

# The implications of climate change on the range expansion of the mountain pine beetle, *Dendroctonus ponderosae* across the Canadian boreal forest

Daniel van der Merwe

April 23, 2015

---

## *Abstract*

As climate change increases, habitat previously unsuitable for the mountain pine beetle (MPB), *Dendroctonus ponderosae*, is beginning to warm resulting in range expansion opportunities. Global climate change models predict that the MPB range will expand eastward from British Columbia, Canada into the Canadian boreal forest. With current scientific evidence available to verify its recent exploitation of jack pine as a viable host, this paper will address the possibility of the boreal forest to sustain endemic populations, enabling the beetle to move through the prairies into the vast pine stands of Ontario and Quebec.

# Table of Contents

1.1 Introduction.....	2
2.1 Mountain Pine Beetle Life Cycle.....	3
2.2 Brooding .....	3
2.3 Emergence and Dispersal.....	4
2.4 Colonization.....	5
3.1 Availability of Suitable Hosts .....	6
3.2 Lodgepole vs Jack pine resin .....	6
4.1 Future Climatic Conditions.....	7
4.2 Precipitation and Drought .....	8
4.3 Fire.....	8
5.1 Current Mitigation Efforts .....	9
5.2 Description of Treatments.....	10
6.1 Discussion.....	11
Literature Cited.....	13

## 1.1 Introduction

The mountain pine beetle (MPB), *Dendroctonus ponderosae*, is an herbivorous bark beetle native to the forests of North America. The beetle's historical range stretches from northern Mexico at latitude 31°N, to central British Columbia at latitude 56°N, and from the Pacific Coast to the Black Hills of South Dakota (Safranyik et al. 2010). Though this native insect is usually considered innocuous, 4 or 5 outbreaks have occurred in northwestern North America over the past century (Safranyik 2004; Taylor et al. 2006; Aukema et al. 2008), with the current outbreak being the largest since recording began roughly 125 years ago (Taylor & Carroll 2004; Raffa et al. 2008; Cullingham et al. 2011). In 2002, established MPB populations were discovered in the Peace River region of British Columbia by entomologists, indicating the beetle had breached what was assumed to have been a geoclimatic barrier; the Rocky Mountains (de la Giroday et al. 2012). By the year 2006, it was reported that widespread infestations were being noticed as far east as Slave Lake, Alberta (Alberta Sustainable Resources Development 2006; Safranyik et al. 2010). The expansion of the MPB's historical range into areas previously considered uninhabitable is recognized as a consequence of global climate change (Figure 1). Numerous studies

demonstrate that a warming climate is increasing the suitability of available habitat for beetle populations (Logan & Powell 2001; Carroll et al. 2003; Cudmore et al. 2010; Safranyik et al. 2010; Cullingham et al. 2011; Sambaraju et al. 2012). In particular, there is an increased focus on how these epidemic populations result in such widespread infestations. Genetic analysis confirmed the theory of long range transport (Bartell 2008; Safranyik et al. 2010), and subsequent radar observation and aerial capture by Jackson et al. (2008) verified that the MPB can undergo wind aided, long range transport within the planetary boundary layer.

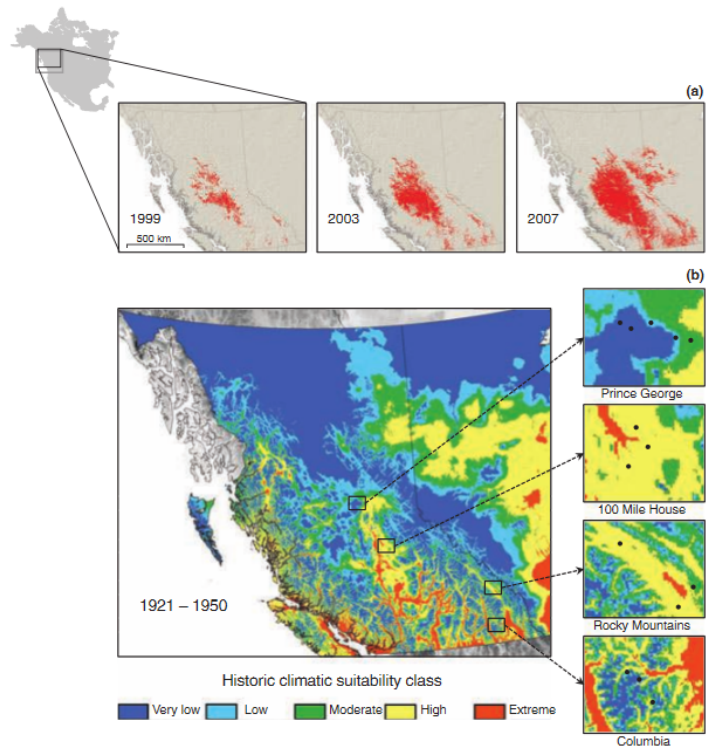


Figure 1: (a) 1999 to 2007 range expansion of the mountain pine beetle *Dendroctonus ponderosae* in western Canada, with infestations indicated in red, and (b) (adapted from Carroll et al. 2004) distribution of historic climatic suitability class from 1921 to 1950, with extreme CSC denoting climatically optimal habitat and very low CSC denoting climatically unsuitable habitat (Cudmore et al. 2010).

As the MPB continues an eastward migration across the landscape into habitats once considered climatically intolerable, it is gradually transitioning from its primary host, lodgepole pine (*Pinus contorta* Dougl.) to jack pine (*Pinus banksiana* Lamb., Lusebrink 2013). This adaptability to alternate hosts is vital in the beetles' eastward pursuit as host-tree selection and the subsequent colonization, brood development and emergence all influence MPB population establishment and persistence (Safranyik et al. 2010). Recent research has confirmed that the lodgepole pine/ jack pine hybrid zone and the boreal jack pine forest are susceptible to MPB attack (de la Giroday et al. 2010; Cudmore et al. 2010; Cullingham et al. 2011). As successful colonization depends on the death of the host tree, MPB establishment is easily identified (Safranyik et al. 2010). Cullingham et al. (2011) found 19 hybrid trees within the zone that had been attacked, as well as 8 pure jack pine trees on the leading edge of the outbreak. Although several trees are nowhere near an indication of a shift towards an epidemic population, the concern lies in the fact that the boreal forest is outside of the MPB's historic range (Cullingham et al. 2011).

In a 2014 report released by Alberta's ministry of Environment and Sustainable Resource Development (ESRD), beetle winter survival assessments indicate that overall, populations in northwest Alberta showed signs of being static to increasing. Extremely successful beetle survival was recorded south of Grand Prairie, and just east of Manning (Alberta ESRD 2014). In central Alberta, the population around Slave Lake has shown to be decreasing, with the exception of a few patches northwest of Edson that showed moderate to high overwintering success, indicating an increasing population. This is thought to be due to migrating beetles from the increasing population in Grand Prairie (Alberta ESRD 2014). Cold winter temperatures and aggressive mitigation techniques have resulted in a low number of infested trees in southern Alberta (Alberta ESRD 2014).

This paper will assess the likelihood that mountain pine beetle will be able to move across the Canadian Boreal into Ontario and Quebec given our current climate change regime, host availability on the land base, as well its ability to overcome current mitigation efforts being employed by the province of Alberta.

## **2.1 Mountain Pine Beetle Life Cycle**

### **2.2 Brooding**

The MPB typically has a univoltine life cycle that contains 4 stages of development including egg, larvae, pupa and adult (Safranyik & Carroll 2006). Female beetles are the first to select and colonize new host trees during late July to mid-August, showing preference to damaged or stressed trees with compromised defense systems (Cullingham et al. 2011). Once a host tree has been identified, following a

successful gustatory assessment of bark compounds, the female beetle will bore through the outer bark into the phloem initiating gallery construction, and ultimately a mass attack (Safranyik & Carroll 2006). Galleries are constructed vertically in the direction of the wood grain (Safranyik & Carroll 2006). Following mating, females oviposit (up to 60 eggs per female) into chambers cut into the sides of the parental gallery (Safranyik & Carroll 2006). Within roughly a week, the deposited eggs covered in boring dust will hatch, and the emerging larvae begin feeding immediately on phloem tissue, in a direction perpendicular to the parental gallery (Safranyik & Carroll 2006). During this feeding stage, larvae undergo four moulting cycles called instars (Safranyik & Carroll 2006). Feeding continues through the summer into the fall, at which point the larvae have progressed through the second, into third or early fourth instar by the time decreasing temperatures halt further development (Safranyik & Carroll 2006). This is the stage at which the importance of biological synchrony is demonstrated, as late instar larvae have a much higher cold tolerance than early instar larvae, resulting in greater overwintering survival rates for synchronous populations (Safranyik & Carroll 2006). Larvae, the most cold-tolerant of the four life stages, have lethal low temperatures of  $-23^{\circ}\text{C}$  to  $-29^{\circ}\text{C}$  for the first instar,  $-23^{\circ}\text{C}$  to  $-34^{\circ}\text{C}$  for the second instar, and  $-29^{\circ}\text{C}$  to  $-40^{\circ}\text{C}$  for the their and fourth instars (Logan et al. 1995, Safranyik & Carroll 2006).

### 2.3 Emergence and Dispersal

Maturation is completed with newly developed beetles consuming the lining of their pupal chamber, which includes the inner bark, blue stain fungi spores, and other microorganisms (Safranyik & Carroll 2006). The significance of this final meal before emergence is that it aids in the development of flight muscles and facilitates the transport of fungal and yeast spores to new host trees (Safranyik & Carroll 2006). MPBs have developed a symbiotic relationship with several blue fungi species, which aid in the colonization of host trees (Safranyik et al. 2010). The mechanisms involved in this process are discussed in detail in sections 2.4 and 3.2.

The duration until emergence depends largely on summer temperatures (Safranyik & Carroll 2006). While most MPB populations are univoltine, warmer than average summer temperatures can result in bivoltine tendencies (Figure 2; Reid 1962; Mitton & Ferrenberg 2012). In northern latitudes and high elevations, cool summer temperatures may retard brood development

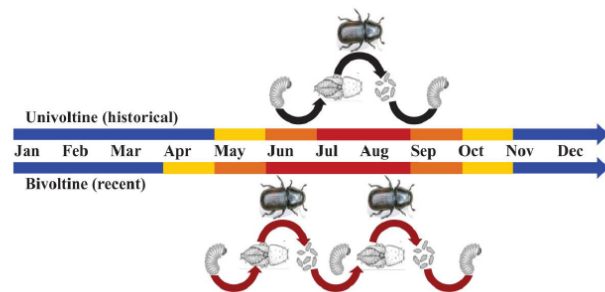


Figure 2: Historical univoltine life cycle of the mountain pine beetle and the recent bivoltine life cycle. Colors represent monthly temperature regimes, blue is  $< 0^{\circ}\text{C}$ , yellow is  $0^{\circ}\text{C}$ - $4.99^{\circ}\text{C}$ , orange is  $5^{\circ}\text{C}$ - $9.99^{\circ}\text{C}$ , and red for  $\geq 10^{\circ}\text{C}$  (Mitton & Ferrenberg 2012).

and require up to two years for maturation (Amman 1973). Emergence is also temperature dependent, only transpiring after ambient temperatures rise to over 16° C (Reid 1962). This usually occurs from mid-July to mid-August (Reid 1962; Sambaraju et al. 2012), at which point the beetle is able to survive outside for a few days before locating a viable host tree (de la Giroday et al. 2012). The optimal temperature range for beetle flight is between 22° and 32° C (Safranyik 1978).

Upon emergence, the beetle will either undergo short range dispersal within the same stand by flying in the area between the bottom of the crown and the top of the understory, or attempt long range dispersal flying above the canopy (Schmitz et al. 1980; Safranyik et al. 1989; Safranyik & Carroll 2006). Long range dispersal is predicted to occur in outbreak situations where local host species have been fully depleted (Jackson et al. 2008). During periods of long range dispersal, beetles can be found at heights exceeding 800 m above the forest canopy within the atmospheric boundary layer, and have the capacity to travel anywhere from 30 to 110 km per day (Jackson et al. 2008). Host trees are selected using a combination of sight and smell, where large, dark silhouettes (Shepherd 1966; Safranyik & Carroll 2006) and vertically oriented cylinders (Billings et al. 1976; Safranyik & Carroll 2006) are deemed preferable by the beetles. These long range dispersal events are predicted to be increasingly influential in the successful spread of epidemic populations (Safranyik & Carroll 2006).

#### **2.4 Colonization**

The MPB is an extremely resilient species that has adapted several distinct characteristics to overcome host defense systems (Safranyik et al. 2010). The first is a mutualistic relationship between MPB and several species of blue fungi and bacteria, which the MPB distributes from the tree it emerged from to a new host tree (Safranyik et al. 2010). Once within the host tree, these microorganisms quickly spread through the phloem and xylem inhibiting resin production, the main defense system in conifers (Lusebrink et al. 2013). In order to be effective, female beetles initiate a mass attack by releasing aggregation pheromones (Lusebrink et al. 2013). This second mode of attack involves the female beetle oxidizing  $\alpha$ -pinene, a monoterpene resin constituent, to produce an aggregation pheromone that attracts both MPB sexes (Safranyik et al. 2010). When males arrive they release *exo*-brevicommin to attract more females (Lusebrink et al. 2013). These pheromones continue to be released until optimal MPB densities are reached, estimated at approximately 60 attacks per m<sup>2</sup> of bark (Raffa & Berryman 1983). The resulting phenomenon is a swift mass attack on the host tree, usually lasting less than two days (Safranyik et al. 2010).

### 3.1 Availability of Suitable Hosts

In a study conducted in 1967, Furniss and Schenk (1969) identified the successful infestation of jack pine by the MPB in a controlled arboretum environment, and raised the question as to why the beetle had not moved eastward through the lodgepole x jack pine hybrid zone in Alberta and eventually into the pure jack pine beyond. Climatic factors leading to over winter mortality were most notably the source for the beetle's containment, limiting its spread both northward as well as eastward. Conclusive evidence of increasing global temperatures four decades later confirmed the range expansion of the beetle into habitats previously considered climatically marginal (Cudmore et al. 2010), most notably with the beetles breach of the rocky mountains in 2002 (de la Giroday et al. 2012). Not only was the MPB moving into new areas, but it was also displaying greater reproductive success in naïve lodgepole pine stands where co-evolution with the beetle was absent (Cudmore et al. 2010). In addition, very compelling evidence based on previously conducted experiments suggested that Furniss and Schenk's query was not only plausible, but the potential for jack pine to sustain low level populations through the boreal posed great potential risk (Safranyik et al. 2010).

The conclusions drawn by Safranyik et al. (2010) were solidified with the discovery of eight attacked pure jack pine trees, along with nineteen attacked hybrid trees (Cullingham et al. 2011). The hybrid trees discovered in the study were shown to be more biologically descendant from lodgepole pine than jack pine (Cullingham et al. 2011), empirically suggesting the possibility that co-evolved lodgepole defenses could potentially be genetically transferred to naïve populations of jack pine (Cullingham, 2012).

### 3.2 Lodgepole vs Jack Pine Resin

As a first mechanism of defense to a beetle attack, trees will excrete large quantities of toxic resin out of the wound as to flush the beetle from the tree, preventing access to the cambium tissue (de la Giroday et al. 2012). The resin, containing the monoterpene  $\alpha$ -pinene is oxidized by the female beetle, resulting in the production of the aggregation pheromone, *trans*-verbenol, indicating to other beetles that a viable host has been located (Safranyik & Carroll 2006). The production of this aggregation pheromone through the exploitation of the tree's primary defense has been a critical factor in the success of mass attacks and the establishment of epidemic populations (Safranyik et al. 2010).

Though this has been a viable and successful tactic in lodgepole pine, the ability of the beetle to exploit this defence in the same manner within a jack pine stand had yet to be seen in natural conditions. To address this question Erbilgin et al. (2013) compared the ability of the MPB to produce *trans*-verbenol from jack and lodgepole pine bolts, as well as comparing physical size, lipid content and flight propensity

of beetles emerging from each respective host. The results of these findings concluded that female beetles on jack pine emitted two times as much *trans*-verbenol than those on the lodgepole pine (Erbilgin et al. 2013). The quantity of monoterpene excreted from entrance holes in the bolts was much greater in the lodgepole pine for the first 120 hours, but overall, there were greater volumes of  $\alpha$ -pinene and 3-carene released from jack pine (Erbilgin et al. 2013). On average, beetles emerging from jack pine bolts were shown to be physically larger than those from lodgepole pine bolts, and heavier beetles were shown to have a greater tendency towards flight than lighter beetles (Erbilgin et al. 2013).

#### 4.1 Future Climatic Conditions

According to projections by the International Panel on Climate Change Fifth Assessment Report (2013), global mean surface air temperatures are expected to increase by 0.3° to 0.7° C between 2016 and 2035 (Kirtman et al. 2013). These rising temperatures are projected to expand climatic suitability, with a warming of just 3° C resulting in a 500 m elevation gain (Hughes 2000) and a 2.5° C change predicted to shift habitat range northward by 7° (Logan & Powell 2001). British Columbia has already experienced approximately a 1.2° C increase in mean annual temperatures between 1959 and 2002 (Mitton & Ferrenberg 2011). Temperature deviations were most pronounced in the spring and winter, with an increase in minimum temperature of over 2° and 1.5° C, respectively (Fauria & Johnson 2009). Within the boreal forest, this increase in global temperature is expected to alter levels of precipitation, increase the occurrence of drought, and intensify and extend the fire season, ultimately resulting in a shift of the boreal climatic zones (Table 1; Price et al. 2013). The modification of the boreal forest’s thermal regime may result in the dissolution of the climatic barrier currently believed to be limiting MPB distribution (Logan & Powell 2001; Carroll et al. 2003; Cullingham et al. 2011; Sambaraju et al. 2012) and increasing the vulnerability of the boreal forest to MPB attack as it copes with climate change stressors (Peng et al. 2011).

Table 1: Predicted mean daily temperature by 2100 for Canadian boreal forest terrestrial ecozones (Price et al. 2013).

Terrestrial Ecozone	Summer Temperature Change		Winter Temperature Change	
	Mean Min. T	Mean Max T	Mean Min T	Mean Max T
Aspen Parkland and Boreal Plains	↑ 4.5°C	↑ 3.5-4°C	↑ 6.5°C	↑ 5.5-6°C
Boreal Shield and Hudson Plains	↑ 5°C	N/C	N/C	↑ 8°C
Taiga Cordillera and Taiga Plains	↑ 4°C	↑ 4.5°C	↑ 7.5-8°C	↑ 5.5°C
Taiga Shield	↑ 3.5-6°C	↑ 2.5-5°C	↑ 9-10°C	↑ 2.5-5°C



## ***4.2 Precipitation and Drought***

Global climate change is projected to increase the average annual precipitation of the Canadian boreal forest, particularly during the winter and spring (Price et al. 2013). However, this does not necessarily translate to an increase in soil moisture as rising winter and spring temperatures will also result in higher evapotranspiration (Price et al. 2013). Rather, general circulation models (GCM) predict trends toward longer but drier growing seasons, (Price et al. 2013) and more frequent and severe droughts (Peng et al. 2011).

There are two main implications of an increase in frequency and severity of droughts in the boreal forest. The first is the direct stress droughts place on tree health. Within the western boreal forest, summer water deficit is considered the main factor limiting tree growth (Peng et al. 2011). GCMs overwhelmingly predict that cumulative moisture depletion in soils will increase by the end of the 21<sup>st</sup> century (Bergeron et al. 2010). There have already been significant increases in tree mortality rates in the boreal forest, which Peng et al. (2011) attributed to extensive drought periods, particularly in western Canada. Their study found that mortality rates in western Canada were significantly positively related to temperature and water deficits (Peng et al. 2011). The second repercussion is that droughts increase the vulnerability of trees to other ecosystem disturbances. During droughts, trees are less likely to spend a lot of energy on resin production, thus increasing the chances of successful MPB infestations (Mitton & Ferrenberg 2011). As well, droughts may also intensify the boreal forest's susceptibility to fire (Peng et al. 2011). As with droughts, fire frequency involves a trade-off between changes in the mean annual precipitation and temperature levels (Bergeron et al. 2010).

## ***4.3 Fire***

There is a general consensus that based on the projections from GCMs; climate change will increase the frequency, severity, duration, and spatial distribution of wildfires in the boreal forest (Soja et al. 2007; Bergerson et al. 2010). Within the boreal forest, an increase in extreme weather events is predicted to increase the occurrence of lightning ignited fires (Soja et al. 2007). Fire suppression has historically kept the burn rate of the boreal forest artificially low (Bergerson et al. 2010), which has contributed to the MPB outbreak (Sanfranyik & Carroll 2006; Kurz et al. 2008). By 2100, the burn rate of the boreal forest is expected to double, however as the burn rate is currently maintained at an unnaturally low level, these projections are still within the natural range of variability for the boreal forest (Bergerson et al. 2010). In Canada an estimated \$500 million/ year is spend on fire suppression (Flannigan et al. 2006), therefore any increase in fire frequency will have significant management implications both environmentally and socioeconomically (Bergerson et al. 2010). In particular, an increase in fire frequency is raising concerns over greenhouse gas emissions and the uncertainty over whether future

forests will turn into carbon sources (Kurz et al. 2008). If the burn rate doubles as predicted, forest emissions could double as well, increasing up to 100 Mt CO<sub>2</sub>e yr<sup>-1</sup> (Kurz et al. 2008).

### 5.1 Current Mitigation Efforts

The objectives set forth by the Alberta Sustainable Resource Development (ASRD) are two fold; to start with, the program aims to contain current MPB populations as well as minimizing longitudinal spread along the eastern border of the province, and additionally, to prevent populations from spreading further east into the boreal forest (ASRD 2007). In order to implement effective control practices, it is crucial to have an understanding of the population processes of established infestations (Carroll et al. 2006) so that the state of the population can be determined. Based on the stand susceptibility risk and rating model developed by Shore and Safranyik (1992), ASRD modelled and mapped out the Stand Susceptibility Index (SSI), or potential risk to pine stands throughout the province (ASRD 2007). This provided an initial starting point in assessing the urgency associated with the various infestations, with focus and priority being placed on stands with the highest SSI. These stands were prioritized for determining current conditions including distribution and infestation status, brood survival and population trends (ASRD 2007). Ground surveys were conducted within infested stands to determine the rate of overwintering survival, while aerial surveys were used to assess the rate of spread (Figure 3; ASRD 2007). Based on these population estimates, management objectives were allocated between infested stands, and target operational objectives were determined and distributed accordingly with the intention of overall population containment (ASRD 2007).

In areas where overwinter survival rates are high and populations display signs of eastward progression, top priorities are placed on aggressive management techniques. These areas are collectively known as the leading-edge management zone, and control practices are very aggressive, aimed at returning populations to an endemic level (ASDR

2007). Areas identified as the holding zone are given secondary priority to management activities, as their

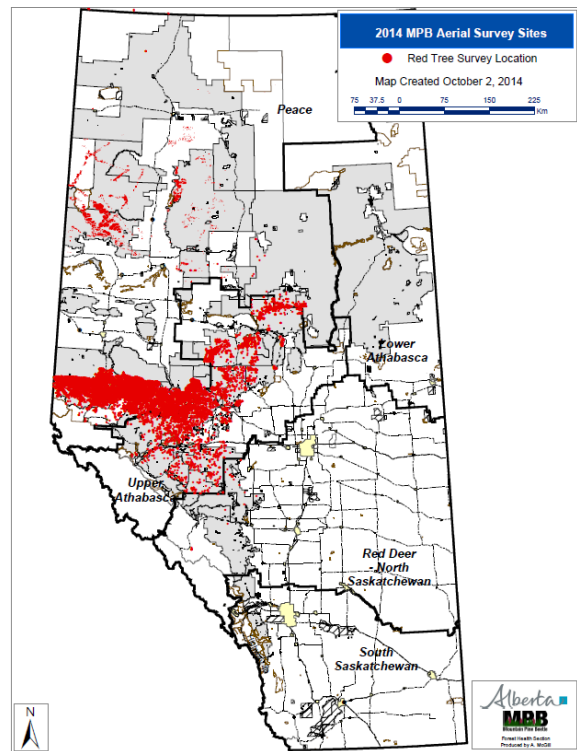


Figure 3: 2014 mountain pine beetle aerial survey sites assessing the rate of spread in Alberta, Canada by the Alberta Sustainable Resource Development program (ASRD 2007).

composition consists of considerably more infested trees in much larger clump sizes than the leading edge zone (ASRD 2007). The objective set forth in this zone is to either reduce or maintain static beetle populations. Lastly, the salvage zone contains areas that are infested to the point where any control methods are futile, and as such, areas within the timber harvest land base are salvage logged (ASRD 2007).

## ***5.2 Description of Treatments***

The most common treatment used in the leading edge management zone is intensive, single tree selection, along with small group selection (ASRD 2007). Depending on the allocation of the land, proximity to infrastructure or ecosystem sensitivity, single tree treatments can be carried out in a number of ways (Carroll et al. 2006). The most desirable situation occurs when the target tree is within close proximity to a road network. In this case the tree, or groups of trees, will be felled and transported to the mill where processing will effectively kill the beetles (Carroll et al. 2006). In isolated areas where log extraction is not possible, the single trees or small groups are hand felled, bucked into small manageable sizes, piled on top of the stumps and burned (Carroll et al. 2006). In this zone, treatment needs to occur in 80% of the priority sites where surviving beetle brood was identified (ASRD 2007).

Selective harvesting of small to medium sized patches of infested trees followed by single tree selection if required is the primary treatment within the holding zone (ASRD 2007). In order to maintain populations at a static level, control needs to be established within 50% to 80% of controlled sites (ASRD 2007). If possible, the wood is transported to the mill for processing, otherwise it is bucked up, stacked up and burned in a high intensity fire with the aid of a bit of fuel (Carroll et al. 2006).

Within the salvage zone where control efforts are ineffective, large cut blocks are used as a management technique known as “sanitation logging” (Carroll et al. 2006). The trees are harvested, limbed and transported to the mill. Caution must be exercised when conducting this method as harvesting alone will not result in beetle mortality (Carroll et al. 2006) and there is the risk of inadvertently spreading beetle populations via human transport (ASRD 2007). In addition, logs decked at the mill are still fostering developing broods, and if left for long enough, new adults will emerge (Carroll et al. 2006). In many instances, this method is followed up by pheromone baiting a handful of standing residual trees within the area in a process labeled “post-logging mop-up” (Carroll et al. 2006). The trees, once full of beetles, are then harvested and transported to the mill to be processed (Carroll et al. 2006).

In rare instances, chemical pesticides have been used as method of control targeting small numbers of high value trees in locations such as parks or campsites (ASRD 2007). Other than this small application example, the use of chemicals as a means of pest control has been almost completely

terminated due to their detrimental impacts to the environment, as well as the huge health risks posed to those that work with them (Carroll et al. 2006).

## 6.1 Discussion

Following the MPBs breach of the Rocky Mountains and its subsequent movement into naïve lodgepole pine stands, Cullingham et al. (2011) found the first evidence to show that mass attacks had not only happened within hybrid lodgepole/ jack pine, but also in pure jack pine. This initial movement into the boreal through the hybrid zone is predicted to have happened due to the very close chemical composition of both the beetle's traditional host and the new novel host. Erbilgin et al. (2013) demonstrate under a controlled setting that not only is the beetle able to exploit the defense compounds of jack pine in a similar manner to that of lodgepole, but it in fact was found that jack pine contains higher amounts of  $\alpha$ -pinene. This was echoed in the findings that more trans-verbenol was excreted from the entrance holes in jack pine than the lodgepole pine, indicating that female beetles are able to produce more aggregation pheromones in jack pine suggesting the new naïve host is even more prone to mass attack than historical hosts. The slight variations in the chemical compositions of the two species' resins had further surprising implications, revealing that beetles emerging from jack pine showed higher overall fitness with larger body sizes and greater tendencies towards flight. All of these factors become extremely interesting when assessing the environmental changes predicted within the boreal, and definitely appear to suggest that the odds of making a comfortable living in the boreal are stacked in favour of the beetle.

In the next 20 years, climate models predict an increase in global temperatures anywhere from 0.3° C to 0.7° C, with even greater increases predicted for Canada's boreal region (Kirtman et al. 2013). By the year 2100, temperature changes will show signs of increase anywhere from 3° C to 10° C in some areas, which will result in the physical shift of the boreal climatic zones (Kirtman et al. 2013). Precipitation regimes are expected to change fairly substantially, with annual precipitation increasing, particularly during the winter and spring months (Price et al. 2013). Even though precipitation is predicted to increase, the summer growing months will be longer and drier as a result of increased evapotranspiration. Water stress experienced by the trees during the summer months will increase susceptibility to infestations (Mitton & Ferrenberg 2011). Fire will become more prevalent on the landscape, creating huge implications for greenhouse gas emissions leading to increased positive feedback. Jack pine as well as black spruce will both benefit from this increased fire regime in terms of regeneration as they both have serotinous cones (Price et al. 2013).

When all of these factors are considered, the beetle's increased tendency towards flight, greater production of aggregation pheromones and larger body sizes, both ground and aerial surveys will become

essential to the prevention of the MPB reaching Ontario and Quebec. Timely detection and active response plans will be essential as the ability of beetles emerging from jack pine for long distance dispersal flights provide adequate causes of concern for increased invasion risk, resulting in the increased probability of sustained endemic populations (Erbilgin et al. 2013). Although there is need for supplemental research, especially related to species composition, age class and density across the boreal, this review suggests that there is strong evidence supporting the ability of the MPB to successfully exploit jack pine, and if volumes are sufficient to sustain endemic populations, the possibility of range expansion could be a real threat (Cullingham et al. 2011).

## Literature Cited

---

- Alberta Environment and Sustainable Resource Development. 2014. Beetle survival success varies within, across regions [online]. Available from <http://esrd.alberta.ca/lands-forests/mountain-pine-beetle/default.aspx> [accessed 8 February 2015].
- Alberta Sustainable Resources Development. 2006. Beetle bulletin: mountain pine beetle activities in Alberta, December 1, 2006. Alberta Sustainable Resources Development, Edmonton, Alberta.
- Alberta Sustainable Resource Development. 2007. Mountain Pine Beetle Management Strategy, December 2007. Alberta Sustainable Resources Development, Edmonton, Alberta.
- Amman, G.D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environmental Entomology* 2: 541-547.
- Aukema, B.H., Carroll, A.L., Zheng, Y., Zhu, J., Raffa, K.F., Moore, R.D., Stahl, K. and Taylor, S.W. 2008. Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. *Ecography* 31: 348-358.
- Bergeron, Y., Cyr, D., Girardin, M.P., and Carcaillet, C. 2010. Will climate change drive 21<sup>st</sup> century burn rates in Canadian boreal forest outside of its natural variability: collating global climate model experiments with sedimentary charcoal data. *International Journal of Wildland Fire* 19: 1127-1139.
- Carroll, A.L, Shore, T.L and Safranyik, L. 2006. Direct Control: Theory and Practice. – In: Safranyik, L and Wilson, B. (eds). *The mountain pine beetle: a synthesis of biology, management and impacts on lodgepole pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, pp. 155-172.
- Cudmore, T.J., Björklund, N., Carroll, A.L. and Lindgren, B.S. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. *Journal of Applied Ecology* 47: 1036-1043.
- Cullingham, C.I., Cooke, J.E.K., Dang, S., Davis, C.S., Cooke, B.J., and Coltman, D.W. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. *Molecular Ecology* 20: 2157-2171.
- Cullingham, C.I., James, P.M.A., Cooke, J.E.K. and Coltman, D.W. 2012. Characterizing the physical and genetic structure of the lodgepole pine x jack pine hybrid zone: mosaic structure and differential introgression. *Evolutionary Applications* 5: 879-891.
- de la Giroday, H-M. C., Carroll, A.L., Aukema, B.H. 2012. Breach of the northern Rocky Mountain geoclimatic barrier: initiation of range expansion by the mountain pine beetle. *Journal of Biogeography* 39: 1112-1123.
- Erbilgin, N., Ma, C., Whitehouse, C., Shan, B., Najjar, A. and Evenden, M. 2013. Chemical similarity between historical and novel host plants promotes range and host expansion of the mountain pine beetle in a naïve host ecosystem. *New Phytologist* 201: 940-950.
- Fauria, M.M., and Johnson, E.A. 2009. Large-scale climatic patterns and area affected by mountain pine beetle in British Columbia, Canada. *Journal of Geophysical Research* 114: 1-19.

- Flannigan, M. D., Amiro, B. D., Logan, K. A., Stocks, B. J., and Wotton, B. M. 2006. Forest fires and climate change in the 21st century. *Mitigation and adaptation strategies for global change 11*: 847-859.
- Furniss, M.M. and Schenk, J.A. 1969. Sustained natural infestation by the mountain pine beetle in seven new *Pinus* and *Picea* hosts. *Journal of Economic Entomology* 62: 518-519.
- Hughes, A.D. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15: 56-61.
- Jackson, P.L., Straussfogel, D., Lindgren, B.S., Mitchell, S. and Murphy, B. 2008. Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Canadian Journal of Forest Research* 38: 2313-2327.
- Kirtman, B., Power, S.B., Adedoyin, J.A., Boer, G.J., Bojariu, R., Camilloni, I., Doblas-Reyes, F.J., Fiore, A.M., Kimoto, M., Meehl, G.A., Prather, M., Sarr, A., Schär, C., Sutton, R., van Oldenborgh, G.A., Vecchi, G. and Wang, H.J. 2013. Near-term climate change: projections and predictability - In: *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Logan, J.A., Bolstad, P.V., Bentz, B.J. and Perkins, D.L. 1995. Assessing the effects of changing climate on mountain pine beetle dynamics. *in* R.W. Tinus, ed. *Proceedings of the interior west global change workshop, April 25-27, 1995, Fort Collins, Colorado, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-262*. Pp. 92-105.
- Logan, J.A., and Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Naturalist* 47: 160-172.
- Lusebrink, I., Erbilgin, N. and Evenden, M.L. 2013. The lodgepole x jack pine hybrid zone in Alberta, Canada: A stepping stone for the mountain pine beetle on its journey east across the boreal forest? *Journal of Chemical Ecology* 39: 1209-1220.
- Mitton, J.B., and Ferrenberg, S.M. 2011. Mountain pine beetle develops and unprecedented summer generation in response to climate warming. *The American Naturalist* 179: 163-171.
- Peng, C., Ma, Z., Lei, X., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., and Zhou, X. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change* 1: 467-471.
- Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M., McKenney, D.W., Pedlar, J.H., Stratton, T., Sturrock, R.N., Thompson, I.D., Trofymow, J.A. and Venier, L.A. 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews* 21: 322-365.
- Raffa, K.F., Aukema, B.H., Berntz, J. et al. 2008. Cross-scale diversity of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58: 501-517.
- Raffa, K.F., and Berryman, A.A. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 53: 27-49.

- Reid, R.W. 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia. I. Life cycle, brood development, and flight periods. *The Canadian Entomologist* 94: 531-538.
- Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations – In: D.L. Kibbee, Berryman, A.A., Amman, G.D., and Stark, R.W. (eds). *Theory and practice of mountain pine beetle management in lodgepole pine forests. Symposium Proceedings, University of Idaho, Moscow, ID*, pp. 77-84.
- Safranyik, L., Silversides, R., McMullen, L.H., and Linton, D.A. 1989. An empirical approach to modelling the dispersal of the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Col., Scolytidae) in relation to sources of attraction, wind direction and speed. *Journal of Applied Entomology* 108: 498-511.
- Safranyik, L., and Carroll, A.L. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. – In: Safranyik, L and Wilson, B. (eds). *The mountain pine beetle: a synthesis of biology, management and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre*, pp. 3-66.
- Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G. and Taylor, S.W. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist* 142: 415-442.
- Sambaraju, K.R., Carroll, A.L., Zhu, J., Stahl, K., Moore, R.D. and Aukema, B.H. 2012. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography* 35: 211-223.
- Schmitz, R.F., McGregor, M.D., and Amman, G.D. 1980. Mountain pine beetle response to lodgepole pine stands of different characteristics. – In: Berryman, A.A. and Safranyik, L. (eds). *Proceedings of the 2<sup>nd</sup> IUFRO Conference on Dispersal of Forest Insects: Evaluation, Theory and Management Implications. Aug. 27-31, Sandpoint, ID. Cooperative Extension Service, Washington State University, Pullman, WA*. Pp. 234-243.
- Shore, T.L. and Safranyik, L. (1992). *Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands (Inf. Rep. BC-X-336)*. Victoria, BC: Canadian Forest Service, Pacific Forestry Centre.
- Soja, A.J., Tchebakova, N.M., French, N.H., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin, F.S., and Stackhouse, P.W. 2007. Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change* 56: 274-296.
- Taylor, S.W. and Carroll, A.L. 2004. Disturbance, forest age dynamics, and mountain pine beetle outbreaks in BC: a historical perspective. – In: Shore, T.L. et al. (eds), *Challenges and solutions. Proc. Of the Mountain Pine Beetle Symp., Kelowna, BC, Canada. October 30-31, 2003, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, NRC Research Press*, pp. 41-51.
- Taylor, S.W., Carroll, A.L., Alfaro, R.I., Safranyik, L. 2006. Forest climate and mountain pine beetle outbreak dynamics in western Canada. In: *Mountain Pine Beetle Symposium: Challenges and Solutions* (eds Shore TL, Brooks JE, Stone JE), Report BC-X-339, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Pp 67-94.