom of the crown, while cones on dead trees were opened with lower char height. However, there was a wider variation in cone opening in relation to char height observed in the dead trees likely due to lower foliar moisture content and crown bulk density than living trees.

Acknowledgement

First, I would like to thank my advisor Dr. Victor Lieffers for his great guidance, patience, knowledge, and help throughout my master's program. I am also grateful for my thesis committee, Drs. Mike Flannigan and M. Derek MacKenzie for their insightful comments and suggestions on my research.

This research would not have been completed without financial support by Foothills Research Institute. I also want to give special thanks to Dave Schroeder from Alberta Environment and Sustainable Resource Development and Colleen Mooney from FPInnovations for providing access to the original Archer Lake project data. Cordy Tymstra, Greg Baxter, Ray Ault, Rex Hsieh, Jarret Whitbread, and Waterways Wildfire Management Area also helped us with personal expertise, technical support, and logistics.

For the last three years, I had a lot of opportunities to work with amazing people who helped me complete my master's program: Dr. Xianli Wang gave me valuable advice and a lot of statistical help. Maria Sharpe shared her knowledge, time, and pieces of her life with me. Kirk Johnson provided constructive criticism, suggestions, and encouragement. I was also very lucky to work with members of the Western Partnership for Wildland Fire Science at the University of Alberta and research assistants Drew McDonald and Cassidy Van Rensen.

I am particularly thankful to Dr. Joohoon Lim for mentoring me since my research assistantship at the Korea Forest Research Institute and providing encouragement to pursue fire ecology in Canada. My thanks also go out to my dear friends from Korea, Canada, and elsewhere for their moral support.

Most importantly, I would like to thank my mother and family for their unconditional support and love. Such an accomplishment would not have been possible without them.

Table of Contents

Abstract	
Acknowledgements	
Table of Contents	
List of Tables	
List of Figures	
Chapter 1	7
1. Literature Review	7
1.1. Introduction	7
1.2. Cone Serotiny as an Opportunistic Trait in Jack Pine	8
1.3. Cone Opening Mechanism	9
1.4. Fire as a Means to Regenerate MPB-killed Forests	10
1.5. Fuel Alteration by MPB	12
1.6. Research Objectives	14
1.7. Thesis Outline	14
2. References	17
Chapter 2	24
1. Introduction	24
2. Materials and Methods	28
2.1. Study Area	28
2.2. Experimental Design	28
2.3. Prescribed Burns and Data Collection in 2009	29
2.4. Data Collection in 2012	31
2.5. Statistical Analysis	31
2.5.1. Fuel Moisture Content	31
2.5.2. Cone Opening as a Function of Char Height	32
2.5.2.1. Char Height Location	32
2.5.2.2. Regression Analysis	32
2.5.2.3. Variable Selection	33
3. Results	34

3.1. The Impact of MPB Simulation on Fuel Moisture Regime	34
3.2. Fire Behaviour Characteristics Between Living and Dead Stands.....	34
3.3. Cone Opening as a Function of Char Height	35
3.4. Cone Opening Model	36
3.4.1. Variable Selection.....	36
3.4.2. Cone Opening Modeled with Char Height	36
4. Discussion	38
4.1. Cone Opening Between Healthy and Recently Dead Jack Pine	38
4.2. Factors Involved in Cone Opening in Dead Trees	39
4.3. Reliability of the Current FWI System	40
4.4. Application of Fire in MPB-killed Forests.....	42
4.5. Limitation of Using Char Height as a Proxy for Fire Intensity	42
5. References.....	55
Chapter 3	60
1. Conclusion	60
2. Future research.....	61
3. References.....	63
Appendix.....	64
A. Canadian Forest Fire Weather Index System.....	64
B. Van Wagner's (1977) Crowning Initiation Model	65
C. The Relationship Between Predicted and Observed Rate of Spread.....	66
D. Multivariate Nonlinear Regression Models Fits for Cone Opening.....	67
E. Stand Density for Each Study Plot	69
F. Fuel Load Data for the Archer Lake Study Area	70

List of Tables

Table 1. Weather information and Fire Weather Indices of the study plots at Archer Lake in 2009.....	44
Table 2. Correlation matrix among tree and cone opening variables.....	45

List of Figures

Figure 1. Chronological description of mountain pine beetle attack	16
Figure 2. Location of the research site.....	46
Figure 3. Comparisons between measured and estimated moisture content in fine fuels and organic layers in relation to the standard fuel moisture models in Canadian Forest Fire Weather Index System.....	47
Figure 4. Comparisons of moisture content of fine fuel (i.e., litter), duff, and crown foliar between control (L) and MPB-simulated plots (D).....	48
Figure 5. Critical surface fire flame length to initiate crowning in living and dead stands in relation to crown base height with an application of Van Wagner's (1977) crown fire initiation model	49
Figure 6. Critical surface fire intensity to initiate crowning in living and dead stands in relation to crown base height with an application of Van Wagner's (1977) crown fire initiation model	50
Figure 7. Cone opening modeled with different fire types defined by the relationship between char height and CBH	51
Figure 8. Accumulated cone opening by crown layers as a function of char height (char height<CBH)	52
Figure 9. Accumulated cone opening by crown layers as a function of char height (char height>CBH)..	53
Figure 10. Cone opening in relation to char height for both dead and living trees..	54

Chapter 1

1." Literature Review

1.1. Introduction

Mountain pine beetle (*Dendroctonus ponderosae*, MPB) is a natural disturbance agent in western North America with a range from New Mexico to British Columbia and has occurred within the natural habitat range over the last century (Alfaro et al. 2009). MPB infestation plays a critical role in development of stand structure by killing mostly old and large trees and providing space for future regeneration (Amman 1977). Forests in south western Alberta have experienced several endemic levels of MPB outbreak in the last 100 years (Reid 2001, Natural Resources Canada 2012). In recent times, however, a larger scale of MPB outbreaks has been occurring beyond its historical habitat range and invading into novel habitats such as northern British Columbia and western Alberta where MPB outbreak was not recorded in the recent history. Recent large and sustained MPB outbreaks in the new habitats are linked to: a) long-term forest management policies that resulted in large areas of homogenous, mature or over-mature pine forests susceptible to disturbances; and b) climate change providing warmer winter temperatures resulting in increased survival of MPB (Safranyik 1978, Safranyik et al. 2010). Moreover, MPB populations blown by strong winds from northeast British Columbia to Alberta successfully survived in 2006 (<http://www.mpb.alberta.ca/>) and this is threatening intact pine forests in the province today. In British Columbia, 14 million ha of pine forests have been impacted by MPB (Wulder et al. 2010, Coops et al. 2012). Alberta has 6 million ha of pine forests vulnerable to MPB (<http://mpb.alberta.ca/>) and forest protection programs have been conducted to prevent timber loss by removing mature pine trees that are susceptible to MPB (ESRD 2011).

Conifer forests in Alberta are in an ecological hot spot today regarding MPB expansion into new habitats, that is Canadian boreal forests. Lodgepole pine is well known as a primary host species for MPB (Lee 2006, Safranyik et al. 2010). Interestingly, Alberta's forests are composed of lodgepole pine (*Pinus*

contorta) in the west, lodgepole-jack pine hybrid zones in the transitional area, and jack pine (*Pinus banksiana*) in the east (Rudolph and Laidly 1990). Hybridization between these two species is common in the overlap regions due to genetic similarity. Recent studies show successful MPB attack from lodgepole pine-dominated forests into lodgepole-jack pine hybrid zones as well as pure jack pine stands in Alberta and discuss that these hybrid zones might aid MPB to expand into new habitats across the Canadian boreal forests that are jack pine-dominated (Safranyik et al. 2010, Cullingham et al. 2011, 2012). As an outbreak of MPB requires new habitats and it occurs at a large scale, public concerns are raised because the negative consequences of MPB outbreaks on jack pine forests will have economic and ecological implications.

1.2. Cone Serotiny as an Opportunistic Trait in Jack Pine

Jack pine has two different forms of cones: a) non-serotinous (i.e., cones are open at maturity); and b) serotinous (i.e., cones remain closed after maturity). Serotiny level may differ among individual trees even in the same stand (Clements 1910), also depending on age group (Mason 1915, Crossley 1956, Lotan 1975), elevation (Critchfield 1957, Lotan 1976), or soil characteristics (Tower 1909). In jack pine, one tree can have both serotinous and non-serotinous cones (Schoenike 1976); however, most of jack pine populations in Canadian boreal forests are highly serotinous (Radeloff et al. 2004). Gauthier et al. (1993) found that cone serotiny was well correlated with DBH and that non-serotinous cones on young jack pine might be related to resource allocation strategy at young stage of development, i.e., focused more on growth rather than producing resinous compounds at young age. Furthermore, serotiny level was determined by the usual type of fire; highly serotinous populations were an outcome of usually intense fires, whereas low serotinous populations were selected for low intensity fire (Gauthier et al. 1996).

Cone serotiny is an ecological trait that has evolved with frequent occurrence of fire on the landscape (Critchfield 1957, Lotan 1976, Muir and

Lotan 1985, Schwilk and Ackerly 2001). Jack pine is a shade-intolerant species which has better growth under full sunlight (Rudolph and Laidly 1990). Uniform release of a large number of seeds at the same time that competing species are removed allows the pine to dominate the disturbed areas afterwards (Lamont et al. 1991, Flannigan and Wotton 1994, Keeley 1994).

Jack pine also relies on fire for seedbed preparation (Chrosiewicz 1974, Flannigan and Wotton 1994). Cones that drop to the surface by branch breakage can be opened through surface heating from solar radiation, thereby releasing seeds in the absence of fire (Teste et al. 2011a). However, seed release without seedbed preparation may not always result in successful emergence of seedling because thick organic matter develops on the forest floor in the Canadian boreal forests. This coarse organic matter develops due to low decomposition rate in the cold weather and the ground surface is usually covered with a blanket-like layer of feather mosses or ground lichens. Although pine seeds may land on the forest floor, begin germination, and rooting in the absence of disturbances, the coarse organic layers and the feather moss or lichen layers quickly dry out during periods of drought because the germinating roots have not reached a stable moisture supply in the mineral soil (Coates 2002, Vyse et al. 2009).

1.3. Cone Opening Mechanism

Jack pine is the most abundant overstory species in the Canadian boreal forests and accounts for a large part of the timber supply (Rudolph and Laidly 1990). For these reasons, cone opening mechanism has long been of interest to silviculturists. Serotinous pine cones are sealed with resinous bond to seal scales and to protect seeds until the bond is broken by sufficient temperatures (Beaufait 1960). Cone opening could be achieved by two methods: solar radiation and forest fire. Cones near the forest floor may be exposed to both direct radiation and long-wave radiation from the soil surface that is hot enough to melt resin bond and release seeds (Crossley 1956, Lotan 1964). Periodic forest fire can also open jack pine

cones in the aerial seedbanks and the fire consumes part of the forest floor providing a suitable seedbed of mineral soils (Abrams and Dickmann 1982, Knapp and Anderson 1980). Temperature required to open cones is slightly different between lodgepole and jack pine; however, generally a jack pine cone is open at 50°C by melting the resinous bond holding the scales closed and a lodgepole pine cone is at 45.5°C (Cameron 1953). Temperature that exceeds 65°C is known to decrease the seed viability (Wright 1931). Seed viability is influenced by time exposed to heat and even a few seconds of exposure of the cone to high temperature (i.e., >700°C) results in a decrease in seed viability (Beaufait 1960). In nature, however, cones are hanging in the branches in the presence of fine fuels such as needles and a crown fire may not necessarily result in cone ignition or loss of seed viability. Eyre (1938) suggested that aerial fuels will be consumed and generating heat to open cones, but the cone will still protect the seed viability. During a fire, live needles take both time and energy to evaporate moisture, thereby delaying ignition (Bond and van Wilgen 1996, Schwilk and Ackerly 2001, Jolly et al. 2012) and these wet fuels act as a heat sink and protecting cones from direct exposure to high temperature during the fire (Schwilk and Ackerly 2001). In most crown fires, duration of flaming in the canopy is short (10~12 sec) and seed viability is not influenced by the heat generated within the short period of time (Alexander and Cruz 2012b). Interestingly, seed release does occur with a time lag (Alexander and Cruz 2012b) and released seeds might delay germination to avoid unsuitable post-fire conditions (de Groot et al. 2004) such as high accumulation of ash resulting in high soil pH, surface temperature (Thomas and Wein 1985, Herr and Duchesne 1995), as well as toxic effect of ash on germination (Kemball et al. 2006).

1.4. Fire as a Means to Regenerate MPB-killed Forests

The use of prescribed burning might be a feasible regeneration method meeting the purpose of both providing seeds by opening the cones in aerial seedbanks and

preparing a suitable seedbed. This may be both cost- and scale-effective. The Canadian Forest Fire Weather Index System assists with the decision making process for prescribed burning in Canada (Van Wagner 1974, 1987; FWI), and calibrations of the FWI System have been made in European countries (e.g., United Kingdom, Slovenia, Greece), and Asia such as Indonesia and China. FWI System is composed of three fuel moisture codes (i.e., Fine Fuel Moisture Code (FFMC), Duff Moisture Code (DMC), and Drought Code (DC)) and three fire behaviour indices (i.e., Initial Spread Index (ISI), Buildup Index (BUI), and Fire Weather Index (FWI)). FWI System provides daily numeric ratings of moisture content of the forest floor with consideration of the interactions between fuels and weather variables (i.e., temperature (°C), relative humidity (%), wind speed (km/h), and 24-hour accumulated precipitation (mm) taken at 12:00 local standard time or 13:00 daylight saving time). Depending on the degree of decomposition and location, fuel layers are divided into three: litter layer (i.e., needles, other surface litter; 1-2cm in depth (de Groot 1987)), fermentation layer (i.e., organic matter that is decaying but still identifiable; 5-10cm in depth (de Groot 1987)), and humus layer (i.e., organic matter that is too decayed and not identifiable; 10-20cm in depth (de Groot 1987)). Each layer has different bulk density due to the degree of decomposition, thereby different water-holding capacity. FFMC represents moisture content in fast-drying litter layer that is exposed to all of the weather variables in terms of drying and wetting rate. DMC is moisture content in loosely compacted organic layer (i.e., fermentation layer) and it is not affected by wind, but temperature, relative humidity, and precipitation. DC indicates moisture content in deep and compacted organic layer (i.e., humus layer) and temperature and precipitation are the weather parameters affecting moisture content in the layer. FWI System provides ISI based on a combination of FFMC and wind speed which predicts fire spread on the surface. BUI is produced with a combination of DMC and DC and suggests information on smoldering combustion of deep organic matter as well as coarse woody debris on the surface. Finally, FWI describes overall information on predicted fire intensity and danger

in relation to fuel moisture and weather conditions in an area (Van Wagner 1987, Wotton 2009).

FWI System is generally applicable to Canadian forests where mature jack pine and lodgepole pine are the main overstory fuel types (Van Wagner 1974, Turner and Lawson 1978, Van Wagner 1987, Beck and Armitage 2001). These two species are widely distributed across Canada and similar in stand structure and fire behaviour (Wotton 2009). However, further studies are required to assess application of the FWI System in different fuel types than the standard fuel type, for instance, MPB-altered fuel type.

1.5. Fuel Alteration by MPB

Changes in fuel moisture regime and fuel spatial distribution are observed at the canopy layer and forest floor in MPB-killed forests. In the first few years after MPB infestation, the majority of the fine fuels of the canopy (i.e., needles and twigs) remain on the trees, but have low moisture content (Hoffman et al. 2012) and experience change in the chemical properties in needles (Jolly et al. 2012, Page et al. 2012). Relative amounts of lignin, cellulose, hemicellulose, and extractives such as resins and oils (Kramer and Kozlowski 1960, Page et al. 2012) change with time since tree mortality and this influences fire behaviour characteristics (i.e., time to ignition, flammability, heat yields) in MPB-killed forests (Page et al. 2012). Meanwhile, as MPB cuts off the xylem water transport and transpiration processes, the reduced water uptake leads to increase in water availability in the soil (Hélie et al. 2005). It is noteworthy that MPB outbreak does not increase the total available fuels, but changes the spatial distribution (Hoffman et al. 2012).

Magnitude of MPB outbreak in alteration of fuel distribution depends upon site (i.e., soil texture, moisture) as well as weather conditions. In general, when the MPB-killed forests are between red- and grey-attack stages (Fig. 1), it is characterized by an accumulation of fine fuels to the ground (Klutsch et al. 2009,

Simard et al. 2011) because crown abrasion breaks off the brittle dead twigs during wind after MPB outbreaks (Teste et al. 2011a). When MPB-killed trees fall to the ground after 10 or more years, they have already lost their canopy fine fuels (Mitchell and Preisler 1998, Simard et al. 2011), and increased sunlight penetration through the gaps created by tree canopy loss and fall down of trees encourages understory vegetation that will sometimes add to surface fuels (Simard et al. 2011; Fig. 1). In Vaartaja's south Finland study (1954), under closed canopy condition, the surface of the forest floor will experience 9 to 13°C on most sunny summer days, whereas if light can penetrate right to the ground, the surface temperature may exceed 50°C, which may lead to drying out the surface fuels. Moreover, as the canopy opens, the increased wind speed may promote drying of the surface fuels, along with the increased sunlight penetration, and increase fire risk to the regenerating forests (Romme et al. 2006, Page and Jenkins 2007, Jenkins et al. 2008).

In accordance with the change in spatial fuel distribution, fire behaviour such as fire intensity, rate of fire spread, and flame residence time would differ between living and MPB-killed stands. Accumulated fine fuels on the forest floor in dead stands increase surface fire hazards and fire intensity (Mitchell and Preisler 1998, Romme et al. 2006, Jenkins et al. 2008, Simard et al. 2011). In addition, dry dead needles retained in the canopy may carry surface fire to the crown much faster. At the snag fall-down stage, most of standing dead trees may have lost readily consumable aerial fuels, resulting in less concern of an active crown fire due to lack of fuel connectivity (Page and Jenkins 2007). However, presence of understory vegetation as well as increased surface fuel loading after snag fall might result in increased surface fire intensity (Simard et al. 2011).

Under these changes caused by massive tree mortality, it is uncertain what the serotinous cones in aerial seedbanks would experience when fire is used for regeneration. The current FWI System may not provide accurate prescription for fire intensity and behaviour in forests killed by MPB because soil and canopy moisture regime and fuel distribution differ from those of standard fuel type as mentioned earlier; therefore, further study of the fuel in dead stands is required.

Prescribed burning in dead stands based on the information given by the FWI System should be applied with care because of these uncertainties.

1.6. Research Objectives

The impact of MPB outbreak on fire behaviour was studied mainly in terms of fuel moisture content at canopy and surface levels and rate of spread in jack pine stands that were mechanically killed for MPB simulation in Alberta. Serotinous cone opening in response to fire was also compared between healthy and MPB-simulated trees. Cone opening was modeled with char height as a post-fire measurement and a proxy for fire intensity. Factors determining different patterns of serotinous cone opening are discussed in connection with spatial fuel distribution, surface and canopy fuel moisture, and crown bulk density post-MPB simulation. The hypothesis was that cones on MPB-simulated trees would be more susceptible to heat than on healthy trees due to altered fuel conditions in dead stands has been discussed previously in this chapter.

1.7. Thesis Outline

This thesis consists of three chapters. Research background and rationales behind the research objectives are described in Chapter 1.

Chapter 2 contains cone opening pattern between healthy and MPB-simulated jack pine trees was compared as functions of char height, crown base height, tree height, and cone location in the crown layers by fitting nonlinear regression models. Cone opening was related to char height in both healthy and MPB-simulated trees. As we hypothesized, fire induced cone opening more easily in dead trees under similar heat intensity than in healthy trees. There were differences in moisture regime at both canopy and surface levels between healthy and MPB-simulated stands. However, surface fire intensity represented as rate of

spread was not significantly different. Different patterns of cone opening might have been driven by factors at the canopy level. We observed a decrease in crown foliar moisture content after tree death and this could have led to increase in foliar flammability. In addition, canopy fuel loss in dead trees might have provided larger surface area to volume ratio, which suggests less heat and time required for ignition, and more oxygen supply during combustion process in crowns.

Chapter 3 provides conclusion of the research and future work. Our findings suggest that the current FWI System predicted moisture condition of organic layer at early stage of MPB outbreak relatively well, but extensive fieldwork is required to capture a long-term trend in moisture content after MPB outbreak.

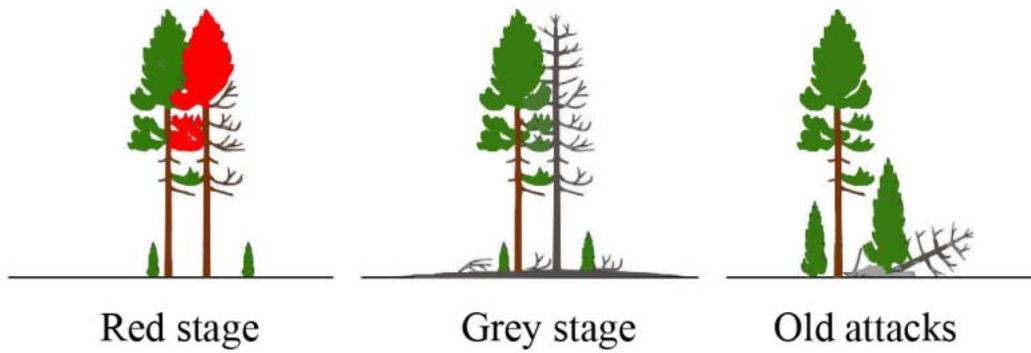


Figure 1. Chronological description of mountain pine beetle attack (adapted from Simard et al. 2011). Red stage begins when needles turn red post-MPB attack. Grey stage is when most of dead needles drop so standing snags look grey in distance. Old attacks are characterized by fall down trees and growth of understory vegetation in the gaps.

2." References

- Abrams, M. D., and D. I. Dickmann. 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. *Canadian Journal of Botany* 60: 946-954.
- Alexander, M. E., and M. G. Cruz. 2012b. Modeling the effects of surface and crown fire behavior on serotinous cone opening in jack pine and lodgepole pine forests. *International Journal of Wildland Fire* 21(6): 709-721.
- Alfaro, R., E. Campbell, and B. Hawkes. 2009. Historical frequency, intensity and extent of mountain pine beetle disturbance in British Columbia. Mountain Pine Beetle working paper 2009-30. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Center.
- Amman, G. D. 1977. Role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession. In: W. J. Mattson (ed) *The Role of Arthropods in Forest Ecosystems*, pp. 3-18. Springer-Verlag, New York.
- Beaufait, W. R. 1960. Some effects of high temperatures on the cones and seeds of jack pine. *Forest Science* 6: 194-199.
- Beck, J. A., and O. B. Armitage. 2001. Diurnal fine fuel moisture characteristics at northern latitude, in Engstrom, R. T., Galley, K. E. M., and de Groot, W. J., *Proceedings 22nd Tall Timbers Fire Ecology Conference: Fire in temperate, boreal, and montane ecosystems*. Kananaskis Village, Alberta, Canada. Tall Timbers Research, Inc., Edmonton, Alberta, Canada [Imperial Printing Ltd.]. pp. 211-221.
- Bond W. J., and B. W. van Wilgen. 1996. *Fire and plants*. London: Chapman and Hall.
- Cameron, H. 1953. Melting point of the bonding material in lodgepole pine and jack pine cones. Canada Department of Resources and Development, Forestry Branch, Silvicultural Leaflet. No. 86. 3pp.
- Chrosciewicz, Z. 1974. Evaluation of fire-produced seedbeds for jack pine regeneration in Central Ontario. *Canadian Journal of Forest Research* 4: 455-457.

- Clements, F. E. 1910. The life history of lodgepole burn forests. USDA Forest Service. Bulletin 79.
- Coates, K.D. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia. *Forest Ecology and Management* 155: 387-398.
- Coops, N. C., M. A. Wulder, 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.
- Crossley, D. I. 1956. Fruiting habits of lodgepole pine. Canada Department of Northern Affairs and National Resources, Forestry Branch, Forest Research Division Technical 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. *Molecular Ecology* 20: 2157-2171.
- Cullingham, C. I., P. M. A. James, J. E. K. Cooke, and D. W. Coltman. 2012. Characterizing the physical and genetic structure of the lodgepole pine × jack pine hybrid zone: mosaic structure and differential introgression. *Evolutionary Applications* 5: 879-891.
- de Groot, W. J. 1987. Interpreting the Canadian Forest Fire Weather Index (FWI) System. 4th Central Region Fire Weather Committee Scientific and Technical Seminar presentation material. Available from: <http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/23688.pdf>
- de Groot, W. J., P. M. Bothwell, S. W. Taylor, B. M. Wotton, B. J. Stocks, and M. E. Alexander. 2004. Jack pine regeneration and crown fires. *Canadian Journal of Forest Research* 34: 1634-1641.
- Environment and Sustainable Resource Development. 2011. Sustainable forest management: current facts and statistics. (On-line Ed). Pub no. 1/605.
- 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.
- Gauthier, S., Y. Bergeron, and J-P. Simon. 1993. Cone serotiny in jack pine: ontogenetic, positional, and environmental effects. *Canadian Journal of Forest Research* 23: 394-401.
- Gauthier, S., Y. Bergeron, and J-P. Simon. 1996. Effects of fire regime on the serotiny level of jack pine. *Journal of Ecology* 84(4): 539-548.
- Hélie, J. F., D. L. Peters, K. R. Tattrie, and J. J. Gibson. 2005. Review and synthesis of potential hydrologic impacts of mountain pine beetle and related harvesting activities in British Columbia. Canadian Forest Service, Mountain Pine Beetle Initiative Working Paper 2005-23. 34 pp.
- 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.
- Hoffman, C. M., C. H. Sieg, J. D., McMillin, and P. Z. Fulé. 2012. Fuel loadings 5 years after a bark beetle outbreak in south-western USA ponderosa pine forests. *International Journal of Wildland Fire* 21: 306-312.
- Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management* 254: 16-34.
- Jolly, W. M., R. A., Parsons, A. M. Hadlow, G. M. Cohn, S. S. McAllister, J. B. Popp, R. M. Hubbard, 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.
- Keeley J.E. 1994. Seed-germination patterns in fire-prone Mediterranean climate regions. In: Arroyo M.T.K., Zedler P.H. and Fox M.D. (eds), *Ecology and Biogeography of Mediterranean ecosystems in Chile, California and Australia*. Springer, Berlin, p. 239–273.

- Kemball, K. J., G. G. Wang, and A. R. Westwood. 2006. Are mineral soils exposed by severe wildfire better seedbeds for conifer regeneration? *Canadian Journal of Forest Research* 36: 1943-1950.
- Klutsch, J. G., J. F. Negrón, S. L. Costello, C. C. Rhoades, D. R. West, J. Popp, 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.
- Knapp, A. K., and J. E. Anderson. 1980. Effect of heat on germination of seeds from serotinous lodgepole pine cones. *American Midland Naturalist* 104(2): 370-372.
- Kramer, P.J., and T.T. Kozlowski. 1960. Fats, oils, terpenes, and related substances. In *Physiology of trees*. McGraw-Hill, New York. pp. 140–158.
- Lamont, B. B., D. C. Le Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. *The Botanical Review* 57: 277-317.
- Lee, S. W. 2006. *Fungi associated with the mountain pine beetle, Dendroctonus ponderosae*. Ph. D. Thesis, University of British Columbia, British Columbia, Canada.
- Lotan, J. E. 1964. Regeneration of lodgepole pine: a study of slash disposal and cone opening. USFS. Research Note INT-16. 4 pp.
- Lotan, J. E. 1975. The role of cone serotiny in lodgepole pine forests. pp. 471-495 in D. M. Baumgartner, editor. *Management of lodgepole pine ecosystems: symposium proceedings*. Washington State University Cooperative Extension Service, Pullman, Washington, USA.
- Lotan, J. E. 1976. Cone serotiny – fire relationships in lodgepole pine. In: *Tall Timbers Fire Ecology Conference Proceedings 14*, Tall Timbers Research Center, Tallahassee, FL. pp. 267-287.
- Mason, D. T. 1915. The life history of lodgepole pine in the Rocky Mountains. USFS Bulletin 154.

- 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.
- Mountain Pine Beetle in Alberta website (<http://mpb.alberta.ca/>)
- Muir, P. S., and J. E. Lotan. 1985. Disturbance history and serotiny of *Pinus contorta* in Western Montana. *Ecology* 66(5):1685-1668.
- Natural Resources Canada website (<http://cfs.nrcan.gc.ca/pages/49>)
- Page, W., and M. J. Jenkins. 2007. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. *Forest Science* 53(6): 662-674.
- Page, W. G., M. J. Jenkins, and J. B. Runyon. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Canadian Journal of Forest Research* 42: 1631-1647.
- Radeloff, V. C., D. J. Mladenoff, R. P. Guries, 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.
- Reid, M. 2001. Can we share the forest with mountain pine beetles? *Wild Lands Advocate* 9(4): 6-7.
- Romme, W. H., J. Clement, J. Hicke, D. Kulakowski, L. H. MacDonald, T. L. Schoennagle, and T. T. Veblen. 2006. Recent forest insect outbreaks and fire risk in Colorado forests: a brief synthesis of relevant research. Colorado State University: Colorado Forest Restoration Institute.
- Rudolph, T.D., and P.R. Laidly, 1990. *Pinus banksiana* Lamb., Jack Pine, pp. 280-293. In R.M. Burns and B.H. Honkala (eds.), *Silvics of North America, Vol. 1, Conifers*, USFS. Agricultural Handbook 654, Washington, D.C.
- Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. In *Proceedings of a Symposium: Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. April 25–27, 1978. Pullman, Washington. Edited by D.L. Kibbee, A.A. Berryman, G.D. Amman, and R.W. Stark. University of Idaho, Moscow, Idaho. pp. 77–84.

- Safranyik, L. A. L. Carroll, J. Régnière, D. W. Langor, W. G. Riel, T. L. Shore, B. Peter, B. J. Cooke, V. G. Nealis, and S. W. Taylor. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist* 142: 415-442.
- Schoenike, R. E. 1976. Geographical variations in jack pine (*Pinus banksiana* Lamb.), Tech. Bull. 304, Agr. Exp. Sta., Univ. of Minn., St. Paul, MN. 47 pp.
- Schwilk, D. W., and D. D. Ackerly. 2001. Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94(2): 326-336.
- 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? *Ecological Monographs* 81(1): 3-24.
- Teste, F. P., V. J. Lieffers, and S. M. Landhäusser. 2011a. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. *Ecological Applications* 21(1):150-162.
- Thomas, P. A., and R. W. Wein. 1985. Delayed emergence of four conifer species on postfire seedbeds in eastern Canada. *Canadian Journal of Forest Research* 15: 727-729.
- Tower, G. E. 1909. A study of the reproductive characteristics of lodgepole pine. In *Society of American Forestry. Proc.* 4: 84-106.
- Turner, J.A., and B.D. Lawson. 1978. *Weather in the Canadian Forest Fire Danger Rating System: a user guide to national standards and practices.* Environment Canada, Pacific Forest Research Centre, Victoria, BC. BC-X-177.
- Vaartaja, O. 1954. Temperature and evaporation at and near ground level on certain forest sites. *Canadian Journal of Botany* 32: 760-783.
- Van Wagner, C. E. 1974. *Structure of the Canadian Forest Fire Weather Index.* Department of the Environment, Canadian Forestry Service, Publication No. 1333. 39 pp.

- 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., C. Ferguson, D. J. Huggard, J. Roach, and B. Zimonick. 2009. Regeneration beneath lodgepole pine dominated stands attacked or threatened by the mountain pine beetle in the south central Interior, British Columbia. *Forest Ecology and Management* 258S:S36-S43.
- Wotton, B. M. 2009. Interpreting and using outputs from the Canadian Forest Fire Danger Rating System in research applications. *Environmental and Ecological Statistics* 16(2): 107-131.
- Wright, E. 1931. The effect of high temperatures on seed germination. *Journal of Forestry* 29(5): 679-687.
- Wulder, M. A., S. M. Ortlepp, J. C. White, T. Nelson, and N. C. Coops. 2010. A provincial and regional assessment of the mountain pine beetle epidemic in British Columbia: 1999-2008. *Journal of Environmental Informatics* 15(1): 1-13.

Chapter 2

1." Introduction

Pine, mountain pine beetle (*Dendroctonus ponderosae*, MPB), and forest fire are a trio of stand development in North American forest ecosystems (Amman 1977, Jenkins et al. 2012). MPB kills large living pine trees and alters fuel distribution in the forests. Increased fire intensity due to accumulation of snags and fine fuels on the surface after MPB outbreaks is able to successfully eliminate competing tree species in pine stands (Brown 1975) and aid the next cycle of pine-dominant ecosystems (Amman 1977: in the second paragraph on page 14).

In modern times, we are dealing with the legacy of old forest management policies including fire suppression and exclusion that have resulted in old and homogenous forests (Samman and Logan 2000). Furthermore, the gradual shift from cold to moderate winters in western Canada has failed to control MPB population size (Bentz et al. 2010, Cullingham et al. 2011). Consequently, MPB population has successfully developed into epidemic levels and invaded novel habitats in high elevation areas such as northern British Columbia and north western Alberta (Bentz et al. 2010, Cullingham et al. 2011).

Alberta pine forests are at the center of attention because lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*) are co-existing and there is a broad zone of hybridization due to genetic similarity between two species (Rudolph and Laidly 1990). One of the issues involved in pine regeneration post-MPB outbreaks on the landscape level is that most of lodgepole pine and jack pine in Canada are serotinous populations that produce closed cones and rely on stand-replacing fire for killing competing species, opening serotinous cones, and providing seedbeds, thereby re-occupying the burned area (Amman 1977, Radeloff et al. 2004). When MPB outbreaks occur in a serotinous pine population, standing dead trees will retain closed cones in aerial seedbanks for a long period of time. Delayed stand development without disturbance would directly impact wood supply and the economy in the long term; therefore, it is

likely that human-induced disturbance will be necessary to re-establish these forests in an acceptable time.

Prescribed burning is thought to be appropriate for pine forest regeneration for two reasons: a) seedbed preparation (i.e., to expose mineral soils); and b) to provide a heat source (i.e., at least 50°C is required for opening serotinous cones). A high intense crown fire with long flame residence time and high flame temperatures would generate high temperature that might directly touch cones in the canopy and overheat the seed to eliminate viability. On the other hand, a low intense surface fire that does not develop as a crown fire or not generate enough heat to the air would fail to open cones in the canopy. Besides, low intense fire may not be able to expose mineral soils for seed germination. Cone opening occurs through three heat transfer processes: convection, radiation, and conduction (Johnson and Gutsell 1993, Alexander and Cruz 2012b). Intense surface fire alone may be hot enough to open cones in aerial seedbanks through convection and radiation processes (Eyre 1938). If the flame length is long enough or there are ladder fuels (i.e., understory vegetation, overstory with lower branches, lichen on the stem, flaky barks) that can carry surface flames to the crown, surface fire may develop into a crown fire. In this case, cones are not only exposed to heat generated from the surface fire, but also to direct flames. Cone opening will occur differently depending on fine fuel availability and its flammability, i.e., moisture content and chemical properties (Jolly et al. 2012); since crown fires mostly consume fine fuels such as needles (Despain et al. 1996).

Lodgepole pine and jack pine are well-known as fire-dependent species; however, fire should be applied with care and a thorough understanding of when it can be used for regeneration. MPB-killed forests are different from healthy pine forests in two ways: moisture regime and fuel distribution at both the ground and canopy level. The lack of water uptake by dead trees leads to increased available moisture in soils, contrarily decreased moisture content in aerial fuels. Although there is no change in total available fuels, dead trees shed aerial fine fuels to the ground within the first few years, resulting in increased surface fuel

loading and fire intensity (Mitchell and Preisler 1998, Romme et al. 2006, Jenkins et al. 2008, Klutsch et al. 2009, Simard et al. 2011).

Most of recent studies on fire behaviour in MPB-killed forests have been conducted in the U.S. where development of a thick organic layer on the forest floor and its role in fire behaviour are not a big concern (Page and Jenkins 2007, Simard et al. 2011). Prescribed burn programs in the U.S. are carried out based on the National Fire Danger Rating System (NFDRS) which focuses on moisture content in fuels of different particle sizes on the forest floor. The impact of MPB outbreaks on fire behaviour in Canadian boreal forests, however, could be more complicated than it was thought because of the presence of thick organic layers on the forest floor. In contrast to the NFDRS or fire behaviour prediction models (i.e., NEXUS, BehavePlus) in the U.S., the Canadian Forest Fire Weather Index System focuses on moisture content in organic matters of the forest floor. There has been little study on the change in moisture regime, specifically at the forest floor level, its interaction with change in fuel loading at surface after massive tree mortality, and its combined impact on fire behaviour in Canadian boreal forest ecosystems. Intense crown fire is a common fire regime in jack pine forests (Flannigan and Wotton 1994, de Groot et al. 2004), but MPB-killed forests will experience somewhat different fire behaviour from healthy jack pine forests and it can be discussed at two scales in the Canadian boreal forests: 1) surface fire behaviour: increased fuel moisture in the forest floor would compensate for increased fire hazard post-MPB outbreaks; and 2) crown fire behaviour: MPB-killed trees would be prone to crowning due to decreased crown foliar moisture and bulk density.

In fire ecology, fire intensity is a term indicating the heat energy generated during combustion processes (Keeley 2009). Direct measurement of fire intensity is often a challenge; thus, other indirect measurements to estimate fire intensity (e.g., flame height, flame length, crown scorch height, char height) have been studied extensively (Van Wagner 1973, 1977, Alexander 1982, Alexander and Cruz 2012a, b). Flame height, vertical length of flame, and flame length, “the distance from the ground at the leading edge of the flame to tip of the flame”

<http://www.firewords.net/>, are not easy to measure because of the nature of burning flames and the difficulty of instrumentation as well discussed by Alexander and Cruz (2012a). On the other hand, crown scorch height and char height are easier to measure post-fire. Crown scorch height is defined as the height of discolored needles by heat or direct flame touch. Crown scorch height is well-correlated to fire intensity (Van Wagner 1973). Also, char height which is the maximum height of charring on the stem is used to estimate fire intensity (Weber et al. 1987).

We hypothesized that fire would induce cone opening more easily in dead trees than in living trees based on previous knowledge. The objectives of the study were: a) to evaluate char height as a surrogate for fire intensity in relation to cone opening; and b) to assess the pattern of cone opening between living and dead stands when burned with different levels of fire intensity.

2." Materials and Methods

2.1. Study Area

The study area was located at Archer Lake, about 165 km northeast of Fort McMurray (58°07' latitude, 110°15' longitude) Alberta, Canada (Fig. 2). The area was dominated by live jack pine (*Pinus banksiana* Lamb., 90% of stems) with a mean diameter at breast height (DBH) of 9.4 cm (SD \pm 2.3 cm), mean height of 8.8 m (SD \pm 1.8 m) and 10% black spruce (*Picea mariana* (Mill.) B.S.P.). Jack pine had a mean DBH of 9.2 cm (SD \pm 1.8 cm), a mean height of 8.6 m (SD \pm 1.2 m). There was no evidence of the recent wildfire in this area (average stand age of 70). The forest floor was covered mostly by lichens (*Cladonia rangiferina*, 70-80% cover), and blueberry (*Vaccinium myrtilloides* Michx.) and bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.) were the dominant understory vascular plants. The topography was generally flat. Soil type was classified as eluviated eutric and dystic brunisols (Alberta Agriculture and Rural Development; [http://www1.agric.gov.ab.ca/\\$department/deptdocs.nsf/all/agdex10307](http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex10307)).

2.2. Experimental Design

Study plots (ranging from 0.12 ha to 4 ha) were laid out in May 2007. Each plot was divided into two subplots and the eastern half was treated, leaving the other half as the control. Originally, 10 plots were established but only 4 of them were used in this study (Table 1). Trees in treated subplots were girdled at breast height in May 2007, aiming for >90% mortality of trees. Girdling simulates MPB attack by stopping translocation of nutrients from crown to roots and causes a gradual death of trees similar to that is caused by the mountain pine beetle galleries attacking the phloem (Miller and Berryman 1986). Girdling, however, does not have the blue-stain fungus attacking the sapwood so there may have been some transpiration for some period after girdling. By the July of 2009, the girdled

trees had dead foliage similar to the “red-stage” of MPB attack; this is the stage when needles turn red and are low in moisture content.

2.3. Prescribed Burns and Data Collection in 2009

In July 2009, 2 years after the girdling treatment, prescribed burns were initiated with 30m of ignition line installation in each plot, ignited with handheld drip torches. The direction of burn and the location of ignition line were decided based upon the weather conditions each day to not direct the fire into designated study areas. The burns were carried out as paired burns; i.e. pairs of control and MPB-simulated subplots were burned at the same time to compare fire behaviour under similar burn conditions. In-fire cameras were placed to assess fire behaviour as well as the rate of spreads in each plot. More information on prescribed burn can be found in Schroeder and Mooney (2012).

An on-site fire weather station recorded air temperature (°C), 24-h precipitation (mm), relative humidity (%), wind speed (km/h), and wind direction on an hourly basis. These weather variables were used for calculating both numeric values of moisture content of forest floor and fire behaviour indices using the Canadian Fire Weather Index System (Van Wagner 1974, 1987; FWI). FWI System provides numerical values that can be used for estimation of moisture content in each fuel layer (i.e., surface litter and twig (<0.5 cm in diameter), loosely compacted organic matter (fermentation layer), deep and compacted organic matter (humus layer)). Sub-indices such as Initial Spread Index (ISI), Buildup Index (BUI), and FWI (Fire Weather Index) are derived from the interaction between weather variables and fuel moisture and used for fire behaviour. In this study, we only presented FFMC, DMC, ISI, and FWI in the results (Table 1; see Appendix C for ISI chart).

Samples of foliage and forest floor were also taken from each plot to compare the difference in moisture content between control and MPB-simulated plots and to capture the moisture condition at the time of burning. Foliar samples

were randomly collected from 5 trees per subplot using pruning shears immediately before the prescribed fire (n=38 each for living and MPB-simulated trees). Forest floor samples (i.e., litter, organic matter) were taken at 5 m-interval on each ignition line (30-m long) immediately prior to prescribed burning. Needle litter from the forest floor was sampled from the surface and organic layer had a mean of 2.5cm deep (SD ±1.7; recalculated based on their field note, previously it was based on their report and I assume that they averaged litter+duff layer, n=34 each for living and MPB-simulated plots). Organic layer was collected from 30 × 30cm square (n=35 each for living and MPB-simulated plots). Samples were sealed, transported, weighed ('wet' weight), and then oven-dried at 100°C for 24 hours and 'dry' weight was measured to calculate gravimetric moisture content (Eq. 1).

$$\text{Fuel moisture content (\%)} = \frac{\text{Wet weight (g)} - \text{Dry weight (g)}}{\text{Dry weight (g)}} * 100 \quad (\text{Eq. 1})$$

Measured fuel moisture content for the forest floor from Eq. 1 was then compared with estimated fuel moisture content by FWI; i.e., lichen, needle litter on the surface for Fine Fuel Moisture Code (FFMC; Eq. A1 in Appendix A; see Literature review in Chapter 1 of this thesis or Van Wagner 1987 for further information), organic matter for Duff Moisture Code (DMC; Eq. A2 in Appendix A) in order to compare the measured and estimated fuel moisture content at each disturbed area. Also measured fuel moisture content was compared between MPB-simulated and control subplots. FFMC and DMC used in moisture content analysis were taken at 1300 MDT of each day of prescribed burning.

2.4. Data Collection in 2012

The site was revisited in the August 2012, 3 years after the prescribed burns. In order to capture well-distributed data, on a wide range of fire intensities, trees with a range of different char height (ranging from 0 to 10m) were selected across the four burn areas (control with burn sample size $n=34$, control with no burn $n=5$, MPB-simulated with burn $n=32$, MPB-simulated with no burn $n=5$). Trees that were dominant/co-dominant, with crown not touching neighboring crowns, and average char height relative to surrounding trees were selected, and cut down with a chainsaw; its GPS location was also marked. Tree height, DBH, height to crown base (CBH), and char height (CHT) were obtained afterwards. Crown scorch height is useful to estimate fire intensity by visually distinguishing height of heated crown (Van Wagner 1977, Alexander and Cruz 2012a); however, we did not measure crown scorch height because it was 3 years after the prescribed burning and it was not clear whether discoloration of foliage was due to burning or MPB simulation treatment. Crown length was divided equally into three layers to analyze cone opening pattern depending on the cone's location in the canopy in relation to char height between healthy and MPB-simulated trees. Cones from the five youngest cohorts were counted and recorded as either open or closed for each crown layer. Cohort was estimated from bud scale scars on the twigs.

2.5. Statistical Analysis

2.5.1. Fuel Moisture Content

FWI-predicted moisture content for litter and organic layers were compared to measured moisture content for corresponding layers to evaluate the reliability of the FWI System in MPB-killed forest fuel type. Measured moisture content was further compared between control and MBP-simulated plots using Student's t test after logarithmic transformation of data to evaluate the MPB simulation treatment effect on moisture content. If the assumptions for Student's t test (i.e., normality,

equal variance) were not satisfied, then we employed alternative t tests: Kolmogorov-Smirnov test for non-normal and differently distributed data; Welch's t test for normal, but unequal variance data.

2.5.2. Cone Opening as a Function of Char Height

2.5.2.1. Char Height Location

Cone opening data were grouped depending on char height location: i.e., char height < CBH was classed as surface fire; CBH < char height < tree height was classed as scorched; tree height = char height (i.e., flame height most likely exceeded tree height) was classed as crowning in further comparisons. Re-grouped cone opening was analyzed using Student's t test to compare differences in cone opening between trees in control and MPB-simulated plots.

2.5.2.2. Regression Analysis

Cone opening in relation to char height was modeled by a nonlinear regression model in R (R Core Team 2012; version 2.15.2) using 'nls' function (library "nls2" and "proto" for finding starting values of the parameters). Nonlinear regression was selected because residual plots of data transformations (i.e., logarithmic, square root transformation) indicated nonlinearity in the model. A power function and logistic function were used for curve fitting procedures for control and treatment, respectively (Eq. 2, 3):

$$y = \frac{a}{1 + \exp(b - c * x)} \quad (\text{Eq. 2})$$

$$y = ax^b \quad (\text{Eq. 3})$$

where y is cone opening, x_i is independent variable, and a, b, c are parameters.

2.5.2.3. Variable Selection

Other possible variables such as CBH, tree height, standardized char height to CBH, standardized char height to tree height, and crown length (tree height – CBH) were also considered in possible models for cone opening. Standardized char height to CBH or to tree height was obtained using Eq. 4:

$$CHT_{STDZ} = \left(\frac{CHT}{x} \right) * 100 \quad (\text{Eq. 4})$$

where x is CBH or tree height. Eq. 4 was employed to take the effect of CBH or tree height on cone opening into account. Pearson's product-moment correlation coefficient was applied in this procedure.

3." Results

3.1. The Impact of MPB Simulation on Fuel Moisture Regime

The fine fuel moisture content at the research site was generally higher than FWI-predicted moisture content derived from the standard FFMC model (Eq. 1 for measured moisture content, Eq. A1 in Appendix A for predicted fine fuel moisture content; Fig. 3a, Fig. 4a). The standard DMC model did not well explain the measured moisture content in control plots, yet it fitted the increased moisture content in MPB-simulated plots relatively well (Fig. 3b).

There was no big difference in measured fine fuel moisture content between control and MPB-simulated plots (Kolmogorov-Smirnov test $p=0.67$, Fig. 4a). Increase in moisture content at organic layer was observed in MPB-simulated plots (Student's t test $p<0.05$, Fig. 4b). At canopy level, green needles from the healthy stands had 5 times as much moisture as the red needles in MPB-simulated stands (Fig. 4c, Table 1; Welch's t test $p<0.05$).

3.2. Fire Behaviour Characteristics Between Living and Dead Stands

The impact of MPB simulation on surface fire behaviour seemed minor (Table 1, Fig. C1 in Appendix C). There was no significant difference in terms of rate of spread (m min^{-1} ; ROS) at the surface level between control and MPB-simulated plots (Fig. C1 in Appendix C).

The critical surface fire intensity and flame length required to promote crowning combustion was estimated using Van Wagner (1977)'s crown fire initiation model (Fig. 5, 6; see Eq. B1 & B2 in Appendix B). This model projected that crowning needed higher critical surface fire intensity and flame length in living trees than in dead trees. In other words, it was expected through figure 5 and 6 that crowning could start much earlier in dead trees than living trees.

3.3. Cone Opening as a Function of Char Height

There was no significant difference found in char height within the same fire type between living and dead trees (Student's *t*-test $p > 0.05$), except for surface fire category ($p = 0.003$; Fig. 7). Crown base height or tree height within the same categories was not significantly different ($p > 0.05$). Surface fire category had a mean char height of 1.8 m (SD ± 0.78) for living trees and 3.88 m (SD ± 1.95) for dead trees, scorching category had a mean char height of 7.15 m (SD ± 1.42) and 7.28 m (SD ± 1.6), and crowning category had a mean char height of 10.38m (SD ± 0.71) and 11.04 m (SD ± 1.16); (The definition on crowning in this research was char height was equal to the tree height or seemed to exceed the tree height, so yes it was the mean height of the trees that fell into crowning category). There was more cone opening with low intensity fires on dead trees than living trees ($p = 0.0002$; Fig. 7b). Cones where char height did not exceed CBH were mostly still closed in living trees (Fig. 7a; see surface fire), whereas cones found in dead trees were mostly open by low intensity fire (Fig. 7b; see surface fire). Cones in scorching category also showed higher cone opening success in dead trees compared to those in living trees (Fig. 7a and 7b; see scorched) (Student's *t*-test $p = 0.003$).

When char height was below CBH, most cones were opened in the bottom third of the crown as char height increased, while cones at upper crowns still remain closed (Fig. 8a). In contrast, most of the cones at lower crowns were open and there were substantially more cones open in the upper layers of the crown compared to living trees with 1-3 m of char height (Fig. 8b). When char height exceeded CBH, cones in the bottom layer of the crown were generally nearly 100% opened in both living and dead trees (Fig. 9a and 9b).

3.4. Cone Opening Model

3.4.1. Variable Selection

Cone opening was well correlated with char height in both living ($r=0.77$, $p<0.05$) and MPB-simulated trees ($r=0.50$, $p<0.05$; Table 2). In living trees, CBH ($r=0.08$, $p=0.7$), tree height ($r=-0.17$, $p=0.4$), and crown length ($r=-0.33$, $p=0.09$) did not significantly explain cone opening. However, those predictor variables were fitted with cone opening using nonlinear regression models as covariates between individual trees and the results were presented in Appendix D. Dead trees had insignificant negative relationship with CBH and tree height ($r=-0.24$, -0.25 for CBH and tree height, respectively), but char height alone was a good predictor variable because of the nature of the dead trees data and covariates did not change the relationship between cone opening and char height much. Therefore, char height was chosen as an independent variable for cone opening un dead trees.

Cone opening was highly correlated with standardized char height to CBH ($r=0.67$, $p<0.05$ for living, $r=0.54$, $p<0.05$ for dead trees; Eq. 4 used) and standardized char height to tree height ($r=0.80$, $p<0.05$ for living, $r=0.56$, $p<0.05$ for dead trees; Eq. 4 used). However, the relationship between char height and standardized char height to CBH or tree height was significantly correlated to each other (standardized char height to CBH: $r=0.90$ for living and 0.92 for dead, ($p<0.05$), standardized char height to tree height: $r=0.98$ for living and 0.95 for dead ($p<0.05$)). These strong correlations mean that char height standardization that was employed to take the impact of different crown characteristics among individual trees into account was not necessarily needed in the cone opening model.

3.4.2. Cone Opening Modeled with Char Height

Cone opening was related to char height (CHT), and the relationship was best fit by a nonlinear model (Fig. 10). The obtained model equations were as below:

$$Cone\ opening_{LIVING} = \frac{80.5563}{1 + \exp(5.9556 - 1.1795 * CHT)} \quad (Eq. 5)$$

$$Cone\ opening_{DEAD} = 40.8181 * CHT^{0.3923} \quad (Eq. 6)$$

In living trees char height needed to be quite high before there was a steep increase in cone opening (see empty circles and solid line in Fig. 10, Eq. 5). Data from dead trees were fitted with 5 different simple nonlinear models and the model fitted with power function was the best according to goodness-of-fit, i.e., AIC (broken line on Fig. 10; for detail, see Table D1-b in Appendix D).

Overall, cones in dead trees were more likely to open by relatively low intensity fire with low char height compared to those in living trees but there was much greater variation in dead tree; it appears that in some trees, cones were opened by relatively low fires, while in another group opening only occurred with higher char height similar trend to cone opening in living trees (solid circles in Fig. 10).

4." Discussion

4.1. Cone Opening Between Healthy and Recently Dead Jack Pine

Char height, as a substitute for fire intensity, was related to cone opening in both healthy and dead trees (Fig. 7-10). Interestingly, our results suggest that there was greater opening of cones with only moderate char height on dead trees. Cones on dead trees tended to open higher in the crowns compared to healthy trees of the same char height range (Fig. 7-10). Convection and radiation heat is the key factor to cone opening in aerial seedbanks. First of all, surface fuel conditions such as fuel loading and fuel moisture determine the amount of heat generated towards the atmosphere. We observed no significant difference in moisture content of fine fuels on the forest floor between control and MPB-simulated plots, but moisture content in the organic layers was higher in MPB-simulated plots than in control plots (Fig. 3, 4). Though we did not quantify the fine fuel loading on the forest floor as a result of MPB simulation treatment prior to burning, it was reported that accumulation of dead needles on the forest floor was observed 2 years after the MPB simulation (Schroeder and Mooney 2012). However, the increase in surface fuel loading in MPB-simulated plots was thought to have been offset by increased moisture content in the organic layer because fire behaviour observation (i.e., fire rate of spread) was not significantly different between control and MPB-simulated plots at the surface level in this study (see Fig. C1 in Appendix C or refer to Schroeder and Mooney 2012 for more information). This implies that fuel conditions at the canopy level hold the key to explaining the different pattern in cone opening between healthy and dead trees. Van Wagner (1977)'s crowning initiation model showed the different energy required to start crowning combustion between healthy and dead trees mainly because of lower crown foliar moisture in dead trees (Fig. 5, 6; Eq. B1, B2 used in Appendix B). Moisture content plays a critical role in crowning initiation and it would explain the different likelihood of crowning initiation between healthy and dead trees (see crown foliar moisture between control and MPB-simulated plots described in Table 1, Fig. 4c). Consistent with Van Wagner's

models (Fig. 5, 6), our results showed that cone opening on dead trees occurred relatively easily (Fig. 7, 8).

4.2. Factors Involved in Cone Opening in Dead Trees

We hypothesized that cone opening on dead trees would be induced much more easily due to increased flammability of aerial fuels. Flammability of aerial fuels after MPB outbreak increases through three mechanisms: a) lowered or arrested transpiration system (i.e., lower foliar moisture content, more environmental-driven moisture regime on dead needles) (Jolly et al. 2012, Page et al. 2012); b) decomposition (i.e., increases in relative proportion of fiber carbohydrates (i.e., lignin, cellulose, hemicellulose) and decreases in proportion of crude fat (i.e., waxes, oil, resins)); and c) a decrease in crown bulk density from the loss of needles (Simard et al. 2011, Hoffman et al. 2012). Not only do the chemical properties influence foliar flammability, but also structural change in needles may impact flammability (Page et al. 2012). Unlike green needles with cylindrical shape, needles become flatten after tree mortality; thereby increasing surface area to volume ratio (Page et al. 2012). In addition, MPB-killed trees shed dead needles, resulting in a decrease in crown bulk density which allows more oxygen supply during crown combustion (Schwilk and Ackerly 2001). Again, low crown bulk density in dead trees has higher surface area to volume ratio which takes a shorter time to ignite compared to healthy trees. Further, we suggest that cones covered with green and moist needles were protected from direct exposure to the heat (i.e., convection and radiation from the fire; Schwilk and Ackerly 2001). As a consequence, more heat may be required to ignite the moist living crowns and to open serotinous cones on living trees compared to that required for dead trees with drier aerial fuels (Bond and van Wilgen 1996, Schwilk and Ackerly 2001). Thus, cones on dead trees with increased flammability in crowns were more susceptible to exposure to heat with a similar range of char height as living trees (Fig. 7-10). Cone opening in aerial seedbanks could also be influenced by ladder

fuels such as shrub or overstory species that have lower branches capable of carrying flames to the canopy. Black spruce was present as ladder fuels in the research site; however, we did not find the effect of the ladder fuels on the great cone opening with low heat on MPB-simulated trees in Fig. 10. Jack pine trees with the great cone opening were mostly from 3T, but there was no black spruce found through vegetation inventory that might have influenced cone opening on those trees (Table E1 in Appendix E). Finally, given that dead trees are more likely to be charred by a given amount of heat, it is likely that we are underestimating the impact of fire on cone opening in dead trees. Therefore, we can state that fire would induce cone opening more easily in MPB-killed trees.

4.3. Reliability of the Current FWI System

The foregoing literature review about the impact of MPB outbreak on fire behaviour underscores the increase in fire hazard and intensity (i.e., rate of spread) after MPB (Page and Jenkins 2007, Jenkins et al. 2008, Simard et al. 2011). Of the prominent concerns, an increase in fire intensity in MPB-killed forests is the most significant issue with regard to application of prescribed burning for pine regeneration. That is, fire should be hot enough to prepare suitable seedbed and open the cones in the canopy, but not too hot to damage the aerial seedbanks. There has been some calibration work done to improve the current FWI System in various regions (Lawson et al. 1997, Wilmore 2001, Wotton et al. 2005, Beverly and Wotton 2007). Lawson et al. (1997) proposed a localized DMC model for Southern Yukon lodgepole pine/white spruce (*Picea glauca*) stand with reindeer lichen (*Cladonia* spp.) fuel type and it seemed to predict moisture content in MPB-simulated plots better than the standard DMC model at the research site (Fig. 3b). Wotton et al. (2005) improved the current DMC model for sheltered fuel type such as organic layer near tree bole where the amount of rainfall reached at surface and bulk density are different from less sheltered fuel type that the standard DMC represents. Sheltered DMC model

predicted similar moisture content to measured moisture content in MPB-simulated plots (Fig. 4b). Compared to the standard DMC, sheltered DMC model provided lower moisture content estimation, but suggested higher moisture content than Lawson's DMC model for our research site (Fig. 4b). However, the data shown was restricted to the early stage of MPB outbreak (i.e., prescribed burning was carried out 2 years since MPB simulation) and was not able to provide the seasonal or time-since-MPB outbreak changes in duff moisture. There may be a need for a specified model to apply fire in MPB-killed forest; this is especially so in the Canadian boreal forests, where a thick feather moss layer is prominent and able to contain moisture during drought periods. Therefore, more work should be done to take into account the increase in duff moisture content under MPB outbreak conditions since moisture is the key factor determining the amount of heat required in ignition and the rate of propagation.

Exposed mineral soil is regarded as a suitable seedbed for pine regeneration (Nyland 1998, BC Ministry of Forests 2001). The magnitude of duff consumption is a function of duff moisture content (i.e., heat required to start ignition), bulk density (i.e., surface area to volume ratio), and depth of duff (i.e., available fuel) (Miyaniishi and Johnson 2002). Therefore, increase in duff moisture content under overstory mortality may slow fire ignition and sustainability at the surface and but still leave fairly thick organic layer for pine roots to reach mineral soils. However, as the impact of MPB outbreak progresses over time, decrease in canopy closure and increase in solar radiation arriving at the surface are expected to influence moisture regime of the surface; i.e., drying out of litter as well as duff layer. All the complexity of MPB outbreak in Canadian boreal forests should be quantified and reflected in the current FWI System in order to provide accurate prescription for proper seedbed preparation purpose.

4.4. Application of Fire in MPB-killed Forests

Our findings suggest that moderate intensity fire could open cones fairly well in dead trees; however, it is still a concern that massive loss of cones in active crown fires will reduce seed availability and seedling recruitment (de Groot et al. 2004), especially in dead trees. Jack pine is a fire-adapted species that is mostly propagated by stand-replacing fires. Fine fuels in the crowns (i.e., needles, twig) are readily consumed in the crown combustion process (Stocks 1987, 1989). de Groot et al. (2004) reported that seed rain in serotinous jack pine forests after crown fires was mostly from the upper canopy, meanwhile cones at the bottom of the crown which were directly exposed to the flame and heat were consumed and not able to provide viable seeds for the stand re-development. Another issue with use of fire in MPB-killed forests is increased flammability of aerial fuels. Dead fine fuels in the canopy are more flammable, but sparsely distributed; therefore, lack of fuel connectivity between trees may not support active crown fire (Page and Jenkins 2007, Schroeder and Mooney 2012). More importantly, closed cones after MPB outbreaks are thought to have good viability for 15 or more years after cone production (Teste et al. 2011b); thus, burning may need to be accomplished before this decline.

4.5. Limitation of Using Char Height as a Proxy for Fire Intensity

Cone opening had a nonlinear relationship with char height (Fig. 10); however, it was not feasible to estimate fire intensity based on char height information using available equations (Van Wagner 1977, Alexander 1982, Alexander and Cruz 2012a, b) due to lack of data (i.e., fuel loading, crown scorch height, fire residence time, flame angle) and limit of model assumptions (i.e., Weber et al.'s (1987) fire intensity equation using char height tended to be overestimates when char height exceeds the 0.3-2.0m range). Fire intensity at the crown level could be quantified using allometric equations (Schneider et al. 2008) after adjusting for

the decrease in fine fuel loading in the dead canopy (i.e., estimated foliage mass was multiplied by a constant based on the amount of dead needles present in the canopy; lodgepole pine in Simard et al. 2011), but fall rate and needle loss in jack pine forests after MPB attack requires further research.

Table 1. Weather information and Fire Weather Indices (taken at 1300 MDT) of the study plots at Archer Lake in 2009. FFMC, ISI, and FWI, which provides information on fire intensity (i.e., moisture content, rate of fire spread, surface fire intensity), were also recorded hourly and those for the time of burning were given in the brackets on the table.

Plot ID	Burn Time	Temp. (°C)	Wind (km/h)	Rain (mm)	Relative Humidity (%)	Crown foliage Moisture (%) (Mean±SD)		ROS ¹ (m/min)		FFMC (Hourly FFMC)	DMC	ISI (Hourly ISI)	FWI (Hourly FWI)	Fire Type ²	
						Dead	Living	Dead	Living					Van Wager/	FBP
3	July 26 16:11	24	12	0	35	19±3.4	174±24.9	4.0	4.0	91.1 (88.8)	36	7.9 (6.6)	20 (17.5)	Passive/ Intermittent	
4	July 27 11:34	22	6	0	35	8±2.4	234±28.1	3.0	3.0	91.2 (85.6)	40	7.2 (3.1)	19.5 (9.7)	Surface/ Surface	
5	July 27 15:09	23	5	0	31	17±2.1	139±11.9	2.6	3.1	91.2 (87.9)	40	7.2 (4.1)	19.5 (12.7)	Surface/ Surface	
6	July 28 12:22	21	10	0	37	16±3.3	139±39.6	6.5	8.8	90.9 (86.5)	43	8.9 (4.8)	23.5 (14.9)	Passive/ Intermittent	

Data provided by Alberta Environment and Sustainable Resource Development and FPInnovations.

¹ Rate of spread measured by in-fire cameras.

² Van Wagner suggested 4 criteria for fire types (surface, passive crown, active crown, and independent crown fire), whereas Canadian Forest Fire Behaviour Prediction System has 3 fire types (surface, intermittent crown, continuous crown fire). Fire types were determined by fire behaviour specialists using on-site assessments (e.g., canopy fraction burned in percent) as well as photographs and video footage.

Table 2. Correlation matrix among tree and cone-opening variables (Pearson’s product-moment correlation)

A. Living trees

Variable	Cone opening	CBH	Height	Char height	Crown Length	*STDZ _{h_c} CBH	**STDZ _{h_c} height
Cone opening	1	0.08 (0.7)	-0.17 (0.4)	<i>0.77 (<0.05)</i>	-0.33 (0.09)	<i>0.67 (<0.05)</i>	<i>0.80 (<0.05)</i>
CBH		1	<i>0.42 (<0.05)</i>	0.19 (0.3)	-0.50 (<0.05)	-0.16 (0.4)	0.12 (0.5)
Height			1	0.07 (0.7)	<i>0.38 (<0.05)</i>	-0.09 (0.6)	-0.13 (0.5)
Char height				1	-0.15 (0.4)	<i>0.90 (<0.05)</i>	<i>0.98 (<0.05)</i>
HTCBH					1	0.14 (0.4)	-0.24 (0.2)
STDZ _{h_c} CBH						1	<i>0.91 (<0.05)</i>
STDZ _{h_c} height							1

B. Dead trees

Variable	Cone opening	CBH	Height	Char height	Crown Length	STDZ _{h_c} CBH	STDZ _{h_c} height
Cone opening	1	-0.24 (0.2)	-0.25 (0.2)	<i>0.50 (<0.05)</i>	-0.04 (0.9)	<i>0.54 (<0.05)</i>	<i>0.56 (<0.05)</i>
CBH		1	<i>0.56 (<0.05)</i>	-0.14 (0.5)	-0.36 (0.06)	-0.24 (0.2)	0.01 (0.9)
Height			1	0.16 (0.4)	<i>0.57 (<0.05)</i>	-0.05 (0.8)	-0.13 (0.5)
Char height				1	0.04 (0.8)	<i>0.92 (<0.05)</i>	<i>0.95 (<0.05)</i>
HTCBH					1	0.18 (0.4)	-0.15 (0.4)
STDZ _{h_c} CBH						1	<i>0.93 (<0.05)</i>
STDZ _{h_c} height							1

Note: Numbers indicate Pearson’s r. Numbers in brackets are *p*-value. Italicized numbers indicate significant correlation with *p*<0.05.

* Standardized char height to crown base height.

** Standardized char height to tree height.

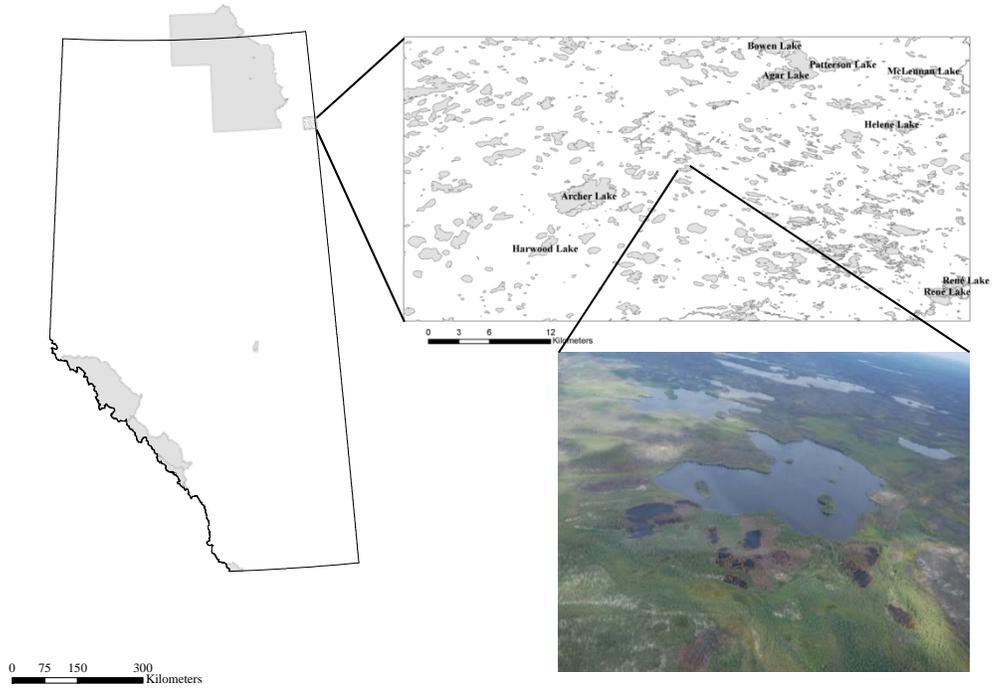


Figure 2. Location of the research site ($58^{\circ}07' N$, $110^{\circ}15' W$). Photograph from the air was provided by courtesy of Alberta Sustainable Resources Development and FPInnovations.

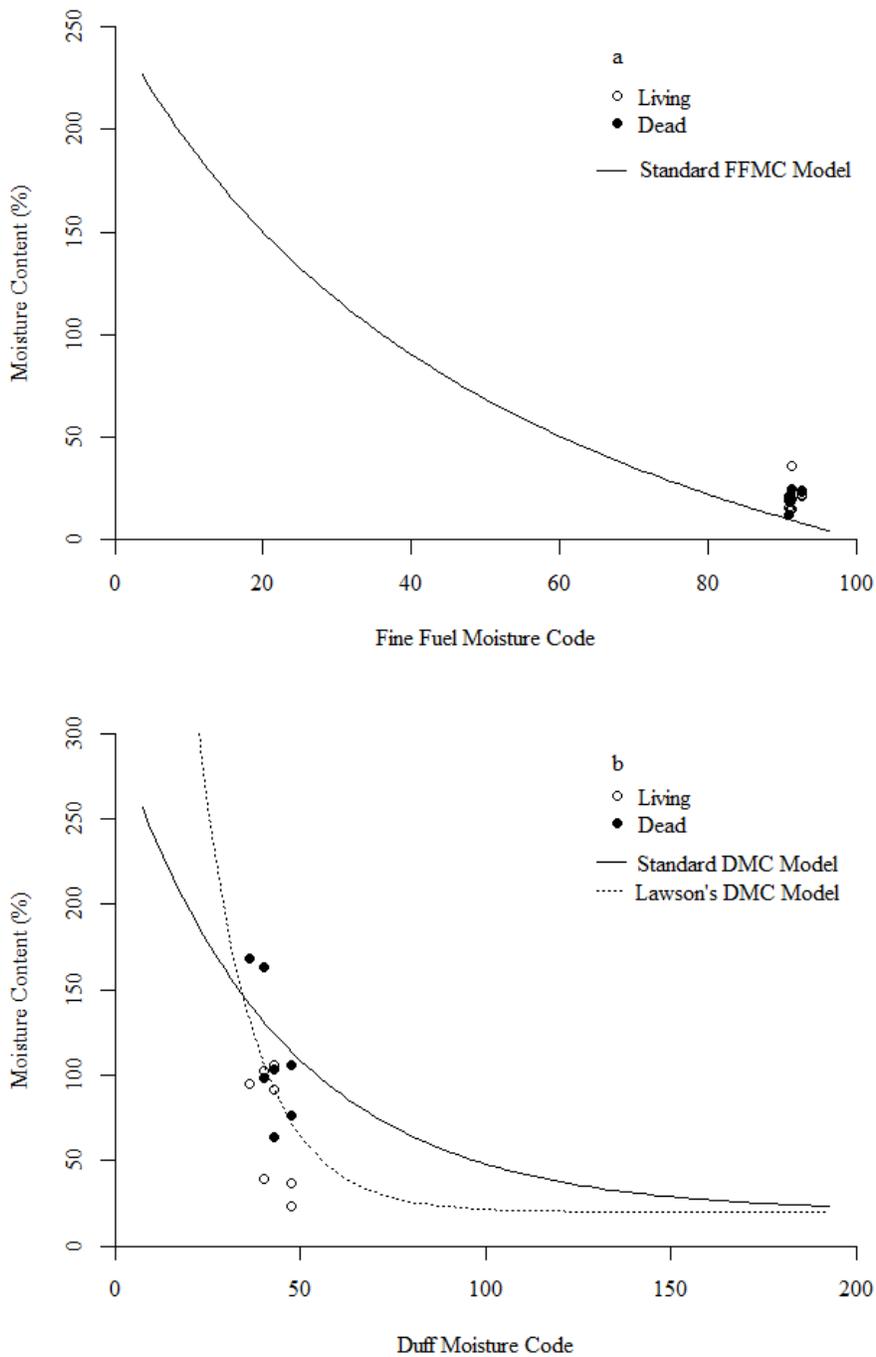


Figure 3. Comparisons between measured and estimated moisture content in fine fuels (a) and organic layers (b) in relation to the standard fuel moisture models in Canadian Forest Fire Weather Index System (solid lines; Van Wagner 1987; broken line indicated Lawson et al (1997)'s localized DMC model, refer to Eq.A3 in Appendix A). FFMC and DMC were taken at 1300 MDT. Data provided by Alberta Environment and Sustainable Resource Development and FPInnovations.

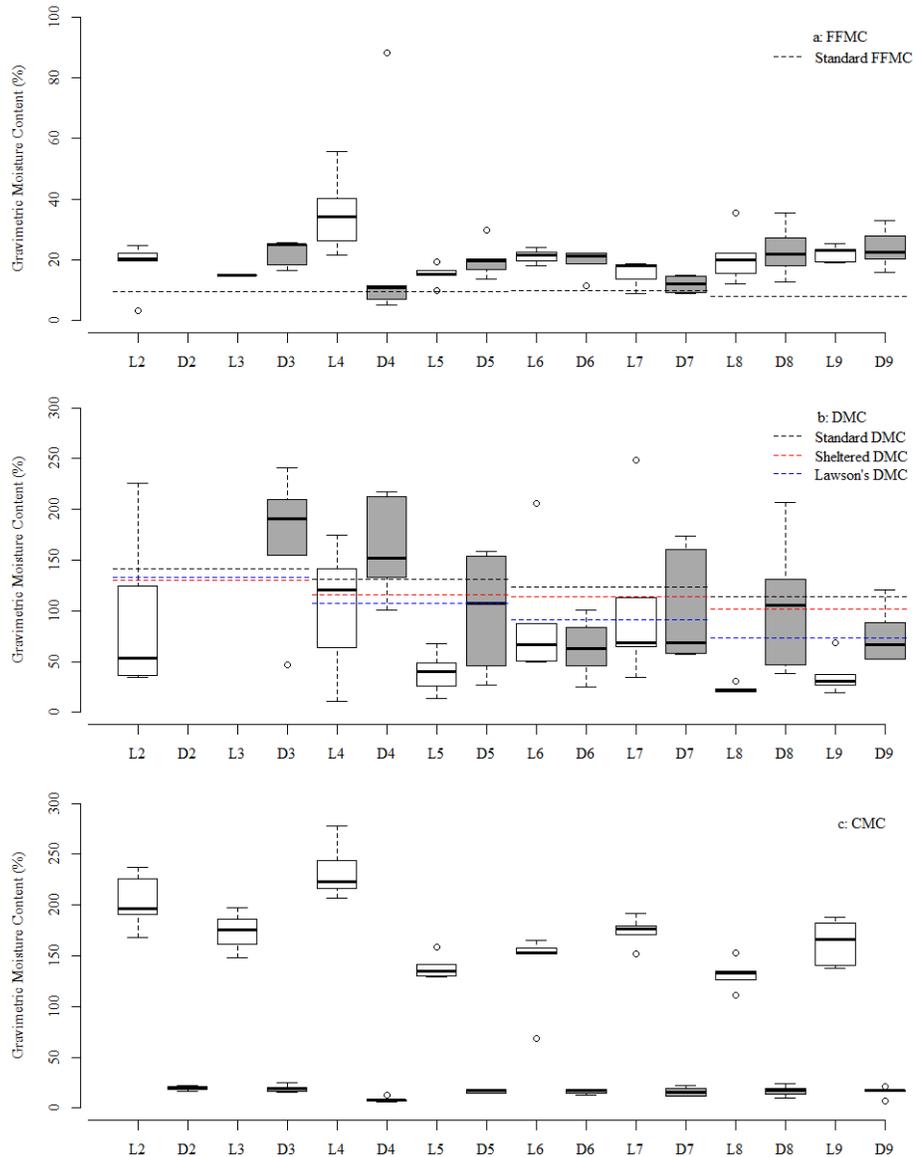


Figure 4. Comparisons of moisture content of a) fine fuel (i.e., litter), b) duff, and c) crown foliar between control (L) and MPB-simulated plots (D). The dashed line in figure (a) indicates predicted moisture content derived from FFMC (refer to Eq. A1 in Appendix A). Dashed lines in figure (b) represent standard DMC (black), sheltered DMC (red), and Lawson’s DMC (blue) (refer to Eq. A2-5 in Appendix A). Solid band inside each box plot is the median; top and bottom of the box show the 75th and 25th percentiles; whiskers show the upper and lower values of the data that fall within $1.5 \times (75\text{th} - 25\text{th percentiles})$; dots indicate outliers which do not fall into $1.5 \times (75\text{th} - 25\text{th percentiles})$ range. Data provided by Alberta Environment and Sustainable Resource Development and FPInnovations.

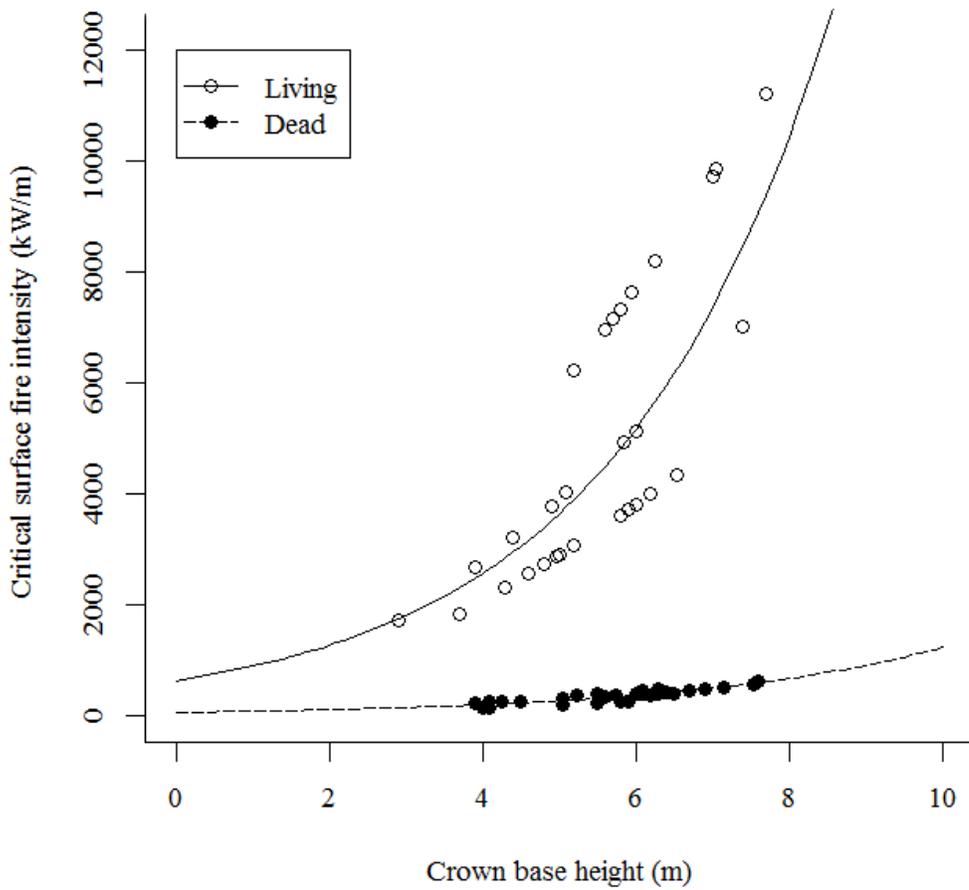


Figure 5. Critical surface fire intensity to initiate crowning in living and dead stands in relation to crown base height with an application of Van Wagner’s (1977) crown fire initiation model. Each point depicts the critical surface fire intensity to initiate crowning was based upon crown base height (m) and crown foliar moisture content (%) (Eq. B1 in Appendix B).

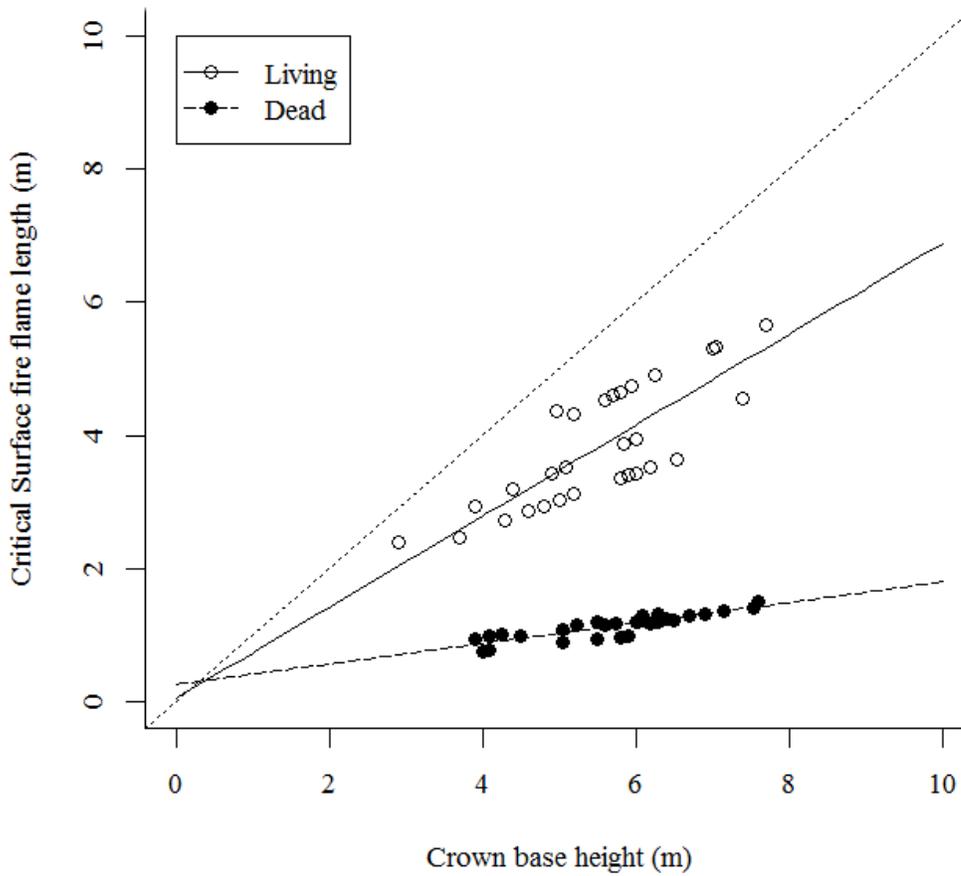


Figure 6. Critical surface fire flame length to initiate crowning in living and dead stands in relation to crown base height with an application of Van Wagner’s (1977) crown fire initiation model. Dashed line indicates one to one regression line and each point depicts the critical surface flame length for a tree using crown base height (m) and crown foliar moisture content (%) (Eq. B2 in Appendix B).

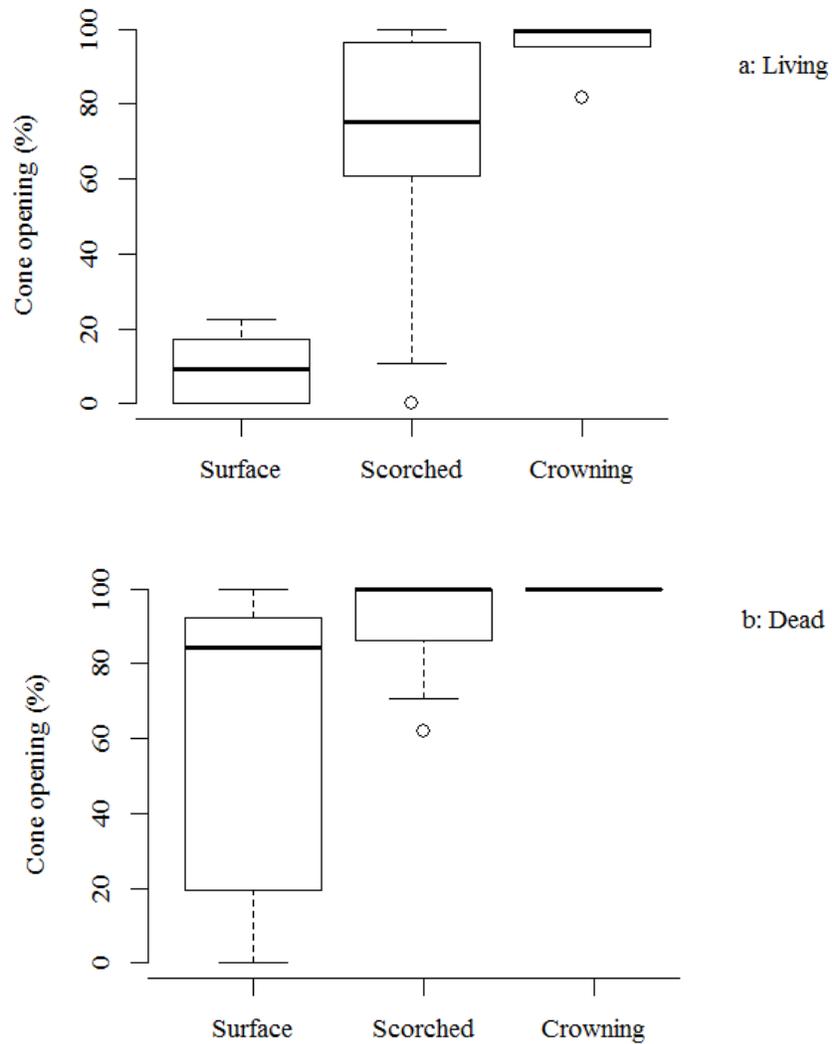


Figure 7. Cone opening modeled with different fire types defined by the relationship between char height and CBH. Surface fire is when char height was found below CBH; scorched is when char height was between CBH and tree height; and crowning is when the char height exceeded CBH. Solid band inside each box plot is the median; top and bottom of the box show the 75th and 25th percentiles; whiskers show the upper and lower values of the data that fall within $1.5 \times (75^{\text{th}} - 25^{\text{th}} \text{ percentiles})$; dots indicate outliers which do not fall into $1.5 \times (75^{\text{th}} - 25^{\text{th}} \text{ percentiles})$ range.

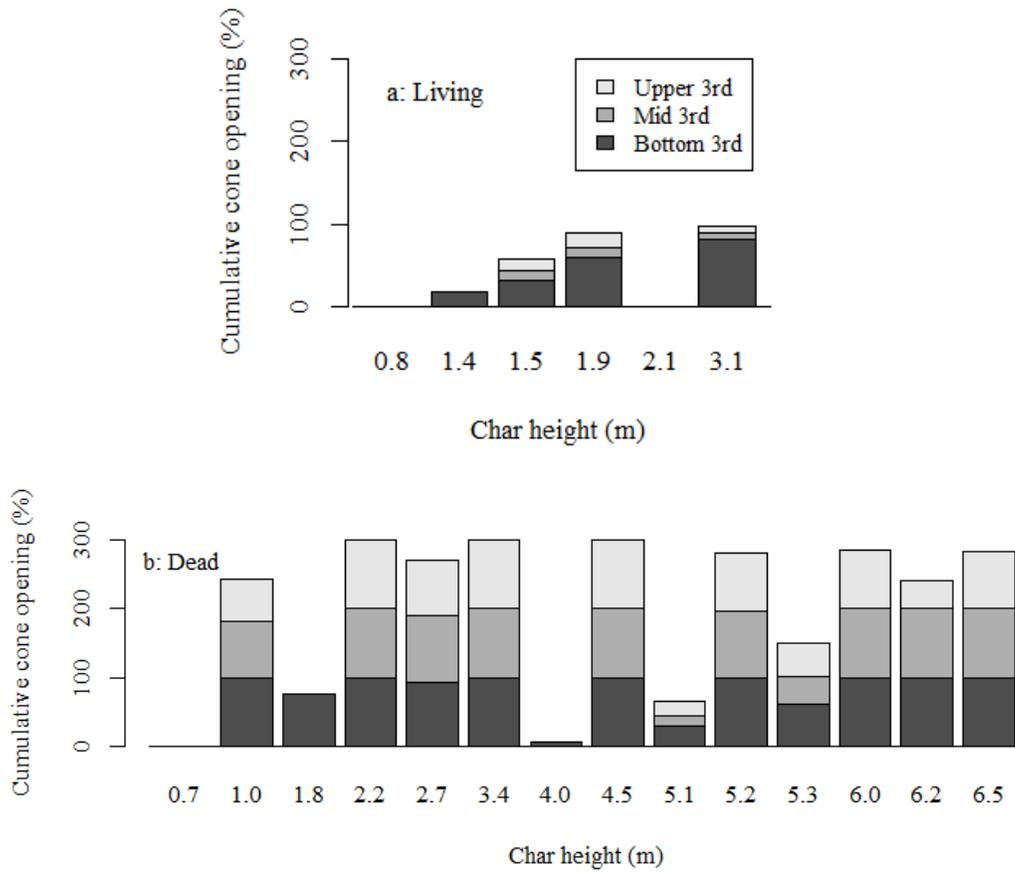


Figure 8. Accumulated cone opening by crown layers as a function of char height lower than crown base height (i.e., surface fire) for a) living trees, and b) dead trees.

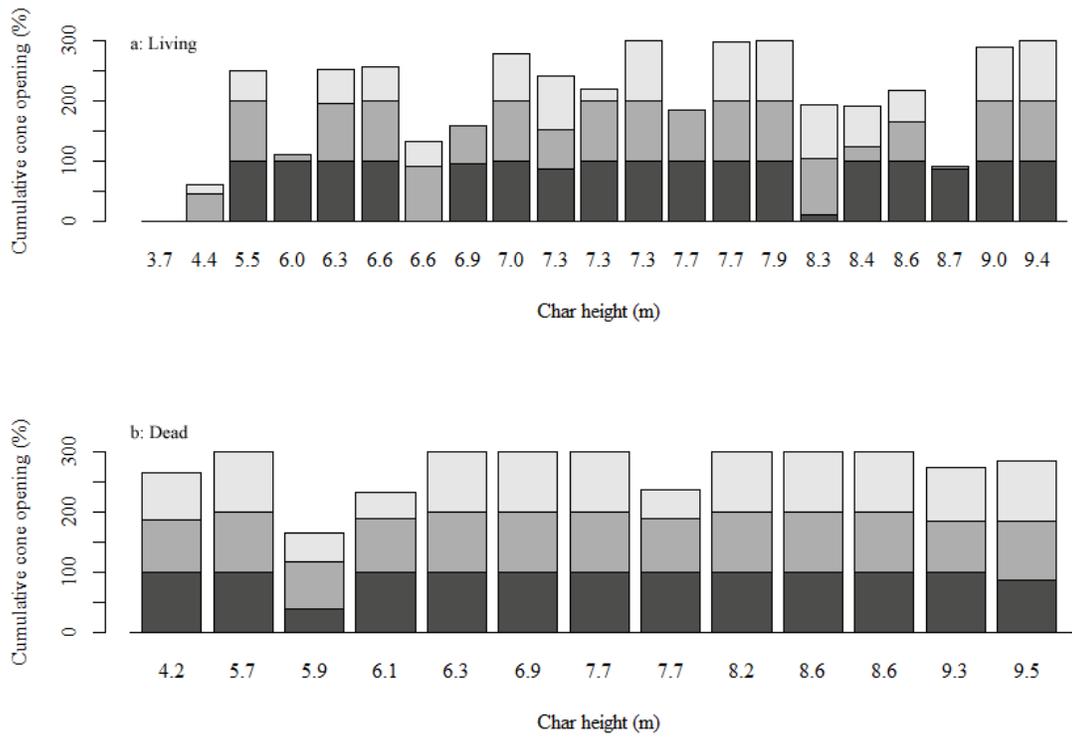


Figure 9. Accumulated cone opening by crown layers as a function of char height higher than crown base height (i.e., scorched) for a) living trees, and b) dead trees.

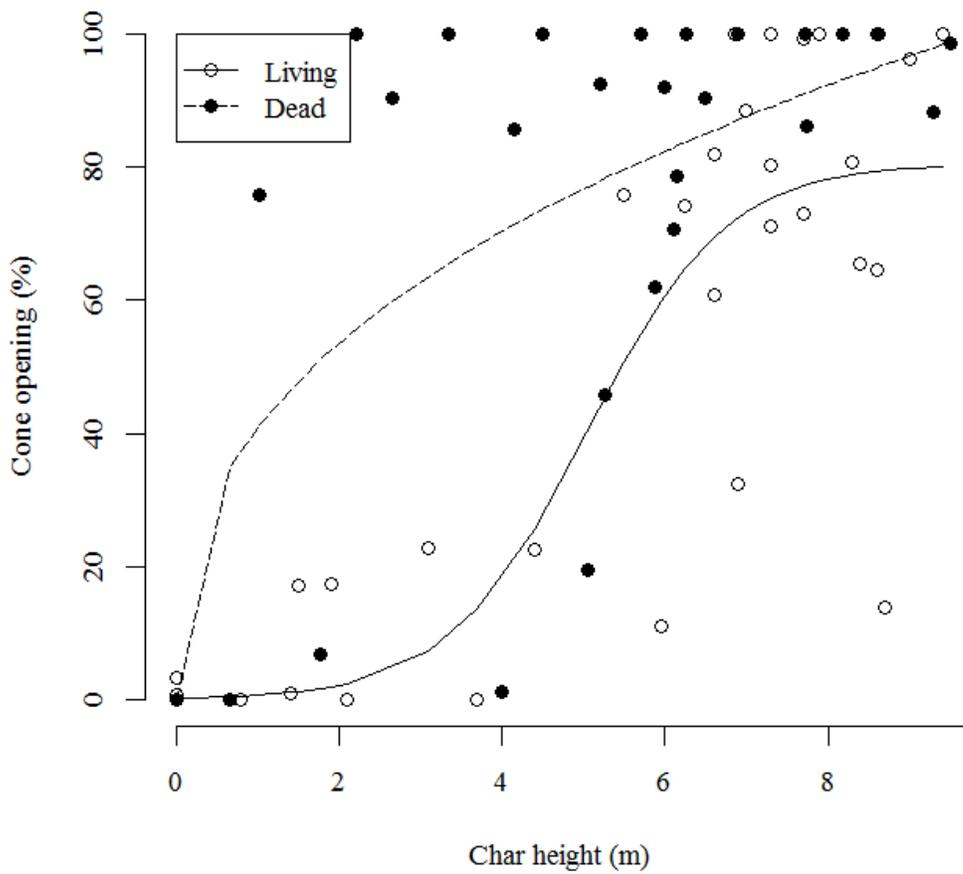


Figure 10. Cone opening in relation to char height for both dead and living trees. Curve was fitted using power function for dead trees (Eq. 5) and logistic function for living trees (Eq. 6).

5. References

- Alberta Agriculture and Rural Development.
[http://www1.agric.gov.ab.ca/\\$department/deptdocs.nsf/all/agdex10307](http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex10307)
- Alexander, M E. 1982. Calculating and interpreting forest fire intensities.
Canadian Journal of Botany 60: 349-357.
- Alexander, M. E., and M. G. Cruz. 2012a. Interdependencies between flame length and fireline intensity in predicting crown fire initiation and crown scorch height. International Journal of Wildland Fire 21: 95-113.
- Alexander, M. E., and M. G. Cruz. 2012b. Modelling the effects of surface and crown fire behavior on serotinous cone opening in jack pine and lodgepole pine forests. International Journal of Wildland Fire 21(6): 709-721.
- Amman, G. D. 1977. Role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession. In: W. J. Mattson (ed) The Role of Arthropods in Forest Ecosystems, pp. 3-18. Springer-Verlag, New York.
- Bentz, B. J., J. Régnière, C. J. Fetting, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60: 602-613.
- Beverly, J. L., and B. M. Wotton. 2007. Modelling the probability of sustained flaming: predictive value of fire weather index components compared with observations of site weather and fuel moisture conditions. International Journal of Wildland Fire 16: 161-173.
- Bond W. J., and B. W. van Wilgen. 1996. Fire and plants. London: Chapman and Hall.
- British Columbia Ministry of Forests. 2001. Fundamentals of natural lodgepole pine regeneration and drag scarification. B.C. Ministry of Forests: Forest Renewal Section Silviculture Practices Branch. pp.34.
- Brown, J. 1975. Fire cycles and community dynamics in lodgepole pine forests. In Proceedings of Management of lodgepole pine ecosystem. pp. 429-456.

- 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. *Molecular Ecology* 20: 2157-2171.
- de Groot, W. J., P. M. Bothwell, S. W. Taylor, B. M. Wotton, B. J. Stocks, 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.
- Hoffman, C. M., C. H. Sieg, J. D., McMillin, and P. Z. Fulé. 2012. Fuel loadings 5 years after a bark beetle outbreak in south-western USA ponderosa pine forests. *International Journal of Wildland Fire* 21: 306-312.
- 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.
- Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management* 254: 16-34.
- Jenkins, M. J., W. G. Page, E. G. Hebertson, and M. E. Alexander. 2012. Fuels and fire behavior dynamics in bark beetle-attacked forests in western North America and implications for fire management. *Forest Ecology and Management* 275: 23-34.
- Johnson, E. A., and S. L. Gutsell. 1993. Heat budget and fire behavior associated with the opening of serotinous cones in two *Pinus* species. *Journal of Vegetation Science* 4(6): 745-750.
- Jolly, W. M., R. A., Parsons, A. M. Hadlow, G. M. Cohn, S. S. McAllister, J. B. Popp, R. M. Hubbard, 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.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18: 116-126.
- Klutsch, J. G., J. F. Negrón, S. L. Costello, C. C. Rhoades, D. R. West, J. Popp, 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.
- Lawson, B. D., G. N. Dalrymple, and B. C. Hawkes. 1997. Predicting forest floor moisture contents from Duff Moisture Code values. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Center, Victoria, BC. Technology Transfer Note No. 6. 6 pp.
- Miller, R. H., and A. A. Berryman. 1986. Carbohydrate allocation and mountain pine beetle attack in girdled lodgepole pines. *Canadian Journal of Forest Research* 16: 1036-1040.
- 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.
- Miyaniishi, 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.
- Nyland, R. D. 1998. Patterns of lodgepole pine regeneration following the 1988 Yellowstone fires. *Forest Ecology and Management* 111: 23-33.
- Page, W., and M. J. Jenkins. 2007. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. *Forest Science* 53(6): 662-674.
- Page, W. G., M. J. Jenkins, and J. B. Runyon. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Canadian Journal of Forest Research* 42: 1631-1647.

- R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Radeloff, V. C., D. J. Mladenoff, R. P. Guries, 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., J. Clement, J. Hicke, D. Kulakowski, L. H. MacDonald, T. L. Schoennagle, and T. T. Veblen. 2006. Recent forest insect outbreaks and fire risk in Colorado forests: a brief synthesis of relevant research. Colorado State University: Colorado Forest Restoration Institute.
- Rudolph, T.D., and P.R. Laidly, 1990. *Pinus banksiana* Lamb., Jack Pine, pp. 280-293. In R.M. Burns and B.H. Honkala (eds.), *Silvics of North America, Vol. 1, Conifers*, USFS. Agricultural Handbook. 654, Washington, D.C.
- Samman, S., and J. Logan. 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area. Report to Congress from Forest Health Protection, Washington Office, Forest Service, U.S. Department of Agriculture. Gen. Tech. Rep. RMRS-GTR-62. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 46 pp.
- Schneider, R., F. Berninger, C-H Ung, P. Y. Bernler, D. E. Swift, and S. Y. Zhang. 2008. Calibrating jack pine allometric relationships with simultaneous regressions. *Canadian Journal of Forest Research* 38: 2566-2578.
- Schroeder, D., and C. Mooney. 2012. Fire behaviour in simulated mountain pine beetle-killed stands. Final Report. FP Innovations. Wildfire Operations Research. pp.17.
- Schwilk, D. W., and D. D. Ackerly. 2001. Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94(2): 326-336.

- 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? *Ecological Monographs* 81(1): 3-24.
- Stocks, B. J. 1987. Fire behavior in immature jack pine. *Canadian Journal of Forest Research* 17: 80-86.
- Stocks, B. J. 1989. Fire behavior in mature jack pine. *Canadian Journal of Forest Research* 19: 783-790.
- Teste, F. P., V. J. Lieffers, and S. M. Lanhäuser. 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.
- Van Wagner, C. E. 1973. Height of crown scorch in forest fires. *Canadian Journal of Forest Research* 3: 373-378.
- Van Wagner, C. E. 1974. Structure of the Canadian Forest Fire Weather Index. Department of the Environment, Canadian Forestry Service, Publication No. 1333. 39 pp.
- Van Wagner, C. E. 1977. Conditions for the start and spread of crown fire. *Canadian Journal of Forest Research* 7: 23-34.
- 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.
- Wotton, B. M., B. J. Stocks, and D. L. Martell. 2005. An index of tracking sheltered forest floor moisture within the Canadian Forest Fire Weather Index System. *International Journal of Wildland Fire* 14: 169-182.
- Weber, M. G., M. Hummel, and C. E., Van Wagner. 1987. Selected parameters of fire behavior and *Pinus banksiana* Lamb. regeneration in eastern Ontario. *Forestry Chronicle* 63(5): 340-346.
- Wilmore, B. 2001. *Duff moisture dynamics in black spruce feather moss stands and their relation to the Canadian Forest Fire Danger Rating System*. Master's thesis. University of Alaska-Fairbanks, Alaska, USA.

Chapter 3

1." Conclusion

Serotinous cone opening as a result of the impact of simulated-MPB outbreak on fire behaviour was studied. Cone opening was modeled with char height at the individual tree scale. Cone opening in both living and MPB-simulated trees could be explained by nonlinear relationships with char height, an indicator for fire intensity. Fire induced cone opening more easily in MPB-simulated trees likely due to increased foliage flammability in MPB-simulated trees. Low foliar moisture content might be a leading factor to cone opening at low fire intensities in MPB-simulated trees. The high foliar moisture content and crown bulk density of healthy trees suppressed cone opening compared to the dead trees, but both living and dead trees showed an asymptotic increase in cone opening with increase in fire intensity.

The impact of killing trees is likely to influence fire behaviour at both the canopy and forest floor level; both of which are different in killed forests compared to living forests. Foliar moisture was lower and canopy fuel distribution was sparser in dead stands compared to healthy forests. Fire behaviour at canopy level was expected to be more active in MPB-killed forests due to changes in canopy fuel conditions, and we observed through cone opening modeling that cone opening in MPB-killed trees was more susceptible to heat exposure than healthy trees. Moisture content in the soil organic layer was increased after trees died likely due to the lack of transpiration processes. Interestingly, this higher soil moisture could mitigate the potential increase in fire intensity associated with the accumulated surface fuel loading from needle cast and broken branches after the tree mortality.

2." Future research

Proper timing to apply prescribed burning, in terms of season and time-since-MPB outbreak is the key to successful regeneration. As discussed earlier, fuel conditions are altered by MPB and the fire intensity and behaviour are expected to be different in MPB-killed forests than what is projected by the current Canadian Forest Fire Weather Index System using mature living jack pine or lodgepole pine forest as standard fuel type. Increase in needle cast at a relatively early stage of MPB outbreak and the eventual accumulation of snags on the surface at a later stage of MPB outbreak results in high fire hazard and fire intensity. Canopy openness after MPB outbreak encourages understory vegetation to grow by providing enough sunlight and nutrition, and depending upon the type and season of the year understory vegetation might also contribute to surface fuel loadings in fire. Alternatively, on richer sites, there may be reduced risk of fire in mid-summer when herbaceous plants are green and well-hydrated.

Besides the alteration of fuels and moisture regime in MPB-killed forests, thick feather moss layers play an important role in controlling moisture content in organic layer as well as soils in cold Canadian boreal forests. Moreover, live feather mosses blanket the ground surface and intercept rainfall. The surface layer dries out quite quickly during the drought period and this break in hydraulic conductivity to the surface impedes evaporation from the deeper organic layer underneath; hence there is likely decrease ignition probability and fire intensity on the ground if fire was applied based on the current FWI System (Fenton and Bergeron 2006, Shetler et al. 2008). Further, killing the overstory and eliminating its capacity for transpiration adds another level of complexity to this question. Therefore, site-specific fuel moisture models taking thickness of feather mosses, moisture retention since rainfall, seasonal moisture variation at feather moss layer into account should be developed for successful pine regeneration using prescribed burning.

In order for fire to open cones in the canopy, adequate fire intensity as well as fuels must be available. In MPB-killed forests, crown foliar moisture

content is dramatically decreased after tree death compared to living trees. In other words, fuels in the dead crown respond more quickly to atmospheric changes (e.g., precipitation, wind, sunlight) than foliage of living trees with intact membranes, cuticle and transpiration stream from the soil. Moisture content in fuels is critical to determining time and heat required for ignition and subsequent fire behaviour. However, the interaction between atmospheric conditions and dead aerial fuels are not well documented. In addition, quantification of fire intensities in MPB-killed forests (i.e., fuel consumption, flame residence time, flame sizes) with taking the increased surface fuel loading and decreased canopy fuel loading should be conducted for improving understanding fire behaviour and cone opening models in relation to fire intensity.

Application of prescribed burning offers good potential as a means to provide fire intensity for cone opening as well as duff consumption. Exposed mineral soils are regarded as suitable seedbeds for pine regeneration in terms of gaining constant moisture and nutrient supply from the soils; however, too intense a fire will hinder good regeneration because of consumption of the seed supply and in some cases an intense fire can impede the physical and chemical conditions of the seedbed. We need to accurately relate available seeds generated from the aerial seedbanks to germination success and seedling survival in MPB-killed stands that have been burned. This will require data on spatial distribution of seed sources, moisture content (litter, duff, and crown foliar moisture), fuel loading data (surface and canopy level), number of cones on individual trees with vertical distribution information, duff consumption, and annual regeneration success and survival rate since burning depending upon different fire intensity and severity.

3." References

- Fenton, N. J., and Y. Bergeron. 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. *Journal of Vegetation Science* 17: 65-76.
- Shetler, G., M. R. Turetsky, E. Kane, and E. Kasischke. 2008. Sphagnum mosses limit total carbon consumption during fire in Alaskan black spruce forests. *Canadian Journal of Forest Research* 38: 2328-2336.

Appendix

A." Canadian Forest Fire Weather Index System

- 1) Standard Fine Fuel Moisture Content equation

$$\text{Moisture content of FFMC (\%)} = 147.2 * \frac{101-FFMC}{59.5+FFMC} \quad (\text{Eq. A1})$$

- 2) Standard Duff Moisture Content equation

$$\text{Moisture content of DMC (\%)} = 20 + \exp\left(\frac{DMC-244.73}{-43.43}\right) \quad (\text{Eq. A2})$$

- 3) Lawson et al (1997)'s DMC model for Southern Yukon-Lodgepole pine/White spruce stand with reindeer lichen duff

$$\text{Moisture content of DMC (\%)} = 20 + \exp\left(\frac{DMC-106.7}{-14.9}\right) \quad (\text{Eq. A3})$$

- 4) Wotton et al.(2005)'s DMC for Sheltered fuel type

$$K = 260.5(Temp + 1.1) * (100 - RH) * Le * 10^{-6}$$

$$DMC = 244.72 - 43.43 * \ln(MC - 20)$$

$$SDMC = DMC + K \quad (\text{Eq. A4})$$

$$MC_{SDMC} = Eq.A2 \quad \text{if } \text{rain} \leq 0.42\text{mm} \quad (\text{Eq. A5})$$

$$MC_{SDMC} = Eq.A2 + 1000 * \frac{\text{rain}_{EFFECT}}{48.77 + b * \text{rain}_{EFFECT}} \quad \text{if } \text{rain}_{EFFECT} > 0$$

$$\text{rain}_{EFFECT} = 0.218 * \text{rain} - 0.094 \quad \text{if } 0.42 < \text{rain} < 7.69\text{mm}$$

$$\text{rain}_{EFFECT} = 0.83 * \text{rain} - 4.8 \quad \text{if } \text{rain} > 7.69\text{mm}$$

where K is drying factor, Temp is air temperature (at 1200 LST), RH is relative humidity (at 1200 LST), Le is day length factor, and rain_{EFFECT} indicates the effective precipitation to change moisture condition in duff layer.

B." Van Wagner's (1977) Crowning Initiation Model

- 1) Critical Surface Fire Intensity

$$I_0 = (0.010 * CBH * (460 + 25.9 * FMC))^{1.5} \quad (\text{Eq. B1})$$

- 2) Critical Surface Fire Flame Length

$$L_0 = 0.0775 * (0.01 * CBH * (460 + 25.9 * FMC))^{0.69} \quad (\text{Eq. B2})$$

where CBH is crown base height, FMC is crown foliar moisture content.

C."The Relationship Between Predicted and Observed Rate of Spread

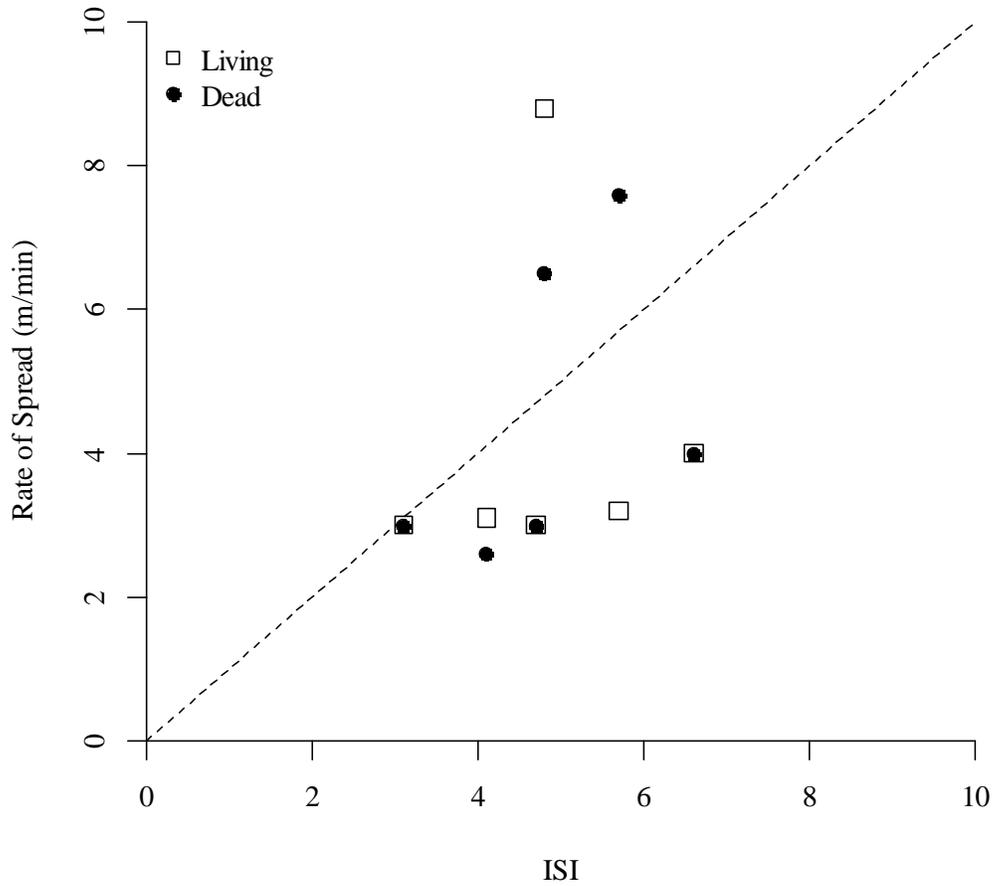


Figure C1. The relationship between FWI-predicted rate of spread (Initial Spread Index) and observed rate of spread. Data provided by Alberta Environment and Sustainable Resource Development and FPInnovations.

D."Multivariate Nonlinear Regression Models Fits for Cone Opening

Table D1. Models Results

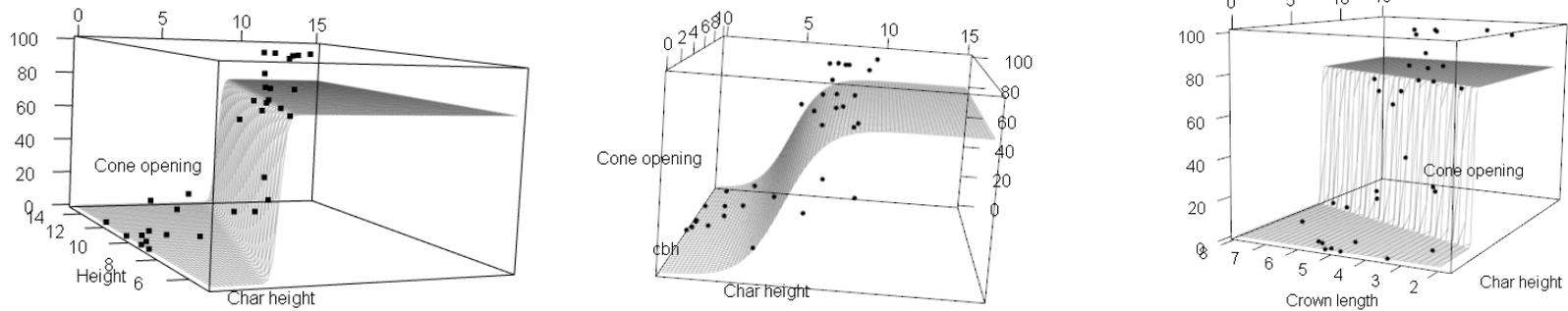
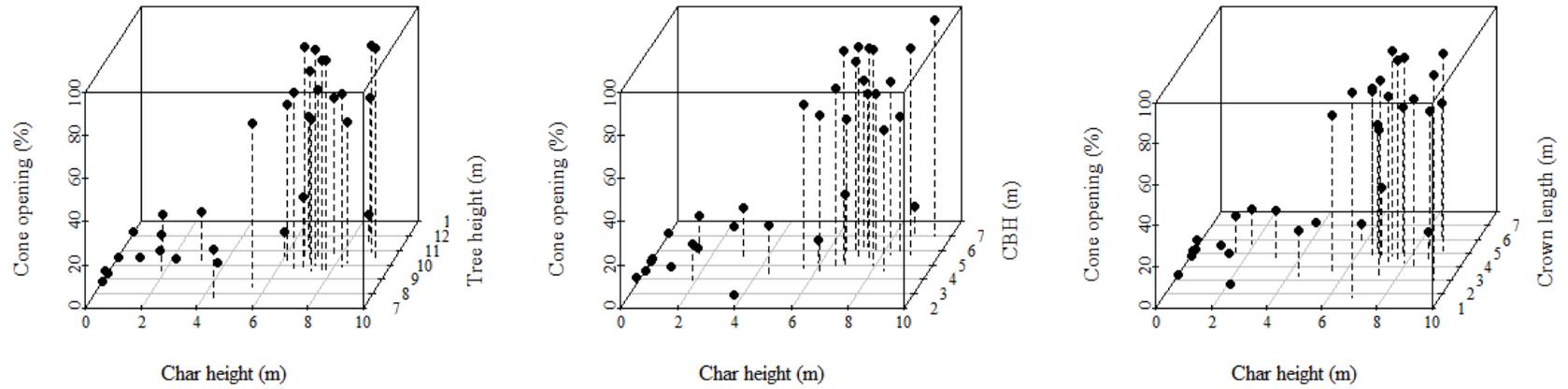
a. Living

No.	Model equation	Variable	Parameters	Coefficient	SE	P	AIC
1	$y=a/(1+\exp(b-c*x))$	Char height (x)	3	a=80.56	9.09	<0.05	301.2
				b=5.96	3.05	0.06	
				c=1.18	0.60	0.06	
2	$y=a/(1+\exp(b+c*x+d*z))$	Char height (x) Height (z)	4	a=77.72	4.55	<0.05	294.2
				b=1.87	5.12	0.72	
				c=-9.94	8.57	0.26	
				d=5.56	5.16	0.29	
3	$y=a/(1+\exp(b+c*x+d*z_1))$	Char height (x) CBH (z ₁)	4	a=80.12	9.09	<0.05	303.2
				b=6.25	4.25	0.15	
				c=-1.14	0.59	0.06	
				d=-0.13	0.78	0.87	
4	$y=a/(1+\exp(b+c*x+d*z_2))$	Char height (x) Crown length (z ₂)	4	a=76.90	4.564	<0.05	295.0
				b=73.53	109.91	0.51	
				c=-35.14	52.60	0.51	
				d=24.84	36.85	0.51	

b. Dead (only simple nonlinear regression fitted)

No.	Model equation	Variable	Parameters	Coefficient	SE	P	AIC
1	$y=a*x^b$ (Power function)	Char height	2	a=40.82	10.82	<0.05	303.6
				b=0.39	0.15	0.01	
2	$y=a-(a-b)*\exp(c*x)$ (Von Bertalanffy growth function)	Char height	3	a=92.91	12.48	<0.05	306.4
				b=1.67	11.50	0.89	
				c=-0.40	0.26	0.06	
3	$y=\exp(a+b*x)$ (Exponential function)	Char height	2	a=3.49	0.23	<0.05	314.5
				b=0.14	0.03	<0.05	
4	$y=a/(1+\exp(b+c*x))$ (Logistic function)	Char height	3	a=82.99	5.93	<0.05	308.1
				b=2.67	1.69	0.12	
				c=-1.99	1.24	0.12	
5	$y=a*\exp(-\exp(b*(x-c)))$ (Gompertz function)	Char height	3	a=83.53	6.19	<0.05	307.7
				b=-1.27	0.77	0.12	
				c=0.95	0.41	0.03	

Figure D1. Model fits for living trees using equations available in Table D1-a of Appendix D. Cone opening was fitted as a function of char height and tree height (far left; equation 2), CBH (middle; equation 3), and crown length (far right; equation 4).



E." Stand Density for Each Study Plot

Table E1. Stand density, mean height, crown base height (CBH), and diameter at breast height (DBH) information for jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*)

BurnID	Fire Classification (Van Wagner/FBP)	<i>Pinus banksiana</i>				<i>Picea mariana</i>			
		Stand density (stem/ha)	Height (m)	CBH (m)	DBH (cm)	Stand density (stem/ha)	Height (m)	CBH (m)	DBH (cm)
1 - 4C	Surface/Surface	1750	9.2	6	10.3	-	-	-	-
	Passive/Intermittent								
	Passive/Intermittent								
	Surface/Surface								
1T	Surface/Surface	1400	8.8	4.5	9.9	450	8.7	4.5	8.6
3T	Passive/Intermittent	1900	8.1	4.3	9.0	-	-	-	-
5C	Surface/Surface	1026	9.0	4.8	9.0	-	-	-	-
5T	Surface/Surface	1427	8.8	4.5	9.9	-	-	-	-
6C	Passive/Intermittent	1650	8.7	4.9	8.9	100	10.0	-	-
6T	Passive/Intermittent	1452	11.7	7.4	11.3	-	-	-	-
7C	Passive/Intermittent	3151	8.4	4.7	9.0	350	8.4	-	10.8
7T	Passive/Continuous	2150	8.0	4.25	8.9	-	-	-	-
8C	Passive/Continuous	2100	7.6	4.5	8.5	500	7.7	-	8.6
8T	Passive/Continuous	1000	6.3	3.6	8.2	-	-	-	-
9C	Passive/Continuous	2050	9.8	4.8	9.5	-	-	-	-
9T	Passive/Continuous	1600	8.5	3.5	8.4	50	-	-	7.2

Data provided by Alberta Environment and Sustainable Resource Development and FPIInnovations. Data for 2T and 4T were not available.

F." Fuel Load Data for the Archer Lake Study Area (from Schroeder and Mooney 2012)

Fuel Characteristic	Value
¹ Forest Floor Depth (cm)	6.8
Forest Floor Load (kg/m ²)	2.4
Forest Floor Bulk Density (kg/m ³)	35.4
² Surface Fuel Load (kg/m ²)	0.75
Tree height (m)	8.7
Live Crown Base Height (m)	4.6
Live Crown Depth (m)	4.2
Canopy Fuel Load (kg/m ²)	0.65
Canopy Bulk Density (kg/m ³)	0.16

¹ Forest Floor: Sum of litter (needles), moss tips, lichen, and duff layers

² Surface Fuel: Dead and down woody paterials