“During stormy nights, I have often camped snugly beneath the interlacing arches of this little pine. The needles, which have accumulated for centuries, make fine beds, a fact well known to other mountaineers, such as deer and wild sheep, who paw out oval hollows and lie beneath the larger trees in safe and comfortable concealment”

John Muir

University of Alberta

Interactions between the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and whitebark pine (*Pinus albicaulis* Engelmann)

by

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Abstract

I compared life history traits between mountain pine beetles (MPB) utilizing whitebark pine and lodgepole pine to better understand how host use could affect MPB impact in the Rocky Mountains of Alberta, Canada. Neither host was obviously better in terms of quality for or susceptibility to the MPB, although whitebark pines with the thickest phloem produced significantly larger adult MPB. Thus, large diameter whitebark pines with thick phloem will contribute as much or more to the transition of MPB populations from endemic to epidemic status than will similarly large lodgepole pines. For some MPBs, a univoltine life-cycle was observed, suggesting that climatic barriers that have constrained high altitude MPB populations in the past are moderating, meaning that this endangered pine is at greater risk of MPB attack. Host species also influenced the assemblage of dead wood inhabiting beetles with seven uncommon species having potential to be specialists in whitebark pine.

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Chapter 1: Whitebark pine and the mountain pine beetle

1.1 Background and rationale

Whitebark pine (*Pinus albicaulis* Engelmann, Family Pinaceae) is a unique and ecologically important component of the sub-alpine forest of western North America. Its closest relatives are the Eurasian stone pines (Subgenus: *Strobus*, Subsection: *Cembrae*), trees with cones that do not open upon maturation; instead pines in this group rely almost exclusively on nutcrackers (Corvidae: *Nucifraga*) to disperse their seeds (Tomback and Linhart 1990, McCaughey and Schmidt 2001). Some time during the Pliocene, it is thought that ancestral Clark's Nutcrackers (*Nucifraga columbiana* (Wils.)) carried ancestral whitebark pines across the Bering Strait land bridge (McCaughey and Schmidt 2001). In the periods of glacial advance and retreat following its introduction to North America, whitebark pine established itself as one of the dominant tree species until the Holocene (8 000 to 4 000 years ago), when changing climate and subsequent competition from other tree species forced whitebark pines to retreat to high elevations (McCaughey and Schmidt 2001). Whitebark pine's current distribution and ecological niche reflects this history, as it is a cold tolerant, high elevation, disturbance adapted species which defines the tree line in subalpine forests across much of western North America (Arno and Hoff 1989, Weaver 2001) (Figure 1.1).

Whitebark pine, somewhat contradictorily, has been described as both a foundation (Ellison *et al.* 2005) and a keystone (Tomback *et al.* 2001) species of subalpine forests. The large and nutritious seeds of whitebark pine are important food for many organisms, including Clark's nutcracker, woodpeckers, jays, ravens, chickadees, nuthatches, finches, chipmunks, ground squirrels, black bears and grizzly bears, although importance varies geographically (Kendall 1983, Mattson *et al.* 1991, Tomback and Kendall 2001 and references therein). Aided by the Clark's nutrcracker, whitebark pine is among the first species to colonize disturbed subalpine forests, where its presence ameliorates extreme conditions and it acts as a nurse tree for many other plant species (Tomback *et al.* 2001). Furthermore, its hardiness enables it to grow where other conifers cannot, making it the last species at the tree line in many areas (Arno and Hoff 1989). At high elevations, its presence regulates snowmelt, runoff and reduces erosion in shallow, poorly developed subalpine soils (Farnes 1990).

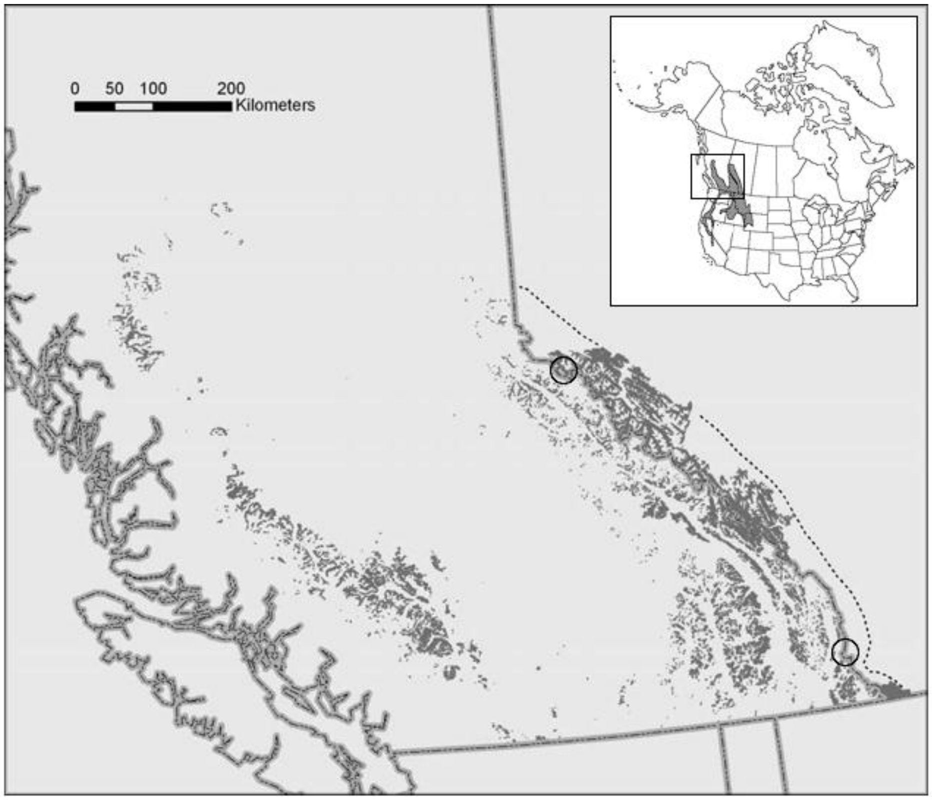

Figure 1.1: Probable distribution of whitebark pine in western Canada and in North America (insert). Gray shading indicates presence of whitebark pine. The dotted line represents the eastern limit of the species distribution. The circled areas indicate the northern (Willmore Wilderness Park) and southern (Crowsnest Pass area) regions where research in this thesis was conducted (after COSEWIC 2010).

Even though whitebark pine has limited economic value (Day 1967), and a substantial component of its distribution lies within protected areas (McCaughey and Schmidt 2001), this species is endangered in both Canada and the United States, although full protection under federal laws are pending in both jurisdictions (Committee on the Status of Endangered Wildlife in Canada 2010, Department of the Interior Fish and Wildlife Service 2010). The main reason for its decline is the accidental introduction of the exotic fungal pathogen, white pine blister rust (WPBR) *Cronartuim ribicola* Fischer (Zeglen 2002, ASRD and ACA 2007, Gibson *et al.* 2008, Smith *et al.* 2008, Tomback and Auchuff 2010). WPBR has a two-host life cycle with three types of spores. One type of spore allows for rapid population amplification, particularly in gooseberries and currants (*Ribes* spp) (this can also happen in *Pedicularis* spp and *Castilleja* spp*)*; a second spore is transmitted from these shrubs to white, foxtail and stone pines, including whitebark pine; and a third type of spore, specialized for long range dispersal, transmits the fungi from pines back to currents and gooseberries (Burns *et al.* 2008). Whitebark pine is further threatened by changes to natural intervals of fire return, as fire suppression has resulted in replacement by later seral species (Tomback *et al.* 2001, ASRD and ACA 2007, Gibson *et al.* 2008). In addition, two climate change related problems are further impacting this species: *i*) the direct loss of habitat as the tree line rises (Romme and Turner 1991, Hamann and Wang 2006), and *ii*) increases from the historical activity of the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) (Logan and Powell 2001, Carroll *et al.* 2004, Taylor and Carroll 2004, ASRD and ACA 2007, Gibson *et al.* 2008, Cudmore *et al.* 2010).

The MPB is among a small group of native, North American bark beetles (Coleoptera, Curculiondiae, Scolytinae) capable of infesting and killing large numbers of mature pine trees over widespread areas. It is considered the most destructive of all western forest insects (Evenden 1943, Furniss and Carolin 1977, Wood 1982, Safranyik and Carroll 2006). MPB population dynamics and the course of its eruptions are generally well understood, although understanding of the driving forces remains inadequate to predict the onset or collapse of population explosions with certainty. MPBs bore into, reproduce in and feed on the sub-cortical tissues, particularly the phloem, of 22 species of pine found in western North America (Furniss and Schenk 1969, Smith *et al*. 1981, Amman and Cole 1983). During the course of an eruption, MPB populations generally become food-limited in stands where temperature is optimal for development (Cole and Amman 1969); in short they kill all vulnerable hosts. MPBs will colonize the best quality trees first, typically those with thick phloem. These allow for the greatest net reproductive rates and the populations will grow (Amman 1984). This local population growth continues until the best trees are used up. Then trees of marginal quality are colonized, net reproductive rates decline and subsequently so do MPB populations (Cole and Amman 1980). In areas where climatic constraints to development and overwinter survival are superimposed on this process, such as at high elevations, MPB populations are adversely affected, regardless of food availability. Thus, there are basic latitudinal and elevation limits for epidemics of the MPB (Cole and Amman 1980). However, the locations suitable for eruptions may change with shifts in climate. In fact it has been suggested that the recent surge of MPB in western Canada into areas without historical evidence of high MPB populations reflects ongoing climate change (see below).

Host trees actively and dynamically defend themselves in multiple ways from bark beetle attack (Shrimpton 1978, Raffa and Berryman 1983, Christiansen *et al.*1987, Raffa and Smaley 1995, reviewed in Franceshi *et al.* 2005). Their ability to stave off MPB attack is thought to depend on their vigor. One of the most important factors determining tree vigor is stand density, with tightly packed trees thought to experience more competition and therefore more stress (Waring and Pitman 1983, 1985, Smith *et al.* 2002, MacQuarrie and Cooke 2011). Furthermore, drought stress is believed to play an important role in predisposing host trees to MPB attack (Waring and Pitman 1983).

Under selection pressure from host defenses, the MPB has evolved a chemically mediated communication system that allows for the synchronous mass attack of a host tree to overwhelm its defenses (Pitman and Vite 1969, Ryker and Rudinsky 1982, Borden *et al.* 1987). More vigorously defended trees require greater densities of beetles to overwhelm and kill the host (or at least part of it), a condition necessary for successful reproduction (Raffa and Berryman 1983). The classic story is that MPB has also co-evolved symbiotic relationships with a number of micro-organisms, most notably blue-stain fungi, organisms which are believed to help overwhelm host defenses (Shrimpton 1972, Raffa and Berryman

1982). However, this paradigm is facing significant criticism at the present time because there is a lack of consistency of virulent fungal associations with tree killing bark beetles (*i.e.*, the most virulent fungal species are not the most prominent among populations of symbiotic fungi in tree killing bark beetles and phytopathogenic fungi are ubiquitously associated with non-tree killing bark beetles) and the rate of fungal colonization does not correspond well with the development of symptoms associated with successful attack (*e.g.*, the fungus grows too slowly disrupt water transport in the sapwood in a way that would contribute to the rapid tree death that is observed after successful colonization by tree killing bark beetles) (Lieutier *et al.* 2009, Six and Wingfield 2011).

Once a host tree has been successfully colonized and killed, a number of tree related variables influence MPB fecundity and survival. One of the most important of these is phloem thickness (Amman 1971, Cole and Amman 1980, Amman and Cole 1983). More eggs are laid and more beetles are produced per unit area of tree bole when phloem is thick (Ried 1963, Amman 1971, Berryman 1976, Cole 1981). MPB success is also influenced by the identity of the fungal symbiont, which is believed to increase the nutritional quality of phloem (Six and Paine 1998, Ayres *et al.* 2000), and pine species (*e.g.*, Amman 1982, Langor 1989, Cerezke 1995).

By far the most important influence on MPB development and survival, however, is climate (Cole 1981, Bentz *et al.* 1991, Bentz and Mullins 1999). Temperature both limits and synchronizes the development of the MPB from egg, through its four larval intars, the pupal stage, then to adult (Bentz *et al.* 1991). Unseasonably cold temperatures in the late fall, winter and early spring are the most important mortality factors affecting the MPB (Amman 1973, Cole 1981), as such events can kill virtually all MPB brood above snowline over large areas. Accumulation of sufficient degree-days in one year is also a key factor allowing for epidemic MPB populations to develop (Amman 1973, Cole 1981, Bentz *et al.* 1991), and depending on temperature, the MPB life cycle can require 1, 2 or 3 years.

The MPB is a natural and important component of the disturbance regime in western North America (reviewed in Rogers 1996). However, anthropogenic influences like fire suppression, alteration of the historical distributions of pine size classes (Taylor and Carroll 2004) as well as a warming climate (Carroll *et al.* 2004, Raffa *et al.* 2008) have created conditions such that the current MPB outbreak in western Canada is an order of magnitude larger than anything previous recorded (Safranyik *et al.* 2010). Though the dramatic expansion north into British Columbia and east into the boreal forest have garnered the majority of attention (*e.g.*, Kurz *et al.* 2008, Cudmore *et al.* 2010, Safranyik *et al.* 2010), sustained outbreaks at high altitudes in other parts of the range are equally novel and potentially devastating (Carroll *et al.* 2004, ASRD and ACA 2007, Gibson *et al.* 2008).

Historically, cold temperatures at the high elevations that whitebark and other five needle pines occupy have protected these trees from frequent, severe MPB infestations (Arno and Hoff 1989, Bartos and Gibson 1990, Logan and Powell 2001). In the past century, however, unseasonably warm summers and mild winters have been associated with severe MPB outbreaks and conspicuous MPB-caused whitebark pine mortality (Logan and Powell 2001, ASRD and ACA 2007). Recently, climatic barriers to the MPB have diminished over much of the range of whitebark pine (Logan and Powell 2001, Carroll *et al.* 2004, Raffa *et al.* 2008), and significant MPB-caused mortality has been observed in this species across the continent (Campbell and Antos 2000, ASRD and ACA 2007, Gibson *et al.* 2008, Bockino 2008, Larson 2010). In the more distant past (10 000 to 8 000 years ago) MPB remains in alpine lake sediments have coincided with a decreases in the ratios of whitebark : lodgepole pine pollen, suggesting MPB activity caused dramatic whitebark pine mortality during those times, revealing the antiquity of the relationship between these two species (Brunelle *et al.* 2008). However more work is needed to fully understand impacts of climate on the historic patterns of MPB activity in ancient whitebark pine forests.

1.2 Objectives

Knowledge of how MPB populations will spread through stands containing whitebark pine is limited. Relatively little work has been done on the MPB in whitebark pine (*e.g.*, Amman 1982, Gross 2008), although our knowledge has grown over the past few decades as MPB caused mortality became increasingly apparent in subalpine forests. The majority of work to date documents patterns of MPB attack (Baker *et al.* 1971, Campbell and Antos 2000, Perkins and Roberts 2001, Bockino 2008, Smith *et al.* 2008, Larson 2010) or models the impacts of climate change on temperature driven development of the MPB in whitebark pine stands (Logan and Powell 2001, Bentz *et al.* 2011). Little is known about the susceptibility or host quality of whitebark pine compared to lodgepole pine (*Pinus contorta* Doug. *ex.* Loud. (*var. latifolia* Engelm.)), the MPB's primary host, particularly inWestern Canada (ASRD and ACA 2007). In this thesis, I endeavored to fill that void through study of MPB life history traits in whitebark pine through both laboratory and field experiments. I also investigated the little known beetle fauna living in MPB killed whitebark pines as a means to assess host effects on the competitors and natural enemies of the MPB, as well as to collect natural history information on many dead wood associated non-pest species. This information will help land managers allocating resources for MPB mitigation and control in ways that will be most effective for whitebark pine conservation.

1.3 Thesis outline

I have arranged this thesis into five chapters. Here, in Chapter 1, I establish the rationale and context for my research and provide pertinent background information about whitebark pine and the MPB.

In Chapter 2, I endeavored to determine the host quality of whitebark pines relative to lodgepole pines through a controlled laboratory experiment. Mountain pine beetles were reared in laboratory using freshly cut whitebark and lodgepole pine bolts. Successful gallery initiation, brood production and brood condition were compared between the two hosts. This work showed that MPB life history traits were influenced by host species and phloem thickness. Interestingly, one species was not of superior quality than the other for all life history traits examined and the relative importance of host species effects varied with phloem thickness.

In Chapter 3, I compared host quality and susceptibility of live whitebark and lodgepole pines in the northern and southern parts of whitebark pine distribution in Alberta. Mountain pine beetle pheromones were used to induce simultaneous attack on similar size, adjacent pairs of whitebark and lodgepole pines. Reproduction, development and survival were monitored in these trees throughout the year. Overall, host effects were relatively small compared to climatic effects, suggesting that quality and susceptibility differed little between whitebark and lodgepole pines. These data also indicated that climatic conditions are becoming more favorable for MPB survival and development, even at the northern part whitebark pine distribution.

In Chapter 4, I compared the beetle (Coleoptera) fauna inhabiting MPB killed whitebark and lodgepole pine stands, in two regions of Alberta. Overall, host influences on the beetle assemblage were smaller than the effects of time since tree death and spatial variables (*i.e.*, region and stand). Notable differences were observed in the two hosts between competitors and predators of the MPB, most important was the apparent preference of *Ips pini* (Say) for lodgepole pine over whitebark pine. Furthermore, with the exception of a few unidentifiable species, we did not find evidence of species exclusively associated with whitebark pine, suggesting that falling and burning MPB killed whitebark pines will not create problems for conservation of non-pest beetle species.

In Chapter 5, I synthesize the results of the three previous data chapters, provide suggestions for future research and outline the management recommendations that could be identified from the outcomes of these experiments.

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Chapter 2: Gallery success, brood production and condition of mountain pine beetles reared in whitebark and lodgepole pine from Alberta, Canada.

2.1 Introduction

The mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, is among a small group of native North American bark beetles capable of infesting and killing large numbers of mature pine trees over widespread areas, and is considered the most destructive of all western forest insects (Furniss and Carolin 1977, Wood 1982). The MPB has a broad host and range distribution, capable of infesting 22 species of pines from northwestern Mexico (31ºN) to northern Alberta and British Columbia (58ºN) (Furniss and Schenk 1969, Wood 1982). The nature of MPB activity, and the role it plays in natural disturbance regimes, varies across different forest types and eco-regions, and has been studied extensively (*e.g.*, Roe and Amman 1970, Amman 1973, Cole and Amman 1980, Rogers 1996, Cudmore *et al.* 2010, Bentz *et al.* 2011). However, the current MPB outbreak in western Canada is unprecedented in terms of geographic scale, and is likely related to anthropogenic factors including fire suppression, which have resulted in huge areas of overmature stands, and winter warming due to climate change (Carroll *et al.* 2004, Taylor and Carroll 2004, Raffa *et al.* 2008, Safranyik *et al.* 2010). Given these novel conditions and expansion of MPB into areas not previously affected, there is need for new empirically based management recommendations to refine best practices for managing the MPB.

The MBP expansion into areas that have historically been climatically unfavorable for the beetle has generated much discussion and interest (Logan and Powell 2001, Carroll *et al.* 2004, Cudmore *et al.* 2010). While the dramatic expansion of the MPB into northern Alberta and British Columbia and eastward into the boreal forest has garnered the majority of attention (*e.g.*, Safranyik *et al.* 2010), sustained outbreaks at high altitudes in other parts of the range are equally novel and potentially devastating. During the past century, high elevation, subalpine forests of western North America have experienced infrequent MPB outbreaks, typically associated with prolonged periods of unseasonably warm summer and winter temperatures (Hiratsuka *et al.* 1981, Logan and Powell 2001, ASRD and ACA 2007, Logan *et al.* 2010). A number of endangered and/or threatened five needle pines including whitebark pine (*Pinus albicaulis* Engelm.), foxtail pine (*P. balfouriana* Grev. & Balf.), Rocky Mountain bristlecone pine (*P. aristata* Engelm.) and Great Basin bristlecone pine (*P. longaeva* Bailey) thrive in these high-altitude forests (Keeley and Zedler 1998, Gibson *et al.* 2008). These species are sensitive to changes in disturbance regimes because they grow slowly and mature late in life. As whitebark pine is a foundational and keystone species in sub-alpine zones (Tomback *et al*. 2001, Ellison *et al.* 2005), the recent expansion and persistence of MPB in high altitudes is a cause for special concern (ASRD and ACA 2007, Gibson *et al.* 2008, Larson 2010, Bentz *et al.* 2011).

Whitebark pine has been devastated throughout most of its range in Canada and the USA by several interacting factors. The accidental introduction of an exotic fungal pathogen, white pine blister rust, *Cronartuim ribicola* Fischer, has been the primary cause for the decline of the species to date (reviewed in Tomback *et al.* 2001, Zeglen 2002, ASRD and ACA 2007, Smith *et al.* 2008, Gibson *et al.* 2008). Fortunately, whitebark pine mortality due to white pine blister rust is not as severe in the central and northern parts of its Canadian distribution as compared to the 'center of abundance' of the species in the northwestern USA (Campbell and Antos 2000, Gibson *et al.* 2008, Smith *et al.* 2008, Logan *et al.* 2010). Nonetheless, the recent MPB outbreak in Alberta and BC, together with the serious impact of the rust, may reduce persistence of whitebark pine as an important ecological player in high altitude ecosystems. In addition, whitebark pine is further threatened by fire exclusion, which favors competing species, and a reduction in suitable habitat due to climate change. Consequently, whitebark pine is recognized as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2010) and by the Fish and Wildlife Service (Department of the Interior Fish and Wildlife Service 2010) in the United States, though full protection under federal law is pending in both jurisdictions.

Whitebark pine stands in Canada are relatively healthy and are important for the conservation and recovery of this pine species nationally and continentally; however, the extent to which whitebark pine stands in Canada will remain relatively healthy is uncertain. The severity and nature of MPB impact on whitebark pine depends on interactions between the beetle and its host. Important life history features of MPB (*e.g.*, survival, fecundity, condition, development) are known to vary in different host tree species (Knight 1959, Reid 1962a, 1962b, 1963, Billings and Gara 1975, Amman 1982, Safranyik and Linton 1982, 1983, Amman and Cole 1983, Langor 1989, Langor *et al*. 1990, Cerezke 1995, Gross 2008). Host associated differences in key life history parameters ultimately determine host suitability and directly influence MPB population dynamics and success.

There is relatively little empirical data about the quality of whitebark pine as a host for the MPB, and the two laboratory experiments that have been published support different conclusions (Amman 1982, Gross 2008). Both of these studies are based on host material from only one or two trees of each species, and thus the contradictory nature of their results could simply reflect natural variation within a tree species. Therefore, to increase understanding of the suitability of whitebark pine as a host for the MPB, and to explore host quality in an unstudied part of the distribution of this host species, I undertook a laboratory study using a larger number of host individuals to compare the population parameters of gallery success, brood production and brood adult condition for MPBs reared in whitebark and lodgepole pine bolts. These parameters were then interpreted in relation to host quality for the beetle. I collected host material from a greater number of trees than in previous studies in an attempt to encompass the range of natural variation for each host within a stand.

2.2 Methods

2.2.1 Collection and preparation of host material and beetles

Host material for rearing MPB was collected near Vickary Creek in southern Alberta (49.7757° N, 114.5282° W), in conjunction with a separate study of blue-stain fungal virulence. Host trees were located on an east-facing slope situated in a mixture of whitebark pine, lodgepole pine (*Pinus contorta* Doug. *ex.* Loud. *(var. latifolia* Engelm.)), Engelmann spruce (*Picea engelmannii* Perry *ex.* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) at 1950 m elevation. Ten whitebark (DBH 16-31cm) and 10 lodgepole pines (DBH 19-29) with no visible signs of insect damage or disease were inoculated at breast height with three species of blue-stain fungi (*Leptographium longiclavatum* Lee, *Ophiostoma montium* (Rumbold), *Grosmannia clavigerum* (Robinson-Jeffrey and Davids)) and an agar control on 17 August 2008. These trees were felled on 22 - 23 September 2008 and a 1 m section of each bole centered on the fungal inoculations was collected for a separate experiment, not discussed here. The remaining portion of the mid-bole (1.8-5.1 m above ground) of each felled tree was used as a source of 2-3 bolts (each 1.1 m in length) for the experiment described here.

When possible, bolts were taken from sections of the bole without forks, branch stumps, or obvious mechanical damage. Bolts were collected from three additional trees of each species (not inoculated as above) to substitute for bolts that were damaged during felling and transportation. Bolts were transported to the Canadian Forest Service, Northern Forestry Center in Edmonton, Alberta, and held in an environmentally controlled greenhouse (22°C:18°C, 12L:12D). The bark surface of each bolt was divided into 1-3 strips, each 1.1m long and $\geq$ 30 cm wide, depending on bolt circumference, by cutting longitudinal grooves with a chainsaw through the bark *ca.* 1 cm into the sapwood. Paraffin wax was used to seal the ends and grooves of each bolt to slow desiccation and reduce infection by saprophytic fungi.

Bolts containing developing MPBs were collected from infested lodgepole pines near Eureka River, in northern Alberta (56.4799° N, 118.5177° W) on 4 September 2008. Infested bolts were held at 5° C until 20 October 2008 and then moved to the greenhouse to allow larvae to complete development. Bolts were placed in large ventilated plastic rearing containers (modified 110-litre black garbage cans) in the greenhouse, and reared under the conditions described above. Emerging beetles were collected daily from the rearing containers, placed in Petri plates lined with fresh pine phloem [sexes separated according to Lyon (1958)], and stored in the dark in a cooler at 8°C until used.

2.2.2 Gallery initiation and beetle collection

I attempted to establish one MPB gallery in each bark strip on each bolt. A newly emerged female beetle was placed in a small hole scored into the bark and phloem *ca.* 30 cm from the base of the bolt. The hole was then sealed with one half of a large gelatin capsule to prevent female escape. After 24 hrs, each hole was checked for gallery initiation, as indicated by boring dust in the gelatin capsule. Females failing to initiate a gallery after 24 hrs were re-inserted into their hole, while dead females were replaced with living females from the Eureka River bolts.

After gallery construction proceeded to the point where females were no longer visible at the entrance of their gallery, a male was inserted into the gallery entrance and the gelatin capsule was replaced to prevent escape. Capsules were checked again after 24 hrs and dead or rejected males were replaced by new males in the gallery entrance. This procedure was repeated daily for seven days (17-23 December 2008), after which I stopped attempting to initiate galleries on those bark sections where galleries had not already been established. In total, I attempted to establish 49 galleries in lodgepole pine and 53 in whitebark pine.

Each bark strip was ‘caged’ with 1 mm^2 nylon screen. To accomplish this, wooden slats (*ca.* 1 cm thick, 3 cm high, and the length of the bolt) were inserted into the chainsaw grooves on each bolt. Then nylon screen was glued and stapled to the top and ends of each slat and to the top end of the bolt. The screen at the bottom end of each cage was formed into a funnel-shape, fit with a collecting jar and then sealed to the bolt with glue and staples to prevent any beetle escape. Emerging F_1 adults were collected daily, placed in individual 1.5 ml microcentrifuge tubes, and stored at -20°C for further analysis.

2.2.3 Gallery dissection and beetle condition

After brood adults stopped emerging (16 March 2009), the bolt diameter and the total number of emergence holes was recorded for each gallery. Bark and phloem thicknesses were measured with calipers (0.01 ± 0.005 cm) at the top and bottom of each bark strip and recorded as an average of these two measurements. The bark was then pealed so that egg gallery length and number of larval galleries could be recorded. The number of eggs laid per gallery (fecundity) could not be assessed because it was impossible to accurately tally dead eggs or identify egg niches in the degraded phloem. Consequently, mating and oviposition could not be used as criteria to identify gallery success. I deemed galleries to be successful if at least one larval gallery was visible along the parent gallery.

To assess the condition of the brood adults, I sexed and determined the size of all 1107 beetles collected from caged galleries. I further investigated the condition of brood adults by determining the mass and percent body fat of 515 female beetles. Pronotal width and length of all beetles was measured to the nearest 0.1 ± 0.05 mm using a Motic K series dissecting microscope (at 8X magnification) and ocular micrometer. Size was calculated for each beetle by generalizing their shape to a prolate spheroid using these measurements.

Measured female beetles were dried at 75° C for 24 hrs before determining their mass to the nearest microgram using a Sartorius CP2P balance. Female beetles were then individually placed in a perforated 1.5 ml microcentrifuge tubes and heated in a Soxhlet apparatus for 8 hrs at 35-60°C in petroleum ether. Beetles were returned to the drying oven a second time for 24 hrs at 75°C and re-weighed. Fat content was determined as the difference in dry mass before and after fat extraction in the Soxhlet apparatus.

2.2.4 Analysis

Both parametric and nonparametric statistical methods were used to analyze the data. Histograms and qq-plots (Harnett 1982) were used to visualize distributions of the data and help select appropriate tests for the questions asked. Possible differences between hosts in the size of bolts used for the experiment were tested by a two-sample Kolmogor-Smirnov test (KS). Relationships between bolt size, phloem thickness, bark thickness and host species were investigated using generalized linear modeling (GLM) with normally distributed errors ($N(\mu,\sigma^2)$) and identity link functions.

Effects of host species, phloem thickness, and bolt size on gallery success were tested by a Generalized Linear Mixed Model (GLMM) with a logistic link function, binomially ($B(n,p)$) distributed errors and the tree from which the bolt was collected included as a random effect. Gallery characteristics were compared between the two host species using two-sample KS tests. Total emergence per gallery was compared between hosts by Poisson-based ($P(\lambda)$) GLMM with a log link function and including the tree from which the bolt was collected as a random effect. GLMMs were parameterized using host species and phloem thickness as fixed effects and tree and gallery as nested-random effects and used to model beetle size ($N(\mu,\sigma^2)$), weight ($N(\mu,\sigma^2)$), and fat content ($G(\kappa,\theta)$). Sex was added as an additional factor to the model of beetle size (analyzing the sexes separately did not drastically alter model results).

Interaction terms with p-values > 0.05 were dropped from all final models. GLMs were fit by maximum likelihood estimates, while GLMMs were fit by penalized quasi-likelihood estimates. Sample sizes and variances differed between host species-phloem thickness combinations for most parameters so inspection of standardized residuals and Cook's distances ($<4/n$) were used to evaluate the models. Measures of beetle condition were compared to one another using multiple Pearson's correlations. Continuous variables in all linear models were normalized (subtract mean and divide by standard deviation) to remove unit effects. All analyses were performed in R version 2.8.1 (R Development Core Team 2008) using the *nlme* (Pinheiro *et al.* 2008) and *MASS* (Venables and Ripley 2002) packages following procedures outlined by Zuur *et al*. (2009).

Since I attempted to establish more than one gallery per bolt, and collected more than one bolt per tree, experimental units were not independent. Therefore, I included nested-random variables into the analysis to partition as much of this variation as possible. The alternative, attaining completely independent experimental units (*e.g.*, establishing one gallery per tree) was not realistic given the conservation status of whitebark pine and consequent limitations on the number of live trees that could be sacrificed.

2.3 Results

2.3.1 Host material

Bolts used to rear beetles ranged in diameter from 15 to 31 cm, with an average of 24 cm, and were similar in size between the two host species (KS, n=48 D=0.333, p=0.134). Furthermore, there were no significant differences in phloem thickness (GLM $N(\mu,\sigma^2)$, $\beta_{sp}=0.0005$, t=0.071, p=0.944) or total bark thickness (GLM $N(\mu,\sigma^2)$, $\beta_{sp}=0.019$, t=1.204, p=0.235) between host species. Phloem thickness (GLM $N(\mu,\sigma^2)$, $\beta_d=0.005$, t=0.756, p=0.459) and total bark thickness (GLM $N(\mu,\sigma^2)$, $\beta_d=0.021$, t=1.271, p=0.210) were not significantly related to bolt diameter, although, some larger diameter bolts of either species had thicker bark and phloem.

2.3.2 Gallery success

Gallery success varied with phloem thickness and host species. Of the 102 attempted galleries, 29 pairings from 12 different lodgepole pine trees and 14 pairings from eight different whitebark pine trees produced brood. Bolts with thicker phloem (GLMM B(n,p), $\beta_{ph}=1.38$, df=73, t=3.629 $p<0.001$) and lodgepole pine bolts (GLMM B(n,p), $\beta_{sp}=2.2$, df=25, t=3.629, p=0.001) were more likely to produce successful galleries (Figure 2.1). Nonetheless, larger bolt diameter did not significantly increase the probability of gallery success (GLMM B(n,p), $\beta_d=0.329$, df=73, t=1.164, p=0.248). For the 59 unsuccessful pairings, 28 (17 in whitebark and 11 in lodgepole) had no egg galleries excavated into the bark. The remaining 31 pairings had egg galleries that were short and varied in length from 1.0 to 15.5 cm with either one (8 whitebark and 6 lodgepole) or both parents dead in the gallery (1 lodgepole pairing), or were seemingly abandoned (12 whitebark and 4 lodgepole).

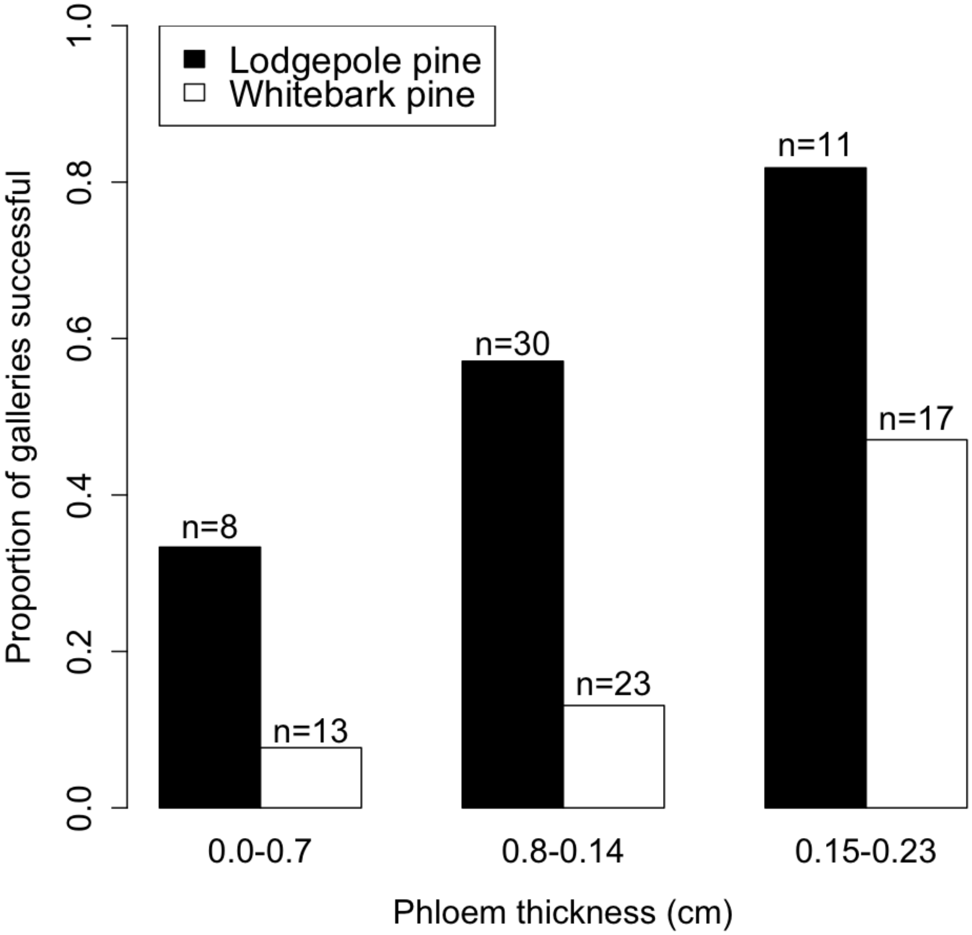

Figure 2.1: Proportion of attempted mountain pine beetle egg galleries that were established successfully on whitebark and lodgepole pine bolts of different phloem thickness (cm). n represents the number of attempted pairings for each size-class/species combination. Egg galleries were deemed successful if they produced at least one larva, as evidenced by larval gallery construction.

2.3.3 *Gallery characteristics*

Mean egg gallery lengths (±SE) were similar (KS, n=38, D=0.179, p=0.877) between lodgepole (38.6 ± 4.38 cm) and whitebark (36.7 ± 6.20 cm) pines. Although the mean number of larval galleries/egg gallery did not differ statistically among hosts (KS, n=39, D=0.380, p=0.149), it was highly variable and there was a trend towards higher numbers of larval galleries in whitebark (76.4 ± 14.21) than in lodgepole pine bolts (54.1 ± 6.74). This trend appears to reflect that a higher relative proportion of the galleries in whitebark pine were in bolts with thick phloem. Larval gallery density (number of larval galleries per cm of egg gallery) differed between host species (KS, n=39, D=0.61, $p<0.001$), and was higher in whitebark pine (3.2 ± 0.43/cm) than in lodgepole pine (2.1 ± 0.27/cm).

Gallery length, number of larval galleries per egg gallery and larval gallery density were all unrelated to phloem thickness in lodgepole pines (Figures 2.2 A, B, C). However, some gallery characteristics were bi-modally distributed in whitebark pine according to phloem thickness: bolts with thin phloem had short egg galleries and fewer larval galleries/egg gallery but those with thick phloem had longer galleries and more larval galleries/egg gallery (Figure 2.2 A, B)

2.3.4 *Brood survival and sex ratio*

A significantly higher proportion of larvae successfully completed development to adulthood in lodgepole pine, 71% ± 4.9 (SE), than in whitebark pine, 53% ± 4.8 (KS, n=39, D=0.528, p=0.008). Interestingly, survival was unrelated to phloem thickness (Figure 2.2 D). The overall sex ratio of brood adults was similar between lodgepole pine (50% female) and whitebark pine (48% female) bolts.

2.3.5 *Brood adult production*

The total number of emerged brood adults per egg gallery is a function of both parental fecundity and larval survival. Brood adults emerged from all successful galleries except one where all larvae died as early instars in a lodgepole pine bolt. The main effects of host species (GLMM $P(\lambda)$, $\beta_{sp}=0.31$, df=17, t=0.907, p=0.377), phloem thickness (GLMM $P(\lambda)$, $\beta_{ph}=0.12$, df=20, t=0.675, p=0.507) and bolt diameter (GLMM $P(\lambda)$, $\beta_{d}=0.15$, df=20, t=1.07, p=0.294) were not significant. However, there was a trend (GLMM $P(\lambda)$, $\beta_{sp*ph}=0.49$, df=20, t=1.929, p=0.068) for brood production to be much higher in lodgepole than in whitebark pine bolts when phloem was thin (<0.15 cm), although brood production was similar between the two species in bolts with thick-phloem (>0.15 cm) (Figure 2.3).

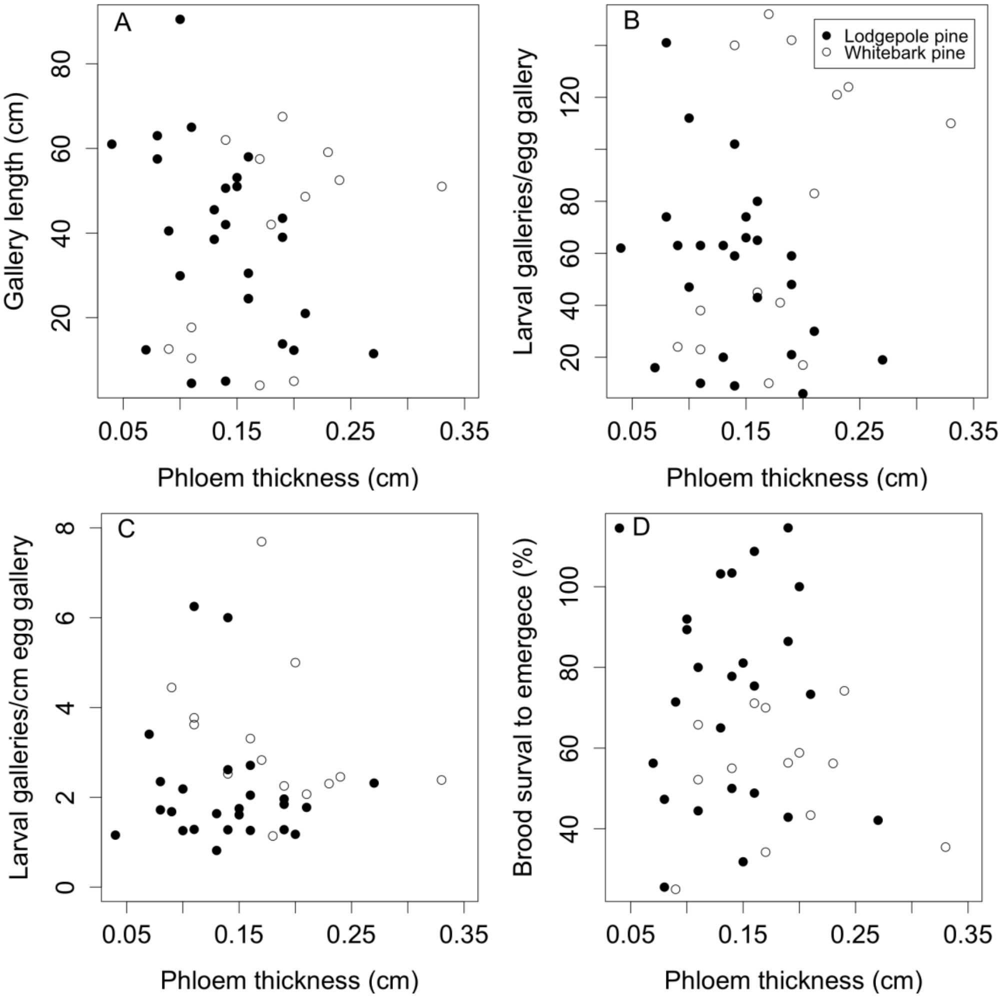

Figure 2.2: Gallery characteristics of the mountain pine beetle reared in two hosts, whitebark pine (white) and lodgepole pine (black). Plots depict: (A) egg gallery length (cm); (B) total number of larval galleries measured along and egg gallery; (C) density of larval galleries along an egg gallery; and (D) survival of brood larvae, calculated as percent of 1st instar larvae that emerged, as they vary with host species and phloem thickness (cm) of bolts.

2.3.6 Brood adult condition

Beetle size varied with host species, phloem thickness and sexes. As is typical for MPB, female adults were significantly larger in volume than males (whitebark pine female: 26.7 ± 0.30 (SE) mm^3; male: 20.4 ± 0.25 mm^3; lodgepole pine female: 24.9 ± 0.27 mm^3; male: 17.7 ± 0.21 mm^3) (GLMM N(μ,σ^2), β_{sex}= 6.5, df=1051, t=27.77, p<0.001). The main effects of phloem thickness (GLMM N(μ,σ^2), β_{ph}= 0.17,

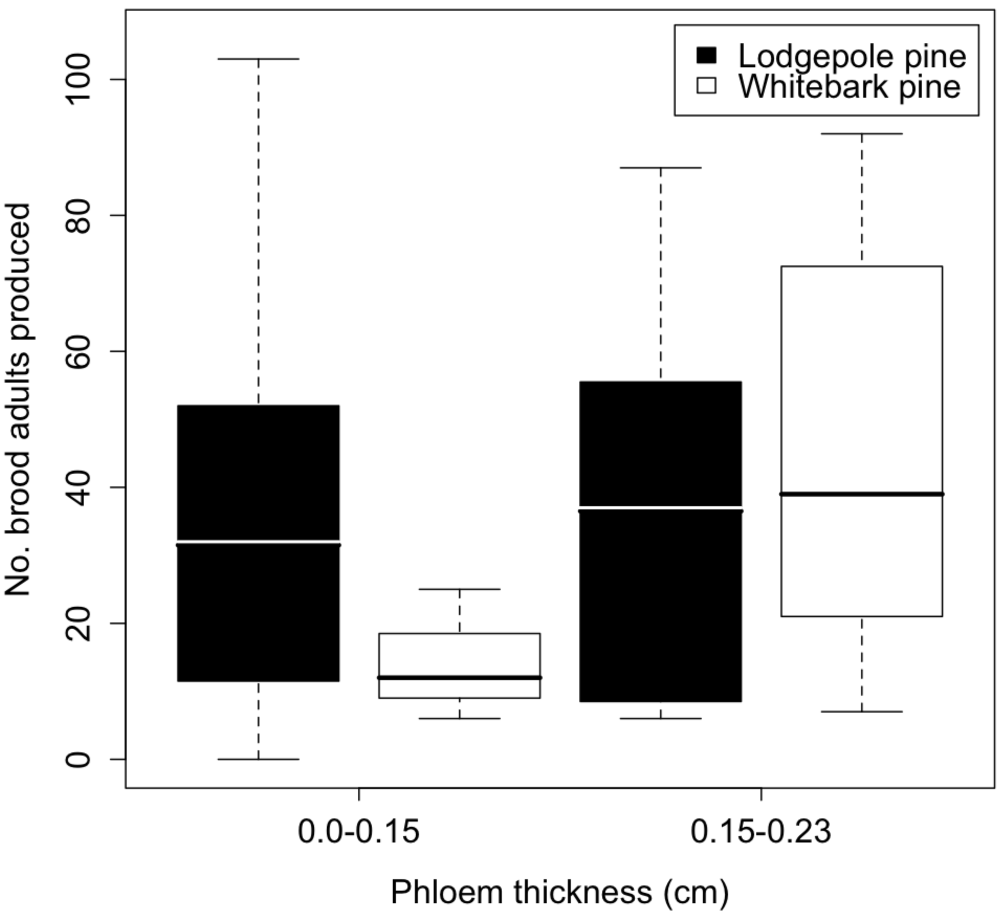

Figure 2.3: Mean number of mountain pine beetle brood adults emerging per egg gallery from experimental rearings in whitebark and lodgepole pine bolts. Box and whiskers represent the quartiles of the distributions of brood sizes from each host and phloem thickness combination.

df=1051, t=0.490, p=0.625) and host species (GLMM N(μ,σ^2), β_{sp}= 0.65, df=51, t=1.14, p=0.260) were not significant. There was, however, a significant interaction between the two main effects (GLMM N(μ,σ^2), β_{sp*ph} = 2.47, df=1051, t=4.47, p=0.001). In general, lodgepole pine produced larger beetles when phloem was thin (< 0.15 cm), but whitebark pine produced larger beetles when the phloem was thick (> 0.15 cm) (Figure 2.4 A, B; sexes plotted separately for clarity, though they were analyzed in the same model)

Mass of brood beetles varied with host species and phloem thickness. Mass was on average greater for females reared in whitebark pine, 5.31 ± 0.074

(SE) mg, than in lodgepole pine, 4.61 ± 0.076 mg, though this difference was not significant (GLMM $N(\mu,\sigma^2)$, β_{sp}= 0.19, df=18, t=0.855, p=0.404). Although female mass also tended to increase with phloem thickness in both hosts, the main effect was not significant [(GLMM $N(\mu,\sigma^2)$, β_{ph}= 0.11, df=19, t=0.67, p=0.510]. However, there was a significant interaction between the effects of host species and phloem thickness (GLMM $N(\mu,\sigma^2)$, β_{sp*ph} = 0.58, df=19, t=2.402 p=0.028). In general, lodgepole pine produced heavier beetles when phloem was thin (< 0.15 cm), but whitebark pine produced heavier beetles when the phloem was thick (> 0.15 cm) (Figure 2.5).

Fat content (% of dry mass) varied with host species and phloem thickness. Fat content was significantly higher in beetles reared in lodgepole pine 36.0 ± 0.6% (SE), compared to those from whitebark pine, 33.4 ± 0.4% (GLMM $G(\kappa,\theta)$,β_{sp} =0.0044, df=18, t=2.957, p=0.008). Fat content increased with phloem thickness (GLMM $G(\kappa,\theta)$, β_{ph} = 0.001, df=20, t=2.39, p=0.027)), and unlike for data about size and mass, tended to be greater in lodgepole pine bolts across the full range of phloem thickness (Figure 2.6).

The three measures of beetle condition were related to varying degrees. Female beetle size and mass were strongly correlated (df=511, ρ=0.606, t=17.221, p<0.001) but size and percent fat were not (df=511, ρ=0.066, t=0.135, p=0.136). Female beetle mass and percent body fat were significantly but only weakly correlated (df=511, ρ=0.136, t=3.110, p=0.002).

2.4 Discussion

2.4.1 Host effects

Interpreting host quality from beetle rearings established in cut bolts is challenging as the host environment is undoubtedly very different in bolts compared to trees attacked naturally, especially insofar as host defenses are

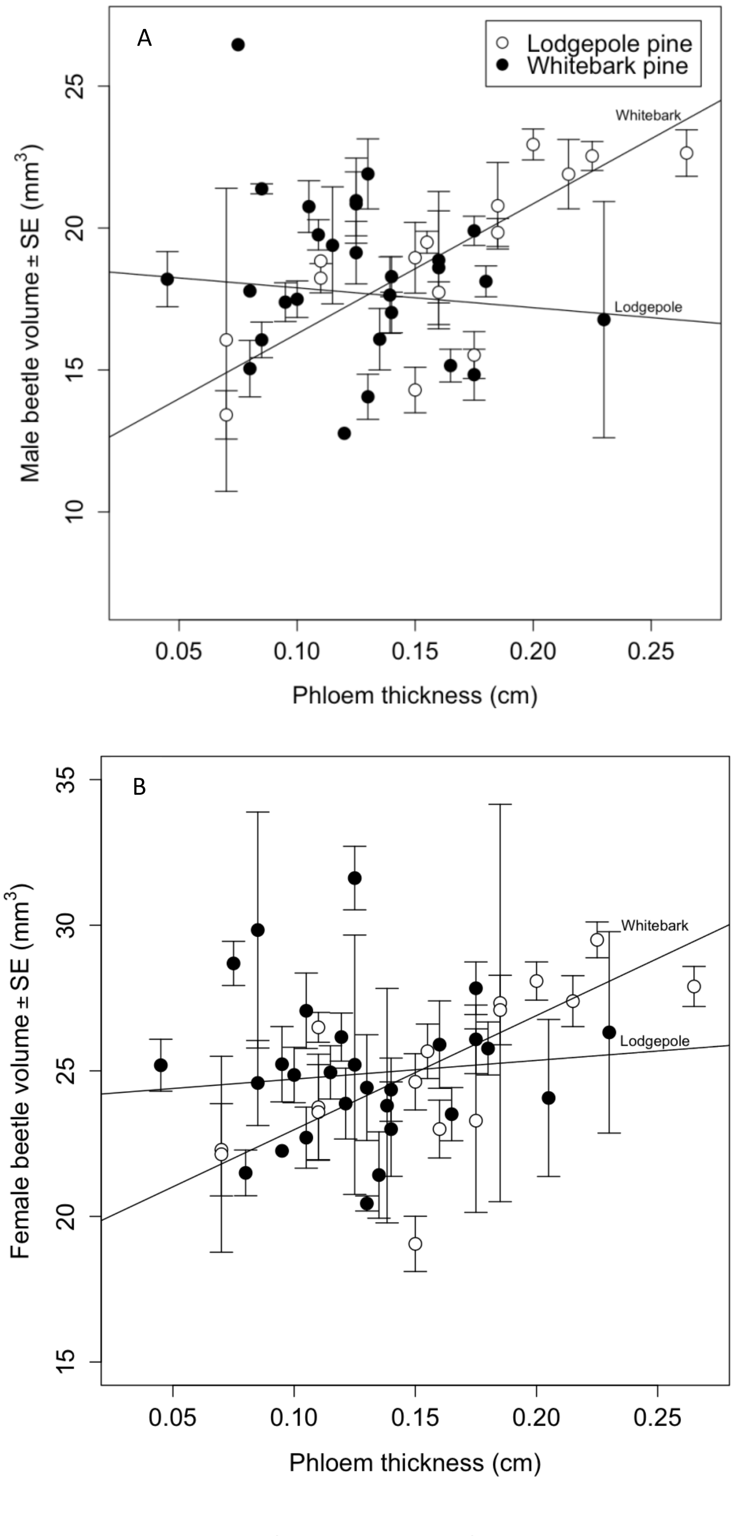

Figure 2.4: Mean ± SE volumes of male (A) and female (B) mountain pine beetles reared in whitebark and lodgepole pine bolts. Each line represents predictions from the fixed components of a GLMM of volume for each host species separately.

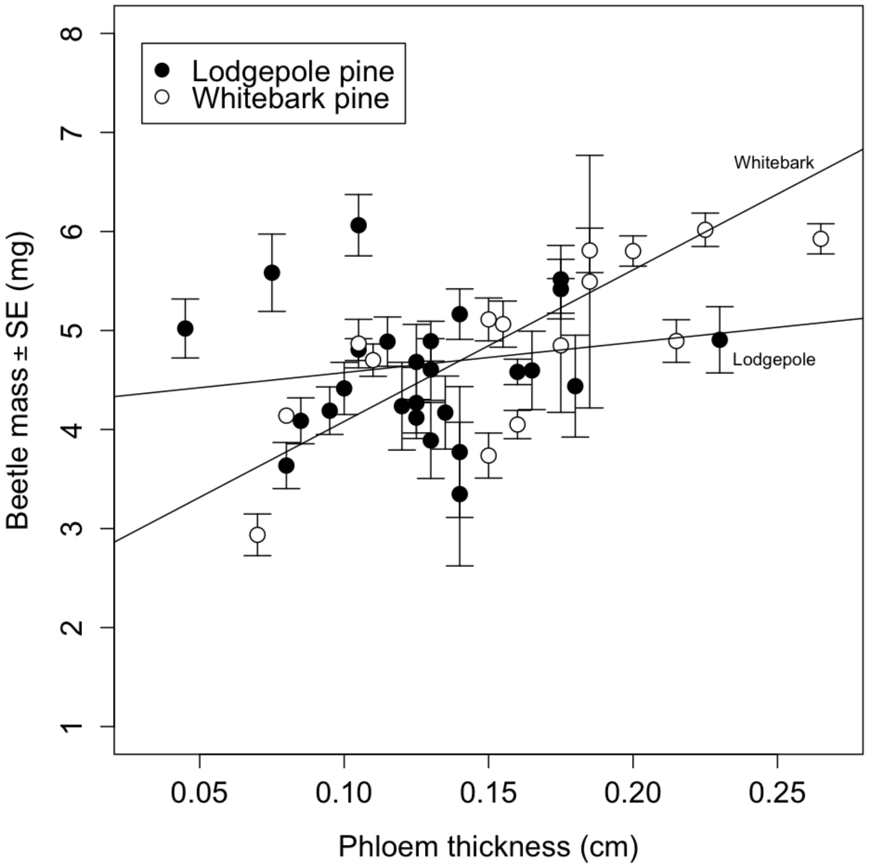

Figure 2.5: Mean ± SE mass of female mountain pine beetles reared in whitebark and lodgepole pine bolts. Each line represents predictions from the fixed components of a GLMM of mass for each host species separately.

concerned. Thus, data like those presented here cannot provide a complete description of host effects; however, they may reveal simple differences in the constitutive qualities of host tissues. My results clearly underscore that bark beetle life history traits vary with host species (Knight 1959, Reid 1962a, 1962b, 1963, Billings and Gara 1975, Amman 1982, Safranyik and Linton 1982, 1983, Amman and Cole 1983, Langor 1989, Langor *et al*. 1990, Gross 2008), phloem thickness (Amman 1969, Roe and Amman 1970, Amman 1971, Amman and Pace 1976, Berryman 1976, Amman and Pasek 1986) and that one host is not always best with respect all life history traits (Amman 1982, Cerezke 1995, Gross 2008), corroborating many previous studies. However, the difference(s) between whitebark and lodgepole that affect life history traits did not vary monotonically, but were a function of phloem thickness. Consequently, one species was not always the best host for the MPB across the entire range of phloem thickness in a stand. Furthermore, two different patterns of variation in life history traits were observed with respect to host species and phloem thickness.

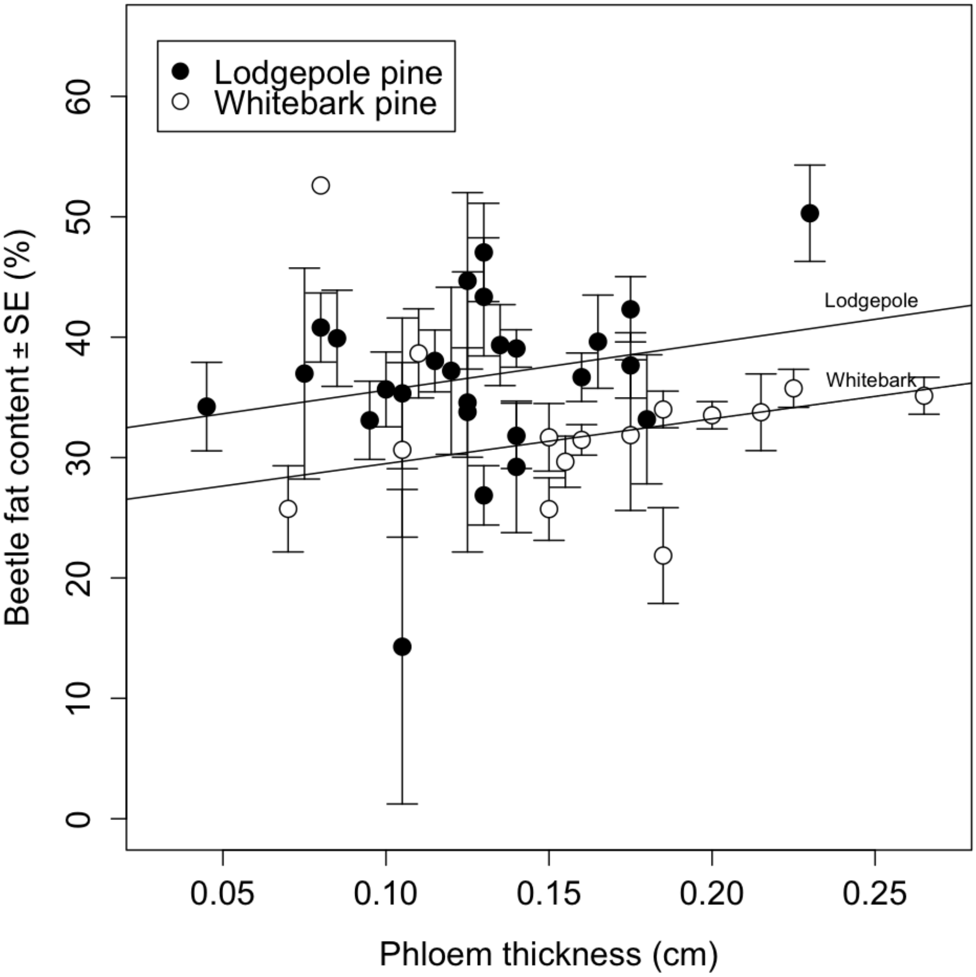

Figure 2.6: Mean ± SE fat content (% of dry weight) of female mountain pine beetles reared in whitebark and lodgepole pine bolts. Each line represents predictions from the fixed components of a GLMM of fat content for each host species separately.

Gallery success, fat content, and brood survival were higher in lodgepole pine, with the latter two traits increasing monotonically with phloem thickness, suggesting these traits are influenced by similar aspects of host quality. Gallery success, as defined in this study, required both egg gallery construction and survival of eggs to at least the 1st instar, and thus reflect the potential effects on two generations of MPBs. Pioneering females are more likely to construct egg galleries on larger trees, because of natural selection for thicker phloem (Cole and Amman 1969, Roe and Amman 1970, Cabrera 1978). In thick phloem the egg gallery can be entirely constructed in the soft phloem whereas in thin phloem gallery construction requires some mining of the outer phloem, tissue that is less nutritious and more energetically costly to tunnel through (Cole and Amman 1980, Amman and Cole 1983). Gallery initiation is also partially controlled by gustatory and olfactory feedback from chemical properties of host tissues (Hodges *et al.* 1979, Sturgeon 1979, Elkinton and Wood 1980, Moeck *et al.* 1980, Cates and Alexander 1982*)* with particular compounds known to attract or repel beetles (Smith 1975, Bordasch and Berryman 1977, Raffa and Berryman 1982a). In contrast, survival of eggs is largely influenced by exposure to resin (Reid 1963, Reid 1970), making quantitative or qualitative differences in the chemical constituents of the sub-cortical tissues of the trees a candidate for explaining the observed pattern of gallery success. Larval survival is also in part influenced by the constitutive levels of defensive compounds found in sub-cortical tissues (Reid and Gates 1970, Sturgeon 1979, Raffa and Berryman 1982b, 1983a, 1983b, Paine and Stephen 1987, Raffa and Smalley 1995, Franceschi *et al.* 2005). The effects of defensive compounds on brood fat contents are not completely understood, though beetles with greater fat contents are more likely to survive exposure to toxic resin vapors (Reid and Purcell 2011). López *et al.* (2011) found that detoxifying these compounds is energetically costly in adult beetles. From this, one might deduce that a host with less toxic sub-cortical chemistry would produce brood beetles with greater fat reserves.

Differences in composition of monoterpenes, a dominant class of insect-related defensive compounds found in the sub-cortical tissues of pines, have been found between whitebark and lodgepole pines (Smith 2000). Lodgepole pine has a greater relative quantity of β-pinene (Smith 2000), a compound which positively affects beetle feeding in laboratory experiments (Raffa and Berryman 1982a). Furthermore, whitebark pine has *ca*. 1.5 times the concentration of limonene, compared to lodgepole pine; this compound is highly toxic to the MPB (Raffa and

Berryman 1982a, 1982b, 1983b) and repels other bark beetles (Smith 1975, Bordasch and Berryman 1977). Thus, concentrations of these two compounds in the two host species likely contributes to the differences in life history traits observed in this experiment.

Interaction of host species and phloem thickness was reflected in patterns of variation in brood size (volume), brood mass, and to a less pronounced extent, brood production, gallery length, and larval galleries/egg gallery. With respect to these traits, whitebark pine was a poorer host than lodgepole pines in instances when phloem was thin (< 0.15 cm) whereas whitebark pine was equal or superior in host quality to lodgepole pine in instances when phloem was thicker (> 0.15 cm). Many trees with thick phloem produce longer, more densely spaced egg galleries and more brood per unit area of bark (Roe and Amman 1970, Amman 1971, Amman and Pace 1976, Berryman 1976, Amman and Cole 1983, Amman and Pasek 1986). In addition, identity of host species also impacts brood production, size and weight (Amman 1982, Langor *et al.*1990, Cerezke 1995). However, interactions like the one featured in our results have not bee commonly reported.

Understanding why the relationships between phloem thickness and host quality differ between host species and how these complex relationships affect various life history traits in bark beetles is challenging. With respect to relative host quality of lodgepole and whitebark pines, results of other research has been perplexing. For example, Amman (1982) found that whitebark pines bolts produced more and larger brood compared to lodgepole pines while, Gross (2008) found that lodgepole pine bolts produced more brood than whitebark pines while whitebark pines produced larger beetles. Unfortunately, these authors did not report the effects of phloem thickness on brood production or brood condition, and thus the interactive effects uncovered by the present study may explain these apparent contradictions.

A number of host factors could be potentially related to the variation in MPB life history traits. Lodgepole pine is a fast-growing, disturbance adapted, early successional species that produce a semi-serotonous seed set early in their growth (5-20 years) (Keeley and Zedler 1998). Whitebark pines are also disturbance adapted, early successional species, but grow more slowly and mature much later (after 20-50 years), produce large, animal-dispersed seeds in mast years and are tolerant of extreme cold (Arno and Hoff 1989, McCaughey and Schmidt 1990, see also Weaver 2001 and references therein). These differences may be associated with different patterns in constitutive chemical defenses, non-structural carbohydrates, C:N ratio, or mineral nutrition along the gradient of phloem thickness. Alternatively, the physical properties of the phloem, particularly its density, may differ between the two host species. Phloem thickness is a function of annual increment, the rate of compression between vascular and cork cambiums and the amount of time dead layers of phloem persist in the inner bark (Cabrera 1978). Thus, different life histories and/or growth forms of these two host species could influence the physical nature of the phloem, though this aspect of host quality was not measured in the study. Further investigation of how life history strategies influence multiple aspects of host quality could help explain how the MPB will affect whitebark pine containing stands and further our understanding of insect herbivore/host interactions in general.

2.4.2 Conclusions and management recommendations

Host-mediated impacts on *D. ponderosae* in lodgepole and whitebark pine do not flow from a simple ranking of host quality; individual tree quality may be of equal or greater importance than host species. Whitebark pines with thin phloem were poor quality hosts with respect to all measured life history traits. These data correspond well with observations that small diameter whitebark pines are rarely ever attacked (Arno and Hoff 1989). Existing data on phloem thickness between these two hosts do not show one species having consistently thicker phloem than another (Baker *et al*. 1971, Six and Adams 2007). Comprehensive inventories of whitebark pine are an essential component of the recovery strategy for whitebark pine (Keane and Arno 2001). Inclusion of data about phloem thickness in these surveys could greatly improve predictive models of mountain pine beetle population dynamics. Presence of large diameter whitebark pines, which likely have the thickest phloem in the stand, will increase the rate of expansion of locally endemic MPB populations, since the largest trees are typically attacked first by MPB. Therefore, the presence of large diameter whitebark pines could contribute more to increasing beetle populations than lodgepole pines of similar size (Amman 1984). Therefore, in high-altitude pine stands at high risk of MPB infestation, large diameter whitebark pine should be prioritized for protection using verbenone pouches (an anti-aggregant) (Bentz *et al.* 2005). In stands already infested, large diameter infested whitebark pine should be prioritized for treatment (*e.g.*, cut and burn).

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Chapter 3: Survival, development and reproductive rates of mountain pine beetles in whitebark and lodgepole pines in northern and southern Alberta, Canada

3.1 Introduction

The mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, is among a small group of native North American bark beetles capable of infesting and killing large numbers of mature pine trees (Evenden *et al.* 1943, Wood 1982). Though usually innocuous, *D. ponderosae* can periodically have eruptive outbreaks and is thus an important component of the natural disturbance regime of pine forests of western North America (Furniss and Carolin 1977, Safranyik and Carroll 2006). The MPB has successfully attacked and reproduced in 22 native and introduced pine species across its historic range (pre-2000) in western North America, *i.e.*, from northern Mexico (31°N) to Central British Columbia (56°N) (Furniss and Schenk 1969, Smith *et al.* 1981, Amman and Cole 1983). Lodgepole pine (*Pinus contorta* Doug. *ex.* Loud. (*var. latifolia* Engelm.)), the main host for MPB in Canada, has co-evolved to benefit from these periodic outbreaks as an opportunity for stand renewal (Geiszler *et al.* 1980, Amman and Schmitz 1988, Stuart *et al.* 1989). In recent years, however, a MPB outbreak first noted in the mid-1990s in central British Columbia has grown dramatically, affecting an estimated 17.5 million ha of pine forest in BC as of April 2011 (BC Ministry of Forests Lands and Natural Resource Operations 2011), an area ten times larger than any previously recorded outbreak (Safranyik *et al.* 2010) with a further 6 million ha at risk in Alberta (Alberta Sustainable Resource Development 2012). Such an eruption has huge economic implications for forest-dependent communities (Wagner *et al.* 2006). The unusually large size and long duration of this outbreak has been attributed to anthropogenic factors including fire suppression, which results in an abundance of overmature stands, and warmer winters, likely due to climate change (Taylor and Carroll 2004, Raffa *et al.* 2008, Safranyik *et al.* 2010).

The current MPB eruption in Canada has expanded into areas where climate has been historically unfavorable for the beetle (Logan and Powell 2001, Carroll *et al.* 2004, Safranyik *et al.* 2010). While the dramatic expansion of the MPB into northern Alberta and British Columbia and eastward into the boreal forest has generated the majority of attention (*e.g.*, Kurz *et al.* 2008, Cudmore *et al.* 2010, Safranyik *et al.* 2010), sustained outbreaks at high altitudes in other parts of the MPB range are equally novel and potentially devastating. During the past century, high elevation, sub-alpine forests of western North America have experienced infrequent mountain pine beetle outbreaks, typically associated with prolonged periods of unseasonably warm summer and winter temperatures (Logan and Bentz 1999, Logan and Powell 2001). A number of endangered or threatened five needle pine species, including whitebark pine (*Pinus albicaulis* Engelm.), foxtail pine (*P. balfouriana* Grev. & Balf.), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), and Great Basin bristlecone pine (*P. longaeva* Bailey), thrive in less-frequently disturbed high-altitude forests (Keeley and Zedler 1998, ASRD and ACA 2007, Gibson *et al.* 2008). The increased frequency and the persistence of MPB outbreaks in high altitude forests pose a serious new risk to these species.

Whitebark pine is a foundation and keystone species of subalpine forests in western North America (Tomback *et al.* 2001, Ellison *et al.* 2005). Populations have been devastated throughout most of the species range in Canada and the USA by the exotic fungal pathogen, white pine blister rust, *Cronartuim ribicola* Fischer, (*e.g.*, Tomback *et al.* 2001, Zeglen 2002, ASRD and ACA 2007, Smith *et al.* 2008). Fortunately, whitebark pine mortality is not presently as severe in the central and northern parts of its Canadian distribution as in the northwestern USA (Campbell and Antos 2000, ASRD and ACA 2007, Smith *et al.* 2008, Logan *et al.* 2010). Whitebark pines are further threatened by fire exclusion, climate change, and the MPB. Consequently, *P. albicaulis* is recognized as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2010) and by the Fish and Wildlife Service (Department of the Interior Fish and Wildlife Service 2010) in the United States, though full protection under federal law is pending in both jurisdictions. Thus, the relatively healthy stands near the northern extent of its range in Canada are important for the conservation and recovery of whitebark, both nationally and continentally; however, the MPB poses an imminent threat to these stands. Furthermore, MPB poses an especially serious risk to whitebark pines in areas where white pine blister rust caused mortality is extensive, as the few remaining trees are likely those with resistance to the rust and thus, are critically important for the persistence of the species.

The severity and nature of the MPB impact on a particular pine species depends on interactions between the beetle and its host. However, important insect life history features of MPB (*e.g.*, survival, phenology, fecundity, development rate) often vary among host tree species (Knight 1959, Reid 1962a, 1962b, 1963, Billings and Gara 1975, Amman 1982, Safranyik and Linton 1982, 1983, Amman and Cole 1983, Langor 1989, Langor *et al*. 1990, Cerezke 1995, Gross 2008). Host-associated differences in key life history parameters ultimately determine host suitability and directly influence MPB population dynamics and success. Much research has been done to quantify and predict the growth and spread of MPB populations (*e.g.*, Berryman 1976, Cole and Amman 1980, Carroll *et al.* 2004, Cudmore *et al.* 2010, Safranyik *et al.* 2010), although research has typically focused on the most abundant pine species in the area of interest. Consequently, little work has been done on MPB in whitebark pine, especially at the northern limits of the host range in Canada.

There is relatively little empirical data on the quality of whitebark pine as a host for the MPB. The majority of studies have focused on describing patterns of MPB-associated mortality in forests containing whitebark pine, and explaining these patterns in relation to stand characteristics, distribution and severity of white pine blister rust, climatic characters, etc. (Baker *et al.* 1971, Campbell and Antos 2000, Perkins and Roberts 2001, Bockino 2007, Six and Adams 2007, Larson 2010). A few studies compared the quality of whitebark pines with other species using cut bolts, often representing only one or two trees in a stand (Amman 1982, Gross 2008, Chapter 2 of this thesis). Such research has contributed valuable information, but basic questions about the quality of whitebark pine as a host must be addressed in natural settings to better predict and mitigate the spread of the MPB under a changing climate.

I aimed to compare the quality of living whitebark and lodgepole pines as hosts for the MPB. Thus, I experimentally induced MPB attack on adjacent pairs of whitebark and lodgepole pines in the field and compared: *i*) densities of attacking MPBs; *ii*) life history parameters including, brood densities, stage dependent survival, and net reproductive rates (Ro); and *iii*) relative MPB development rates between the two hosts by examining the distributions of life stages at key times in beetle development. In addition I related MPB life history parameters to important tree-related variables including: tree size (DBH), total bark thickness, phloem thickness, density of radial resin ducts and area covered by resin blisters.

3.2 Methods

3.2.1 Study area description

I selected two study regions, Willmore Wilderness Park and the Crowsnest Pass area, that characterize the northern and southern limits of whitebark pine range in Alberta, Canada (Figure 3.1). Within each region I identified two sites that contained both whitebark and lodgepole pines in mixed stands and had current MPB activity. In Willmore Wilderness Park, the Deveber Creek site (53.72466°N, 119.54844 °W) had a south aspect at an elevation of 1500 -1550 m, and the Featherstonhaugh (53.78957°N, 119.76147°W) site had a south aspect at 1550-1650 m. In the Crowsnest Pass, the Gould Dome Mountain site (49.91425°N, 114.64792°W) had a west aspect at 1920-2060 m and the Hidden Creek site (49.945859°N, 114.58161°W) was around the crest of a hill at 1960-1990 m. All four sites had relatively continuous canopies that contained different mixtures of Engelmann spruce (*Picea engelmannii* Perry *ex.* Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine and whitebark pine. The higher elevation sites in each region, Featherstonhaugh and Gould Dome Mountain, had more subalpine fir and Engelmann spruce than pine. The lower elevation sites, Deveber Creek and Hidden Creek, were dominated by lodgepole and whitebark pines, with spruce and subalpine fir mostly limited to the understory. Stands were similar to the *major seral* and/or *minor seral* whitebark pine community types described by Arno (2001).

MPB populations in these study sites were low, although beetles have been arriving in these stands from the epidemic populations across the border in British Columbia. Prior to my experiments, infested pines had been felled and burned to aggressively control incipient MPB populations in three of the four stands. At Hidden Creek, MPB activity was low, limited to a handful of attacked trees, and there was no ongoing beetle control activity; however, nearby stands had been heavily attacked by MPB the previous year.

3.2.2 Experimental design

In each site, 3-6 pairs of one whitebark and one lodgepole pine, were selected according to the following criteria: *i*) trees within each pair were of similar diameter at breast height (DBH; range 24.5-44.0 cm, mean difference 2.0 cm, max difference 5 cm); *ii*) trees within a pair were <15 m apart; *iii*) distance between pairs was > 50 m; and *iv*) trees showed no visible signs of insect or disease damage. After data collection began, I observed that one of the apparently healthy trees was infected with white pocket rot (*Phellinus pini* (Thore: Fr.) A. Ames), and therefore, I removed this pair from my analysis. This gave a total of 17 replicate pairs for the study.

To induce MPB attack on trees, each tree was baited with a two-component (trans-verbenol, exo-brevicomin) MPB lure (Contech TM). Two lures were fastened to the north side of each tree 2 m above ground in mid-June, prior to MPB flight. This experiment was carried out in separate years in the two regions to accommodate travel logistics. In Willmore Wilderness Park, three pairs of trees were baited at each site in 2008 and sampled in 2008-2009, and in the Crowsnest Pass six pairs of trees were baited at each site in 2009 and sampled in 2009-2010.

3.2.3 Data collection

All baited trees were attacked by the MPB, as determined by the construction of egg galleries under the bark. In late August, two months following deployment of baits, I counted the number of pitch-tubes and visible gallery entrances centered at breast height (1.3 m) on a 1 m section of the bole of each baited tree to determine the density of attacking beetles. The mountain pine beetle also attacked a number of unbaited trees adjacent to our experimental pairs which were sampled as described below, but only in the last sampling period.

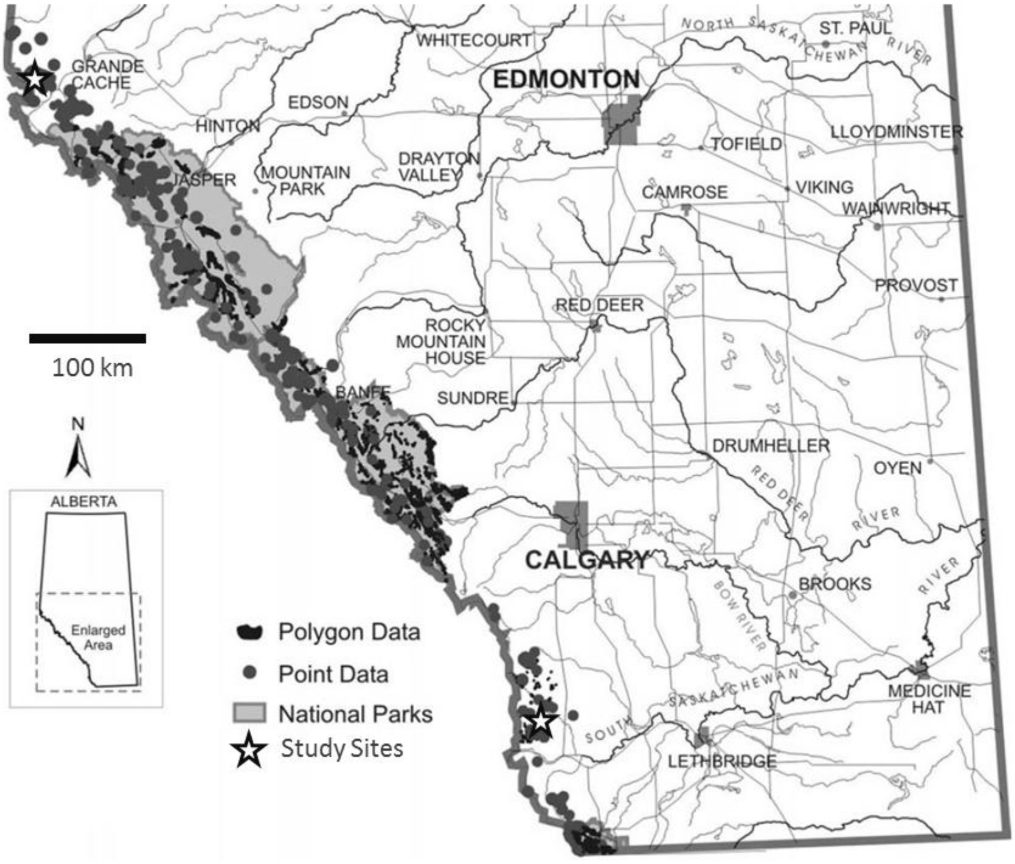

Figure 3.1: Distribution of whitebark pine in Alberta (From ASRD and ACA 2007).

Mountain pine beetle gallery construction and brood development were measured by removing 78.5 cm^2 'bark disks' from the trees. These bark disks provided a 'window' into MPB activity below the bark surface, but allowed adjacent beetles left in the tree to develop in a relatively undisturbed state. Disks were collected by using a drill and 10 cm (diameter) hole saw to make circular cuts 1-2 cm into the xylem on the bole of each tree. The wood within this circular cut was then chiseled out of the tree, making sure not to separate the bark from the sapwood. Disks were collected from the north and south aspects of each tree at 50 cm above and below breast height, and at 4 m above ground, providing 6 bark disks per tree from each sampling event. As weather permitted access to sites, disks were collected at 2-3 week intervals from August to October. Disks were collected again after winter, in June in Willmore Wilderness Park, and in April in the Crowsnest Pass (samples could not be taken from sample trees in Willmore Wilderness Park in April 2009 because of a high avalanche risk). Bark disks were packed in paper bags and immediately returned to the laboratory where they were moistened and placed in cool storage (5°C) until processed, usually within seven days of collection.

Mean bark and phloem thickness (0.01 ± 0.005 cm) for each disk was determined from two measurements taken on opposite sides of each disk with calipers. I dissected bark disks by inserting a blade between bark and sapwood and gently prying the two layers apart, thereby exposing the galleries and brood within. The following data were recorded for each disk: number of egg galleries, length of each egg gallery, success of each gallery (i.e., whether reproduction occurred or adults were pitched out), number of larval galleries, and the number of MPB brood, their condition, and development stage. Eggs could not be counted reliably, even under 8x magnification, because they were often concealed by boring dust and were too fragile to survive the removal of boring dust from egg galleries. Larvae were identified to instar (L1-L4) by measuring head capsule widths (Amman and Cole 1983, Logan *et al*. 1998) with a dissecting scope (16x magnification) fitted with an ocular micrometer.

The number of radial resin ducts and the area of inner bark covered by their associated, terminal resin blisters (Shrimpton 1978, Fahn 1967) were measured for each baited tree. Resin ducts and blisters were measured on two disks from each tree, collected at 50 cm above breast height. A small sanding wheel was used to remove the innermost layers of bark on a randomly chosen 4 cm^2 area of the disk, thereby exposing a polished surface approximately half way into the phloem. A digital photograph was taken of this polished phloem using a Leica MZ125 dissecting scope and DFC320 camera. The percent area covered by resin blisters was determined using image analysis software, ImageJ version 1.43u (Rasband 2010).

DBH was measured for each baited whitebark (25.5-44.0 cm) and lodgepole pine (24.5-42.0 cm). In order to increase the sample size of trees to look at relationships between DBH, bark thickness and phloem thickness, these parameters were also measured for 1-2 whitebark and lodgepole pines nearest to each baited pair of trees. On unbaited trees, a '00' cork-borer was used to remove two small bark disks from the north and south aspects of each tree at 50 cm above breast height. On each of these disks phloem and bark thickness were measured and averaged to give estimates for the tree. Bark and phloem measurements from thirteen whitebark and eleven lodgepole pines collected from a third site in the Crowsnest Pass as part of another study (Chapter 2 this thesis) were also included in this data set.

3.2.4 Analysis

Differences in attack densities between the two hosts were investigated using a linear mixed effect (LME) model that included site and pair as nested-random effects and a variance-covariate structure that accommodated heteroskedasticity between tree species (Zuur *et al*. 2009). Attack densities were further investigated with Pearson correlations of within-pair differences in attack density and various tree-related variables (DBH, bark, phloem, density of resin or percent area covered by resin blisters.

Densities of each larval instar, pupae and brood adults were tabulated from baited trees for each sampling period and averaged for each study site. Larval instar distributions were compared between the two hosts prior to the onset of winter and again in spring before emergence using LME models that included pair, site and region as nested random effects. Trees with no live brood were excluded from these models. Means of the total number of larval galleries per disk and density of larval galleries per cm of egg gallery were calculated using the last sampling period before winter, assuming that the host colonization period was complete by then. Pre-winter larval survival was calculated for each tree as the number of live brood present in the last sample period before winter divided by the total number of larval galleries present in that disk.

I estimated net reproductive rates (Ro) in two ways from baited trees using brood densities from bark disks collected in June 2009 in Willmore Wilderness Park and measurements of attack densities on the 1 m section of the bole. I calculated an upper estimate of the net reproductive rate (Ro_{upper}) for the MPB as the total number of live brood per disk divided by the two times number of attacks observed on a similar area of the bole (assuming each gallery required two parents). However, many of the brood present at this time had not reached the teneral adult stage and would likely experience further mortality before they emerged and reproduced. Therefore I calculated a second estimate of the net reproductive rate (Ro_{lower}) using only the number of brood that had reached the teneral adult stage divided by two times the density of attacks observed on a similar area of the bole. These estimates of Ro assumed MPB progeny emerging from the baited trees would only have one reproductive pairing in their life. Thus, populations with $Ro<1$ were declining whereas those with $Ro>1$ were expanding.

Total larval galleries, larval galleries per cm of egg gallery, pre-winter larval survival, Ro_{upper} and Ro_{lower} were compared between host species with paired-Wilcox tests. Relationships between these characteristics and attack density, tree DBH, bark thickness, phloem thickness, density of resin ducts and area covered by resin blisters were investigated with Pearson correlations.

Relationships between bark thickness (lodgepole: n=41 and whitebark: n=46), phloem thickness (n=47 of each species) and DBH were determined for lodgepole pine and whitebark pine using LME models that included site as a random effect. Means of the density of radial resin ducts and area covered by resin blisters on each tree were compared between host species using paired t-tests.

All models were fit by maximum likelihood estimates. When appropriate, analysis of deviance was performed by F test (Hastie and Pregibon 1992). All analyses were performed in R version 2.11.1 (R core Development Team 2008) using the *nlme* package (Pinheiro *et al.* 2008).

3.3 Results

3.3.1 Bark characteristics

Bark characteristics were strongly related to tree DBH, but differed little between host species. Total bark thickness increased with tree DBH ($F_{1,80}$=43.765 p<0.001) but did not differ between host species ($F_{1,80}$=2.467, p=0.120) (Figure 3.2 A). Similarly, phloem thickness increased with DBH ($F_{1,87}$=13.734, p<0.001) but did not differ between the two pine species ($F_{1,87}$=2.393, p=0.125) (Figure 3.2 B). The density of resin ducts was greater in whitebark pine (t=6.046, df=16, p<0.001) while the area covered by resin blisters did not differ between the two species (t = 0.0768, df = 17, p= 0.940). Number of resin ducts (r=0.357, df=32, p=0.038) and area covered by resin blisters (r=0.40, df=32, p=0.019) were positively correlated with phloem thickness. Neither number of resin ducts (r=0.15, df=32, p=0.409) nor area covered by resin blisters (r=0.11, df=32, p=0.542) were related to tree DBH. Interestingly, the total number of resin blisters and area covered by resin blisters were not significantly related to each other (r=0.160, df=32, p=0.364).

3.3.2 Attack densities

Attack densities differed less between host species within a region than between regions. Overall, median attack densities were higher in lodgepole ($40/m^2$) than whitebark ($30/m^2$) pines, but the differences were of only marginal statistical significance ($F_{1,16}$ = 3.745, p = 0.071). This pattern of host-associated attack density was observed in all sites (Figure 3.3). Differences in attack density within paired trees were not correlated with within-pair differences in DBH (r = 0.109, df=15, p=0.677), bark thickness (r = 0.34, df=15, p=0.177), phloem thickness (r=0.22, df=15, p=0.393), density of resin ducts (r=-0.01, df=15, p=0.989), or percent area covered by resin blisters (r=0.099, df=15, p=0.7046). The accumulated length of all egg galleries per bark disk increased with time, though it was not clear if this was due to new attacks in September and October or lengthening of existing galleries (Table 3.1). Interestingly, 'pitch-outs' were rarely observed. In fact, only eight instances of pitch-out were observed (four in each host) for all the discs collected across the four sampling periods.

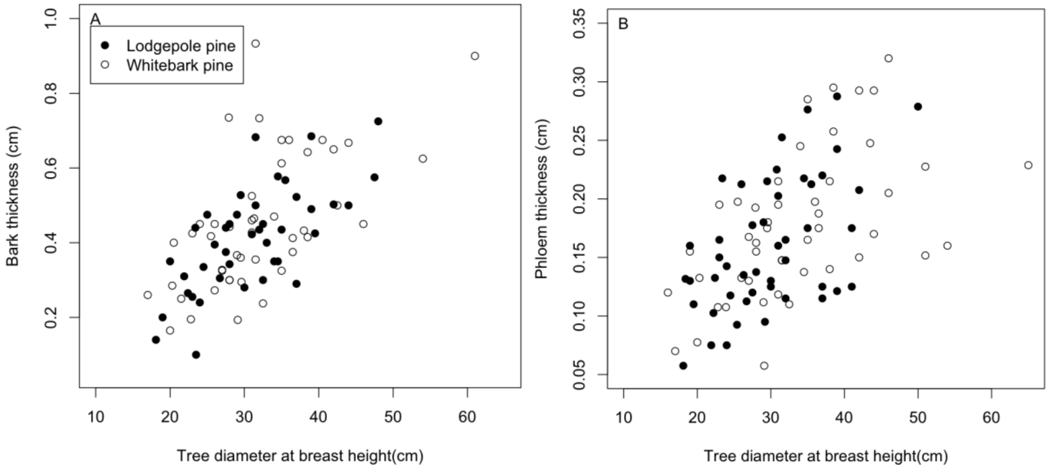

Figure 3.2: Total bark thickness (A) and phloem thickness (B) for whitebark and lodgepole pines of different diameters at breast height (cm). Bark and phloem thicknesses were determined from each tree as averages of four measurements; two measurements taken from north and south aspects of each tree at 50 cm above breast height.

3.3.3 Gallery and brood characteristics

Overall, egg gallery and brood characteristics differed little between host species. The patterns of variation between hosts, however, differed between regions, with host-associated differences more pronounced in Willmore Wilderness Park than in the Crowsnest area (Table 3.1).

The total number of larval galleries per bark disk and the density of larval galleries per cm of egg gallery are characteristics that reflect the total number of eggs laid minus the number of eggs that were infertile and those that were killed (consumed or inundated with resin) before they could hatch. Total larval galleries per disk (n=17, W=175, p=0.301) and larval gallery density (n=17, W=182.5, p=0.197) did not differ significantly between host species, but both parameters tended to be higher in lodgepole pines than whitebark pines in Featherstonhaugh and Hidden Creek (Figure 3.4, 3.5; Table 3.1). Number of larval galleries and density of larval galleries were both significantly and positively associated with attack density (no. larval galleries: r=0.67, t=5.103, df=32, p<0.001; larval gallery density: r=0.365, t=2.222, df=32, p=0.033) and significantly and negatively associated with tree DBH (no. larval galleries: r=-0.37, t=2.275, df=32, p=0.039; larval gallery density: r=-0.44, t=2.804, df=32, p=0.009), bark thickness (no. larval galleries: r=-0.44, t=2.748, df=32, p=0.001; larval gallery density: r=-0.53, t=3.548, df=32, p=0.001) and phloem thickness (no. larval galleries: r=-0.51, t=3.315, df=32, p=0.002; larval gallery density: r=-0.62 t=4.474, df=32, p<0.001) (Table 3.2). Both the number of larval galleries and the density of larval galleries per egg gallery were weakly negatively associated with the density of resin ducts (no. larval galleries: r=-0.23, t=1.332, df=32, p=0.192; larval gallery density: r=-0.25, t=1.440, df=32, p=0.160) and area covered by resin blisters (no. larval galleries: r=-0.21, t=1.245, df=32, p=0.222; larval gallery density: r=-0.26, t=1.512, df=32, p=0.134).

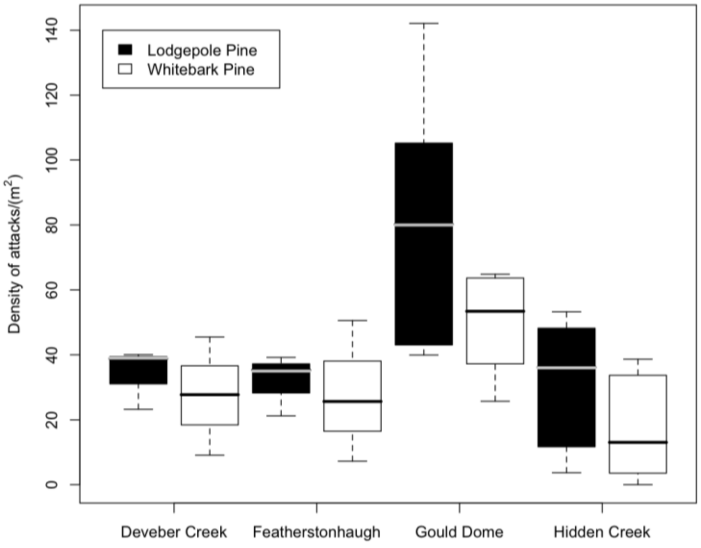

Figure 3.3: Boxplots (boxes represent median + 3rd / - 2nd quartiles, whiskers represent 1st and 4th quartiles) of MPB attack densities on pheromone baited subalpine whitebark and lodgepole pines. Attack densities are presented for each host species at each study site. Deveber Creek and Featherstonhaugh were in Willmore Wilderness Park and Gould Dome and Hidden Creek were in the Crowsnest Pass.

Table 3.1: Tabulation of MPB gallery and brood characteristics of the MPB infesting lodgepole (LPP) and whitebark (WBP) pines. Tables A and B represent separate regions/years of the study. Each value represents an average ± (SE) of all trees of a given species, from a given collection in a 78.5 cm^2 area.

A) Willmore Wilderness

Collection:	August		September		October		July	
Tree Species	LPP	WBP	LPP	WBP	LPP	WBP	LPP	WBP
# of adult galleries	1.2 ± 1.13	0.5 ± 0.59	2.2 ± 1.52	1.9 ± 1.55	2.6 ± 1.38	2.4 ± 1.27	3.1 ± 1.84	2.6 ± 1.72
Egg gallery length	5.9 ± 7.69	1.9 ± 3.05	14.8 ± 10.60	13.0 ± 11.68	17.6 ± 9.60	15.8 ± 13.61	21.9 ± 15.41	17.4 ± 12.50
larval galleries	0.1 ± 0.61	0 ±0.00	6.2 ± 11.65	1.8 ± 4.49	9.9 ± 13.03	2.6 ± 5.07	17.8 ± 19.37	7.8 ± 13.49
1st larval instar	0.1 ± 0.61	0 + 0.0	1.8 + 3.78	1.2 + 2.27	1.1 + 2.04	0.5 + 1.73	0 ± 0.0	0 ± 0.0
2nd larval instar	0 ± 0.0	0 ± 0.0	0 ± 0.2	0 ± 0.0	1.8 ± 3.35	0.3 ± 1.11	0 ± 0.00	0.0 ± 0.16
3rd larval instar	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0.5 ± 1.57	0.1 ± 0.32	0.0 ± 0.26	0 + 0.0
4th larval instar	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0.1 ± 0.50	0.2 ± 0.96
Pupal chambers	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1.1 ±2.79	1.1 ±2.89
Pupae	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0.1 ± 0.48	0.1 ± 0.32
Teneral adults	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0.18 ± 1.20	0.29 ± 1.21
Total Live Brood	0.1 ± 0.61	0 ± 0.0	1.8 ± 3.79	1.3 ± 2.52	3.5 ± 5.68	1.0 ± 2.49	0.4 ± 1.15	0.5 ± 1.32

B) Crowsnest Pass

Collection:	August		September		October		April	
Species	LPP	WBP	LPP	WBP	LPP	WBP	LPP	WBP
# of adult galleries	1.1±0.87	0.7±0.83	1.5±1.46	1.2±1.29	2.3±1.75	2.1±1.5		
Egg gallery length	4±3.92	2.9±4.46	9.3±10.08	7.7±9.18	16.8±13.75	15.1±11.57		
larval galleries	0 ± 0.0	0 ± 0.0	7.6±14.27	1.7± 4.41	22.2±18.48	18.2±20.95		
1st larval instar	0 ± 0.0	0 ± 0.0	1.6±4.21	0.2±0.68	2.4±3.93	2.2±3.34	0 ± 0.0	0 ± 0.0
2nd larval instar	0 ± 0.0	0 ± 0.0	0.1±0.4	0 ± 0.0	3.2±4.71	3±5.08	0 ± 0.0	0 ± 0.0
3rd larval instar	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	1.6±3.07	1±2.9	0 ± 0.0	0 ± 0.0
4th larval instar	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0.2±0.55	0.1±0.6	0 ± 0.0	0 ± 0.0
Pupal chambers	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
Pupae	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
Teneral adults	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0	0 ± 0.0
Total Live Brood	0±0	0±0	1.7±4.53	0.2±0.68	7.5±7.48	6.4±8.02	0 ± 0.0	0 ± 0.0

Table 3.2: Pearson correlations between brood and gallery characteristics and tree related variables. (Significance codes p<0.1,*; p<0.05,**; p<0.01,***; p<0.001****).

Stage	df	Attack Density	DBH	Bark	Phloem	Resin Ducts	Resin Blisters
Total larval galleries	32	0.67****	-0.37**	-0.44***	-0.50***	-0.23	-0.21
Larval galleries / egg gallery	32	0.37**	-0.44***	-0.53**	-0.62****	-0.25	-0.26
Pre-winter survival	32	-0.07	0.02	0.14	0.19	-0.18	0.11
R_{nlow}	10	0.37	0.04	0.02	0.11	0.16	0.17
R_{nupper}	10	-0.02	0.38	0.22	0.42	0.22	0.17

3.3.4 Brood mortality

Pre-winter larval survival did not differ between host species (n=17, w=125, p=0.512). Patterns varied considerably between sites within regions (Figure 3.6). Pre-winter larval survival was unrelated to any of the tree related variables measured (Table 3.2). The total density of all stages of live brood present before winter tended to be higher in lodgepole pines; however, these densities were highly variable (Table 3.1). Overwinter mortality had a dramatic impact on net reproductive rates. In the Crowsnest Pass overwinter mortality was 100%, likely caused by an abrupt drop to -25°C in early October, presumably before the brood had maximized their cold hardiness (Paul Kruger, Alberta Sustainable Resource Development, personal communication, Cole 1981, Bentz and Mullins 1999). Consequently, data from that region are excluded from subsequent analysis of reproductive rate and relative development rates. Overwinter mortality of MPB in Willmore Wilderness Park was also high, again likely caused by cold winter weather (*e.g.*, prolonged periods of extreme cold with minimums reaching of -42°C). Net reproductive rates were highly variable in the trees from Willmore, with brood surviving winter in only 4 of the 6 sampled trees for each species. Ro_{lower} and Ro_{upper} estimates (± SE) ranged from 0.49 ± 0.226 to 0.99 ± 0.469 in lodgepole pine and from 0.25 ± 0.228 to 1.30 ± 0.901 in whitebark pines. Neither Ro_{lower} (n=6, W=22.5, p=0.446) nor Ro_{upper} (n=6, W=20, p=0.803) differed between host species in the six pairs of sample trees from Willmore Wilderness Park. Variation in neither Ro_{lower} nor Ro_{upper} could be explained by any of the variables reordered; there were no significant relationships to attack density, tree DBH, bark thickness, phloem thickness, number of resin ducts or area covered by resin blisters (Table 3.2).

Eleven unbaited whitebark and six unbaited lodgpole pines were also attacked in the vicinity of the experimentally paired trees in Willmore Wilderness Park. Live brood were found in only three of these whitebark pines and in none of the lodgepole pines. Net reproductive rates in the unbaited trees fell within the ranges observed in the baited whitebark pines.

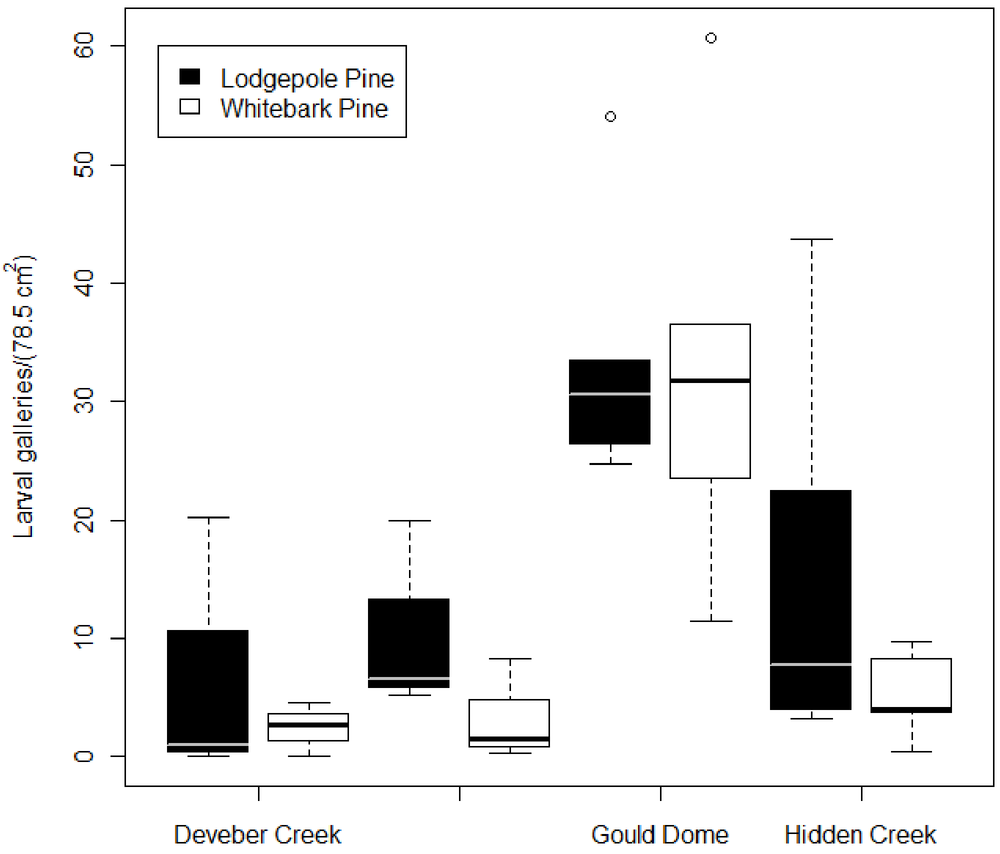

Figure 3.4: Boxplots (boxes represent median + 3rd / - 2nd quartiles, whiskers represent 1st and 4th quartiles) of density of MPB larval galleries on a 78.5 cm^2 area of pheromone baited whitebark and lodgepole pines. Attack densities are presented for each host species in each study site. Deveber Creek and Featherstonhaugh were in Willmore Wilderness Park and Gould Dome and Hidden Creek were in the Crowsnest Pass.

3.3.5 Relative development rates

Relative development rates differed little between the two host species. Prior to the onset of winter, the percent of brood making it to L3 and L4 was slightly higher in lodgepole pine than in whitebark pine ($F_{1,13}$= 5.30, p=0.039). Pre-winter brood (L1:L2:L3:L4) development tended to be more advanced in the Crowsnest Pass (32%:43%:21%:3% in lodgepole and 35%:47%:16%:1% in whitebark), than in Willmore Wilderness Park (34%:52%:14%:0 in lodgepole and 63%:31%7%:0% in whitebark). Prior to the onset of the flight period in Willmore Wilderness Park, only about one-third of live brood had reached the teneral adult stage. Distribution of brood life stages (L1:L2:L3:L4:pupae:teneral adults) was 0%:0%:9%:33%:28%:28% in lodgepole and 0%:6%:0%:48%:16%:29% in whitebark pines. There were no differences between host species in the percent of L3 and L4 ($F_{1,3}$=0.300, p=0.622), pupae ($F_{1,3}$=0.092, p=0.782), or brood adults ($F_{1,3}$=0.647, p=0.480) in Willmore Wilderness Park in April 2009.

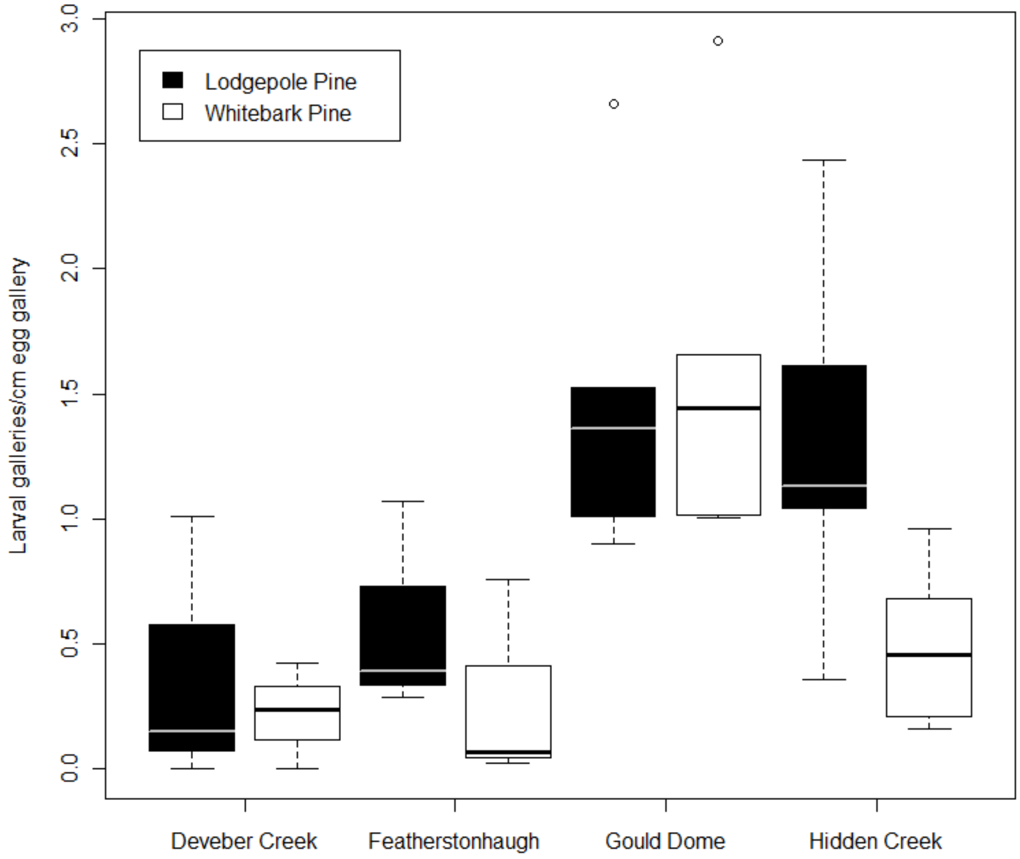

Figure 3.5: Boxplots (boxes represent median + 3rd / - 2nd quartiles, whiskers represent 1st and 4th quartiles) of density of MPB larval galleries per cm of egg gallery on pheromone baited whitebark and lodgepole pines. Attack densities are presented for each host species in each study site. Deveber Creek and Featherstonhaugh were in Willmore Wilderness Park and Gould Dome and Hidden Creek were in the Crowsnest Pass.

3.3.6 Other beetles

A number of other beetles were also collected in the bark disks. The most common included *Ips pini* (Say) (Curculionidae), *Ips latidens* (LeConte)

(Curculionidae), *Trypodendron lineatum* (Olivier) (Curculionidae), *Rhizophagus dimidiatus* Mannerheim (Monotomidae), *Phloeostiba lapponicus* (Zetterstedt) (Staphylinidae) and a large number of unidentified Aleocharinae (Staphylinidae). Interestingly, *I. pini* were commonly collected in lodgepole pine but rarely in whitebark pine while *I. latidens* was only collected on whitebark pine.

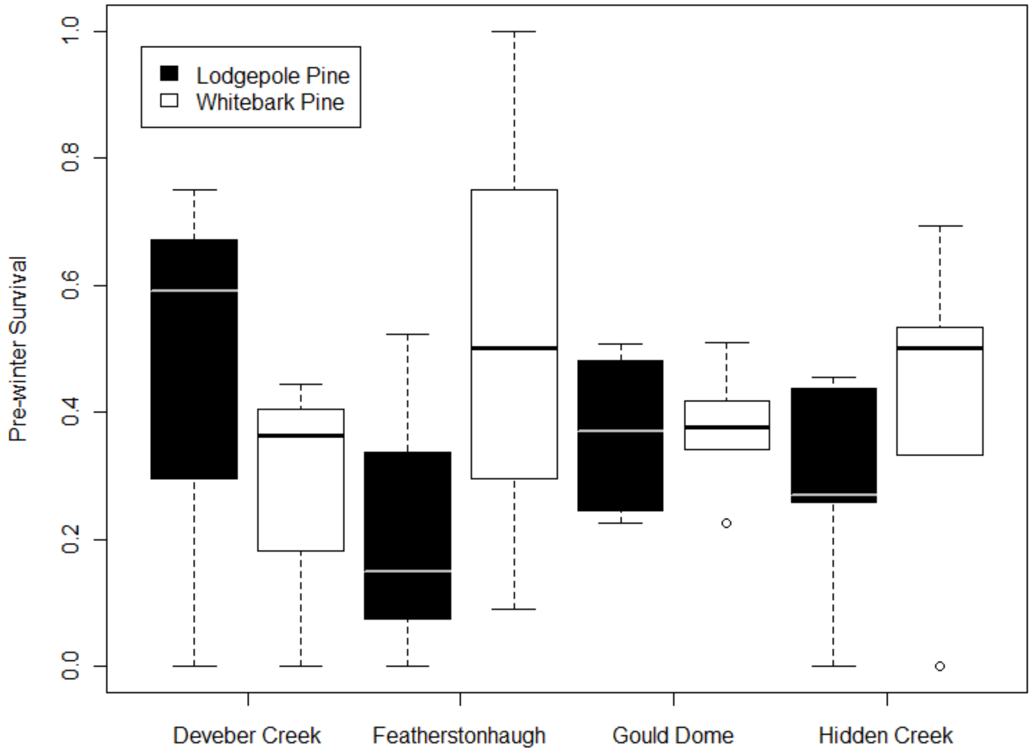

Figure 3.6: Boxplots (boxes represent median + 3rdst / - 2rd quartiles, whiskers represent 1st and 4th quartiles) of pre-winter larval survival of MPBs on pheromone baited whitebark and lodgepole pines. Attack densities are presented for each host species in each study site. Deveber Creek and Featherstonhaugh were in Willmore Wilderness Park and Gould Dome and Hidden Creek were in the Crowsnest Pass.

3.4 Discussion

Climatic factors, particularly cold winter temperatures, had a much more dramatic impact on the MPB in this experiment than did tree host species. The cold winter temperatures (in years prior to and during this experiment), aggressive MPB control efforts, and relatively small MPB in-flights contributed to the local collapse of MPB populations in our experimental sites (Brooks Horne, Alberta

Sustainable Resource Development, personal communication). These circumstances greatly limited the data that could be collected post-winter concerning development rates, post-winter survivorship and phenology. Thus, the most valuable insights were obtained from pre-winter populations.

3.4.1 Bark characteristics

Unlike limber pine (*Pinus flexilis* James), whitebark pine did not have thicker bark and/or phloem than lodgepole pines of similar DBH, at least at our study sites. Langor (1989) attributed much of the superior host quality of limber pine to its thicker phloem. Thus, lack of such differences may explain why we did not observe large differences between the host quality of whitebark and lodgepole pines in this experiment. Other work generally supports our observations about phloem thickness, but suggests that in some sites whitebark pine has thicker phloem, especially in larger trees (Baker *et al.* 1971, Six and Adams 2007, Brooks Horne, Alberta Sustainable Resource Development, personal communication). There is some anecdotal evidence suggesting that there are more large-diameter whitebark pines on the landscape compared to lodgepole pines (Day 1967, Arno and Hoff 1989). However, a recent survey of whitebark pines across Montana, Idaho and Oregon suggests that the size class distributions of these two pines do not differ (Evan Larson, University of Minnesota, personal communication). More likely, one host species does not have consistently thicker phloem than the other through the range of sympatry, but rather phloem thickness of each species varies independently across the landscape according to climatic, edaphic, and stand characteristics (Cabrera 1978, Ying *et al.* 1985, Weaver 2001, Smith *et al.* 2002).

3.4.2 Host defenses and MPB attack

There was significantly higher density of radial resin ducts in whitebark pine than in lodgepole pine. Radial resin ducts and associated terminal resin blisters are an important component of the pitch-out (primary) defense response (Franceschi *et al.* 2005, and references therein) and their abundance has been shown to be negatively correlated with MPB brood survival and gross brood production elsewhere (Berryman 1976). The number of radial resin ducts and the area covered by resin blisters were not strongly correlated with attack density or brood and gallery characteristics. The hypersensitive response (secondary defense reaction) and secondary resin flow occur largely through the activities of polyphenolic parenchyma cells in the secondary phloem; however, less is known about the role of ray parenchyma cells associated with radial resin ducts perform in these reactions (Franceschi *et al.* 2005). The weak correlations between the density of these ducts and survival of early MPB life stages suggest the ray parenchyma cells play a relatively minor role in the secondary defense reactions defending *Pinus* from bark beetles.

Gallery characteristics suggest a tendency for greater egg mortality in whitebark pines. We could not reliably tally the number of eggs laid, but instead measured the number of larval galleries, a function of both eggs laid and egg mortality. The number of eggs laid per cm of MPB egg gallery generally increases with phloem thickness (Amman and Cole 1983); however, we observed a strong negative correlation between phloem thickness and the number of larval galleries per cm of egg gallery (r=-0.62), suggesting that a lower proportion of eggs hatched as phloem thickness increased. This correlation might be explained by the fact that eggs are killed easily by exposure to resin (Reid 1963, Reid and Gates 1970, Berryman 1976) and vigorously growing trees, typically with thicker phloem, generally exhibit more powerful defense responses (Shrimpton 1972, Amman 1973, Cole 1973, Berryman 1976, Cabrera 1978, Raffa and Berryman 1982). The trend towards lower numbers of larval galleries per cm of egg gallery in whitebark pine than in lodgepole pine at Featherstonhaugh and Hidden Creek and lower densities of live brood in Willmore Wilderness Park (Table 3.1) suggest that whitebark pines have stronger induced defense responses than lodgepole pines in some situations. This suggestion is in part supported by observations that one of the three species of blue stain fungi associated with the MPB produced significantly shorter lesions in whitebark pine than in lodgepole pine (Esch, unpublished data) a pattern correlated with resistance to the MPB (Raffa and Berryman 1982).

Inferred egg mortality was strongly and negatively associated with attack density. Greater attack densities exhaust host defenses and limit the quantities of defensive compounds that each attacking beetle and subsequent progeny must contend with (Raffa and Berryman 1983). Attack densities observed in this experiment rarely reached the optimal density of *ca.* 60 attacks/m^2 and were frequently below the ‘threshold’ attack densities of *ca.* 40 attacks/m^2 (Figure 3.3) required to exhaust the defenses of a typical lodgepole pine in Morrow County, Oregon (Raffa and Berryman 1983). Furthermore, Reid (1963) reported average attack densities of *ca.* 70 attacks/m^2 at breast height on lodgepole pines with DBH 20-40 cm and average bark thickness of 0.97 cm in Invermere, BC (trees with thicker bark typically support greater attack densities (Safranyik and Carroll 2006), which may in part explain why greater attack densities were observed by Reid (1963) compared to this study). At Gould Dome Mountain, the only site where attack densities reached or exceeded optimal levels, inferred egg survival and live brood density (data not shown) was substantially higher than at other sites. Thus, the apparently high egg mortality could have been caused by low attack densities. The low attack densities observed in the majority of my sites could have resulted from the MPB control efforts in the area and reduced in-flights of MPB from neighboring stands during the years of these experiments (Brooks Horne, Alberta Sustainable Resource Development, personal communication). Further research into host selection and attack densities under natural conditions (without MPB baits) would be informative.

Logan *et al.* (2010) reported consistently lower attack densities on whitebark compared to lodgepole pines in the Greater Yellowstone Ecosystem (GYE) and that these lower attack densities supported similar brood production between the two pine species, suggesting that whitebark pines are less vigorously defended than lodgepole pines in this region. I also observed consistently lower, though only marginally significant, median attack densities on whitebark (30 attacks / m^2) than in lodgepole (40 attacks / m^2); however, brood and gallery characteristics from this experiment discussed above contrast with Logan *et al.* (2010), and suggest that whitebark pines are more vigorously defended in our study sites. Furthermore, Logan *et al.* (2010) reported that whitebark pines rarely produced conspicuous pitch-tubes in the GYE while these were common on lodgepole pine. Trees of low vigor may not produce pitch tubes (Safranyik and Carroll 2006). I observed similarly large and conspicuous pitch tubes on both whitebark and lodgepole pines in my study site. These contrasts emphasize that the interaction between MPB and whitebark pine will vary regionally, and be influenced by climatic, edaphic and stand related characteristics (Logan *et al.* 2001, Perkins and Roberts 2001, Larson 2010, Bentz *et al.* 2011).

Despite the presence of pitch tubes, 'pitch-outs' were rarely observed in this study. Cudmore *et al.* (2010) reported that trees outside the historical range of the MPB were more susceptible to MPB attack. The absence of frequent pitch-outs may reflect greater susceptibility to MPB attack in the trees at the study sites of this experiment.

3.4.3 Net reproductive rates and development

Unfortunately, my data do not permit a definitive answer about whether Ro differed between the two host species. In Willmore Wilderness Park, two years prior to our experiment, much higher brood production was observed in whitebark than lodgepole pine (Brooks Horne, personal communication). However, I did not observe obviously higher brood production in whitebark than in lodgepole pine in any of my baited trees. This trend was consistently observed in naturally attacked trees adjacent to my baited trees and in the two dozen trees I sampled that were attacked in 2007 in Willmore Wilderness Park (data not shown), with one exception. An unusually large whitebark pine (DBH 62 cm, bark thickness *ca.* 1 cm), located several hundred meters from my study site at Deveber Creek had high numbers of larvae, pupae and teneral adults present under the bark in September 2008. Thus anecdotal evidence suggests that the presence of very large, decadent whitebark pines in sub-alpine forests may contribute significantly to MPB population growth in the initial stages of an outbreak (Amman 1984).

A one-year (univoltine) life cycle with synchronous emergence is among the most important factors influencing MPB population growth (Amman 1973, Cole 1981, Bentz *et al.* 1991, Bentz and Mullins 1999). I observed the completion of development to adulthood for only one-third of the winter survivors; however, a univoltine life cycle in only part of the MPB cohort at high latitudes and altitudes is outside the range of the historic norms for the species (Amman 1973, Safranyik and Carroll 2006). Bentz and Schen-Langenheim (2007), observed similar shifts from 3- and 2-year life cycles towards univoltinism in forests 10° south of our experimental stands. This observation verifies the prediction that, under a changing climate, beetle populations will become increasingly univoltine, which will have serious consequences for the spread and impact of current and future MPB epidemics (Logan and Powell 2001, Carroll *et al*. 2004). Furthermore, recent observations suggest that, given suitable weather conditions, a synchronous univoltine life cycle is not a prerequisite for a MPB outbreak, but rather MPBs are capable of killing whitebark pines and perpetuating outbreaks in instances where a mixtures of one, two and three year life cycles are present in the same stand (Bentz *et al.* 2011). Clearly, the capacity of the MPB to have a univoltine life cycle at high elevations will complicate efforts to conserve this endangered pine species.

3.4.4 Conclusions and management recommendations

The similarity in phloem thickness between whitebark and lodgepole pines, and the fact that there are neither large differences in MPB population parameters nor phenology among the two host species suggests that both species have equivalent quality for the MPB, at least in the range of tree DBHs studied. Nonetheless, anecdotal evidence (my own observations and Brooks Horne, personal communication) that very large whitebark pine trees are superior for MPB production warrants additional investigation. It is recommended that whitebark pine be treated equivalently to lodgepole pine for the parameterization of models that aim to predict MPB population growth and spread. Similarly, management of MPB at high altitudes requires that both pine species need to be incorporated into management plans. The observation of a univoltine life cycle in whitebark pine near its northern limit is a major cause for concern, and it will likely mean continued MPB-caused mortality in whitebark pines, even though the recent cold temperatures have reduced MPB populations in these study sites. The high conservation value of whitebark pine suggests that MPB management in this species should be largely focused on attack prevention, *e.g.*, by the use of anti-aggregants (verbenone), while nearby lodgepole pines may better serve to absorb the resident MPB colonizers and then receive direct control treatment (*e.g.*, cut and burn).

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Chapter 4: Beetle (Coleoptera) diversity in subalpine whitebark and lodgepole pine snags killed by mountain pine beetle

4.1 Introduction

Whitebark pine (*Pinus albicaulis* Engelmann) is a high-elevation, five-needle pine (subgenus: *Strobus*, subsection: Cembrae) found in subalpine forests of western North America (Arno and Hoff 1989, Price *et al.* 1998). The center of abundance of this species is the Greater Yellowstone Ecosystem, with populations extending north to *ca.* 55° latitude in the Rocky and Coastal mountain ranges of Alberta and British Columbia, Canada and south to *ca.* 36° in the Sierra Nevada and Cascade ranges (maps of distribution in Chapters 1 and 3). Whitebark pine populations are declining across much of the species range. These declines are primarily due to impacts of: *i*) the exotic fungal pathogen, white pine blister rust (*Cronartium ribicola* Fischer), *ii*) the mountain pine beetle (*Dendroctonus ponderosae* Hopkins (MPB)), a native bark beetle with populations presently eruptive on an unprecedented scale and *iii*) rapid climate change (Logan and Powell 2001, Zeglen 2002, Gibson *et al.* 2008, Smith *et al.* 2008, Larson 2010, Safranyik *et al.* 2010, Tomback and Achuff 2010). As a result, whitebark pine has been listed as endangered, although full protection under the Species at Risk Act and Endangered Species Act is pending in both Canada and the United States of America (Committee on the Status of Endangered Wildlife in Canada 2010, Department of the Interior Fish and Wildlife Service 2010).

Given its myriad ecological roles, whitebark pine is considered a foundation species for subalpine communities across its range (Ellison *et al.* 2005). For example, the seeds of whitebark pine are an important food source for many animals, including bears, nutcrackers and squirrels, its presence ameliorates extreme microsite conditions, facilitating succession and increasing plant diversity and at the timberline, whitebark pine regulates snowmelt and runoff (reviewed in Tomback *et al.* 2001). However, with the exception of some attention to its major pests, there have been almost no studies of relationships between this tree species and invertebrates (Bartos and Gibson 1990, Gibson *et al.* 2008). Given that invertebrates comprise the bulk of diversity in terrestrial ecosystems (Danks 1979, Danks and Foottit 1989), it is expected that many ecological relationships between whitebark pine and invertebrates exist in these sensitive high elevation ecosystems. Thus, two questions arise: *i*) What are the associations between whitebark pine and particular invertebrate species? and *ii*) To what extent is this associated biodiversity threatened by whitebark pine decline?

Saproxylic invertebrates, those associated with moribund or decaying trees, are extremely diverse, representing a substantial component of forest biodiversity. They are also particularly susceptible to extirpation because of their highly specific microhabitat requirements, which are often spatially and temporally ephemeral (Siitonen 2001, Langor *et al.* 2008). *Ips woodi* Thatcher, is an example, of a saproxylic invertebrate that is likely threatened (D. Langor, Canadian Forest Service, personal communication) because it feeds exclusively on moribund or dead limber pine (*Pinus flexilis* James) (Thatcher 1967, Wood 1982), another endangered five needle pine (Langor 2007). Several other examples of such singular associations have been suggested, though not extensively studied, for other pines species (*e.g.,* DeLeon 1935, Dahlsten and Stephen 1974). Therefore, investigation of whether other invertebrate species have similarly exclusive host relationships with whitebark pine can help identify the full range of threat associated with declines of this important subalpine tree species.

MPB activity has created a large number of standing dead (snags) whitebark and lodgepole pines (*Pinus contorta* Doug. *ex.* Loud. (*var. latifolia* Engelm)) along the east slopes of the Rocky Mountains in Alberta, Canada. We compared the saproxylic beetle fauna between these two pine species in snags existing in close proximity to each other at high elevation to discover the extent to which they support a different fauna. Beetles (Coleoptera) were selected as the focal taxon for this study because they are diverse and sensitive to perturbations in dead wood quantity and quality (Siitonen 2001, Langor *et al*. 2008). Furthermore, taxonomic resources in place allow reliable species level identifications for most beetles.

In this study I sought to meet the following objectives: *i*) conduct the first systematic survey of beetles associated with whitebark pine snags at two locations representing the northern and southern ends of whitebark pine distribution in Alberta; *ii*) determine if the beetle fauna in MPB killed snags differs between whitebark and lodgepole pines in terms of assemblage structure; *iii*) determine if there are species exclusively associated with whitebark pine that might also be threatened by its decline; and *iv*) determine if the composition or abundance of known predators and competitors of the MPB differ between whitebark and lodgepole pines in a way that could affect MPB population dynamics. I hypothesized that fauna composition will differ between the two host species, with the possibility that some species exclusively inhabit whitebark pines. Testing of this hypothesis is of particular importance to forest managers because falling and burning of MPB infested trees is a common management tool, even in protected areas, and such activities could adversely affect a potentially endangered fauna.

4.2 Methods

4.2.1 Study area and sites

The study was conducted in the subalpine forests of the northern and southern Rocky Mountains of Alberta, Canada. It was carried out in 2009 and 2010 in two regions of the province, Willmore Wilderness Park and the Crowsnest Pass, respectively, representing the northern and southern limits of whitebark pine distribution in Alberta.

Research was conducted at two sites in each region with relatively continuous canopies dominated by conifers. Aspect and elevation ranges for the sites in Willmore Wilderness Park were: south, 1500 -1550 m at Deveber Creek (53.72466°N, 119.54844°W); and south, 1550-1650 m at Featherstonhaugh (53.78957°N, 119.76147°W). Site aspect and elevation ranges for the sites in the

Crowsnest Pass region were: west, 1920-2060 m at Gould Dome Mountain (49.91399°N, 114.64803°W); and north 1890-1930 m at Dutch Creek (49.85065°N, 114.62191°W).

Given challenges with access and my determination to focus on sites with a significant proportion of whitebark pine, canopies selected for study contained variable mixtures of Engelmann spruce (*Picea engelmannii* Perry *ex* Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine and whitebark pine. The Featherstonhaugh and Gould Dome Mountain sites were dominated by sub-alpine fir and Engelmann spruce. Dutch Creek was similar to the former sites; however, lodgepole pines were absent. Deveber Creek was dominated by lodgepole and whitebark pines, with spruce and sub-alpine fir mostly limited to the understory.

The MPB had been active in all stands for 3-4 years prior to the study; however, beetle eruptions were still in the early stages, as evidenced by the high ratio of live to dead pine trees. I chose snags in early stages of decay for study, as these stages are most likely to exhibit exclusive host species/invertebrate associations (Langor *et al.* 2008, Wu *et al.* 2010).

4.2.2 Insect collection

Emergence traps and flight intercept traps were used to collect insects associated with snags. Emergence traps were nylon insect screen (mesh size = 0.5 mm) fastened tightly using loops of taught wire and staples to enclose a 1 m long section of each snag chosen for sampling. The bottom portion of each emergence trap was shaped into a funnel of screen that directed emerging insects into a small plastic cup. Prior to completely screening a section of a snag, two 30 cm spikes were driven *ca.* 1-2 cm into the snag at ± 80° from the apex of the funnel. These spikes held the screen away from the surface of the tree, preventing insects from chewing directly through the nylon as they emerged. Flight intercept traps consisted of a clear piece of plastic (Plexiglas®) 1.5 mm X 20 cm X 30 cm attached perpendicularly to the snag (Kaila 1993, Hammond 1997). Intercepted insects fell through a heavy cloth funnel attached to the bottom of the plastic panel into a small plastic cup.

Both types of trap were placed at breast height (*ca.* 1.3 m) and collection cups were filled with ethylene glycol to kill and preserve insects. Traps were oriented down-slope on all snags.

4.2.3 Sampling design

We attached traps to whitebark and lodgepole pines that had been attacked and killed by the MPB 1-4 years previously. The estimation of year of death was based on foliage colour (Safranyik and Carroll 2006). Canopies fading from green to yellow had been attacked the previous year (*fader*), canopies that were entirely red had been attacked 2-3 years previously (*red kill*), and red canopies that had dropped substantial amounts of their foliage had been killed 3-4 years previously (*gray kill*).

At each site in Willmore Wilderness Park, we attached one trap of each type onto three different *fader* and *red kill* trees of each species (2 tree species x 2 snag ages x 3 replicates x 2 trap types x 2 sites = 48 traps on 48 trees in total). In the Crowsnest Pass, MPB populations were being aggressively controlled and all *faders* had been felled and burned the winter previous to the study. Consequently, we attached one trap of each type onto three different *red kill* and *gray kill* trees of each species, except at Dutch Creek where lodgepole pines were absent (36 traps on 36 trees). Emergence traps were installed in Willmore Wilderness Park on 15-17 July 2008 and flight intercept traps were installed there 20-21 August 2008. The accumulated catch from these traps was collected every two to three weeks until 16 September 2008 and once more on 23–24 July 2009. Emergence and flight intercept traps were installed in the Crowsnest Pass 30 June - 1 July 2009. The insects were collected from these traps every 2-3 weeks until 22 September 2009 and once more in 16 May 2010.

All adult beetles were identified to the lowest possible taxonomic level, with most specimens identified to species. Specimens of some groups could not be reliably identified and were excluded from the analysis. These included the Aleocharinae (Staphylinidae), female *Corticaria* (Latridiidae) and female *Podabrus* (Cantharidae). *Pityophthorus* and male *Corticaria* could be reliably assigned to species or morpho-species based on genetalic characters. Singletons of higher taxonomic rank (*e.g.,* Pselaphinae (Staphylinidae) and *Acrotrichis* (Ptiliidae)) were included in the analysis. Family and generic nomenclature follows Arnett and Thomas (2001a, 2001b) and species nomenclature follows Bousquet (1991), unless specimens were described in more recent works. A synoptic collection of all beetles was deposited in the E. H. Strickland Entomological Museum at the University of Alberta.

4.2.4 Analysis

To compare species richness between the two hosts across the range of snag ages, species accumulation curves with 95% confidence intervals were constructed using sample-based rarefaction (Mao-Tao function) in EstimateS version 8.2.0 (Colwell 2009).

The influence of spatial and snag related variables on species assemblages were investigated using multivariate regression trees (MRT) (De'ath, 2002). MRTs dichotomously partition multivariate data (*e.g.*, species data) according to a set of explanatory variables that maximizes within group similarity. Subdivision of groups continues until an 'optimal' fit for the data is found, resulting in a hierarchical 2-dimensional dendrogram or 'tree' showing which explanatory variables explain the majority of variation in the data. Species data were standardized for the cumulative number of trapping days and Hellinger transformed using the *decostand* function in the *vegan* package (Oksanen *et al.* 2011) for R version 2.12.1 (R Development Core Team 2011). Four categorical variables (region: Willmore Wilderness Park or Crowsnest Pass; site: Dutch Creek, Featherstonhaugh, Deveber Creek or Gould Dome Mountain; snag age: *fader, red kill,* or *gray kill*; and host species: whitebark pine or lodgepole pine) were then used to partition the data. A total of 9999 trees were generated in the *mvpart* package for R (Therneau and Atkinson 2010) by selecting the tree that had the greatest number of terminal nodes with a relative error within one standard error of the tree with the lowest relative error. The trees that appeared most frequently, given this constraint, are presented here for each trap type.

To test for relationships between the beetle assemblages, host species and snag age we used redundancy analyses (RDA), a linear constrained ordination method that relates sample composition to constraining and conditional variables (Legendre and Legendre 1998), using the *rda* function in the *vegan* package. Species data were Hellinger transformed (Legendre and Gallagher 2001). The factors host species and snag age-class were included in the RDA as constraining variables. Beetle assemblages from each trap type and region were analyzed separately; and the covariates, site and accumulated number of trap days were included in the RDA as conditional variables. Accumulated number of trap days was included to help account for unequal sampling periods and trap disturbance. Scaling was focused on inter-sample distances (scaling 1) and only vectors that projected outside the circle of equilibrium were plotted. To test if the constraining variables were *significantly* related to species composition an ANOVA-like permutation test with 9999 permutations was performed (Legendre and Legendre 1998). The order of factors in the model did not significantly change the results of any permutation test.

RDA was performed on a sub-set of data from the emergence traps containing the MPB and its known and probable competitors and predators. Emerging MPBs were collected from the first two snag age classes but not the third, and therefore data from *gray kill* traps were removed from this subset before analysis. Overall, 723 individuals in 29 species of phloeophagus scolytines and generalist predators, but not scavengers, were selected for analysis (see Table 4.1). RDA and permutation tests were performed on this sub set of species for a model that included host species and snag age as constraining variables and number of trap days, region and site as conditional variables. Scaling was focused on species scores (scaling 2).

Indicator species analyses (ISA) (Dufrêne and Legendre 1997) were used to detect if any species were strongly associated with one host species and to describe the terminal nodes of the MRTs. These analyses were performed using the *indval* function in the *labdsv* package (Roberts 2010) for R. ISA combines the relative abundance and relative frequency of a species into an indicator value between 0 (no indication) and 1 (perfect indication). In this study, only species with indicator values ≥ 0.6 and p-values < 0.05 were considered good indicators following Jacobs *et al.* (2007). Significance of indicator values was tested with a Monte-Carlo test statistic.

4.3 Results

4.3.1 Beetle assemblage structure

We collected a total of 10 182 individuals, of which 9 270 could be identified to 139 different species or morphospecies in 36 different families. The striped ambrosia beetle, *Trypodendron lineatum* (Olivier) (Curculionidae: Scolytinae) was by far the most abundant species collected, comprising 59% of the total catch. The Scolytinae were the most species rich group, with 25 species collected, including the common species *Hylurgops porosus* (LeConte), *Pityophthorus murrayanae* Blackman, *Ips pini* (Say), and *Ips latidens* (LeConte).

The Staphylinidae were the second most species-rich group with 20 species collected. Most species were represented by only a few individuals while the most abundant species, *Phloeostiba lapponicus* (Zetterstedt), accounted for 65% of all identified Staphylinidae.

Notable among the less species-rich taxa were: two species of Nitidulidae, *Epuraea linearis* Mäklin (2.5%) and *Epuraea truncatella* Mannerheim (3.8%); a species of Tenebrionidae, *Corticeus praetermissus* (Fall) (3.6%); and one species of Monotomidae, *Rhizophagus dimidiatus* Mannerheim (0.7%). These taxa were relatively common and abundant, and, taken together, comprised 10.6% of the overall catch. These insects are commonly associated with the MPB (DeLeon 1935, Dahlsten and Stephen 1974).

As is common in studies of saproxylic insects, the majority of species (93%) were “rare” (< 0.5% of specimens), with 49 species represented by only one individual and 95 species represented by five or fewer individuals. Eighteen species were apparently new records for Alberta, but most of these were minor range extensions for species known from British Columbia (Table 4.1). A few species represented substantial range extensions, including *Microstagetus parvulus* Wollaston (Corylophidae), *Agathidium fenderi* Hatch (Leiodidae), *Epuraea rufida* (Melsheimer), *Phloeonomus suffusus* (Casey) (Staphylinidae), and *Tetratoma variegata* Casey (Tetratomidae). A number of the species collected are likely undescribed, including *Leptophloeus* species1 (Majka and Chandler 2009), a number of the *Corticaria*, and perhaps, some of the *Pityopthorus* (less likely) and Aleocharinae (probable).

Overall, more species were collected in traps placed on whitebark pines (117 species), than on lodgepole pines (90); however, rarefaction analysis showed no differences in species richness between the two host species within any snag age class. This was also true for both trap types (Figure 4.1 A, B). Beetle species richness in both host species tended to be greatest on *gray kill* snags, and this pattern was consistent for both trap types. In flight intercept trap catches, species richness decreased with increasing snag age, while this pattern was not observed for catches in emergence traps. Most host species by snag age class combinations were sampled adequately (as inferred from species accumulation curves approaching some asymptote) to be confident in the estimates of species richness; however, some treatments, most notably those for *gray kill* lodgepole pines snags, were under sampled and estimates of species richness for this group should be considered as tentative.

MRTs gave relatively poor depictions of variation in the data set, explaining only 30% and 10% of the variation in emergence and flight intercept traps catches, respectively. Furthermore, the cross validated errors were relatively

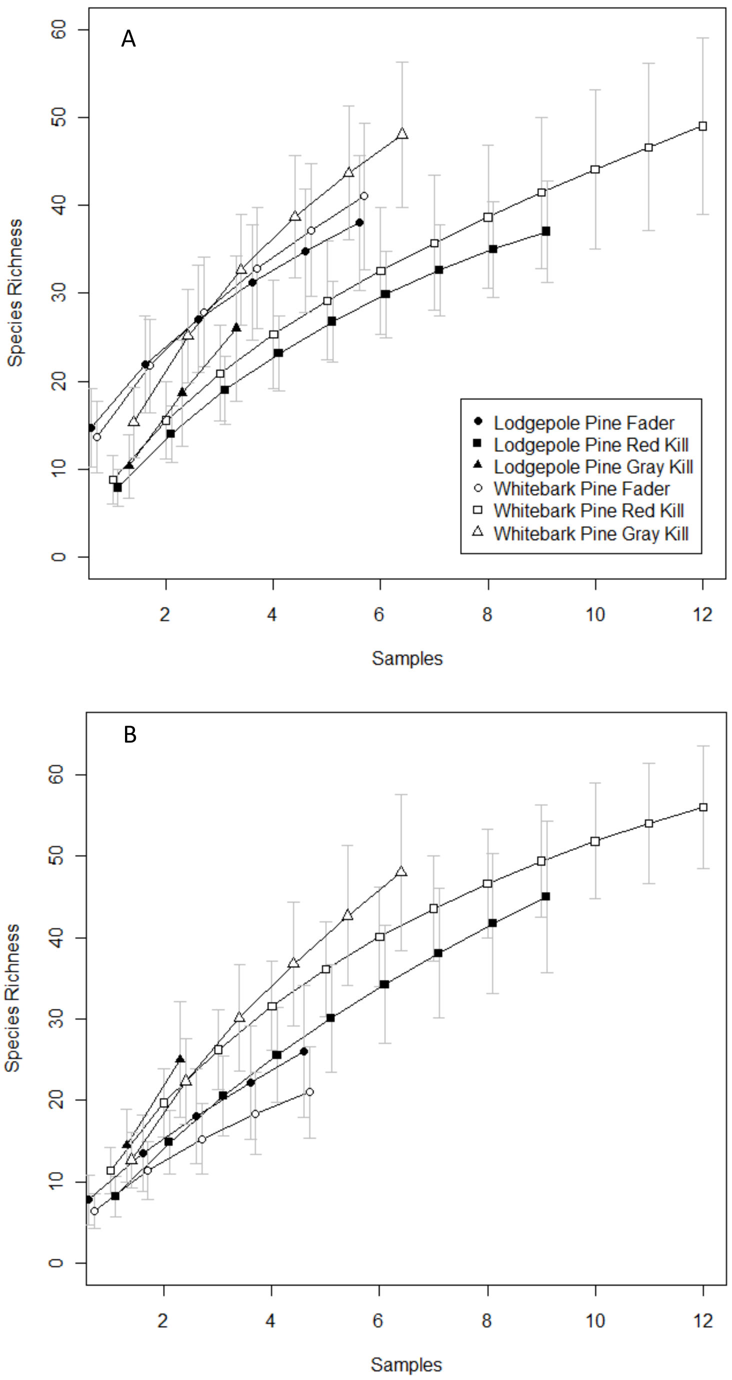
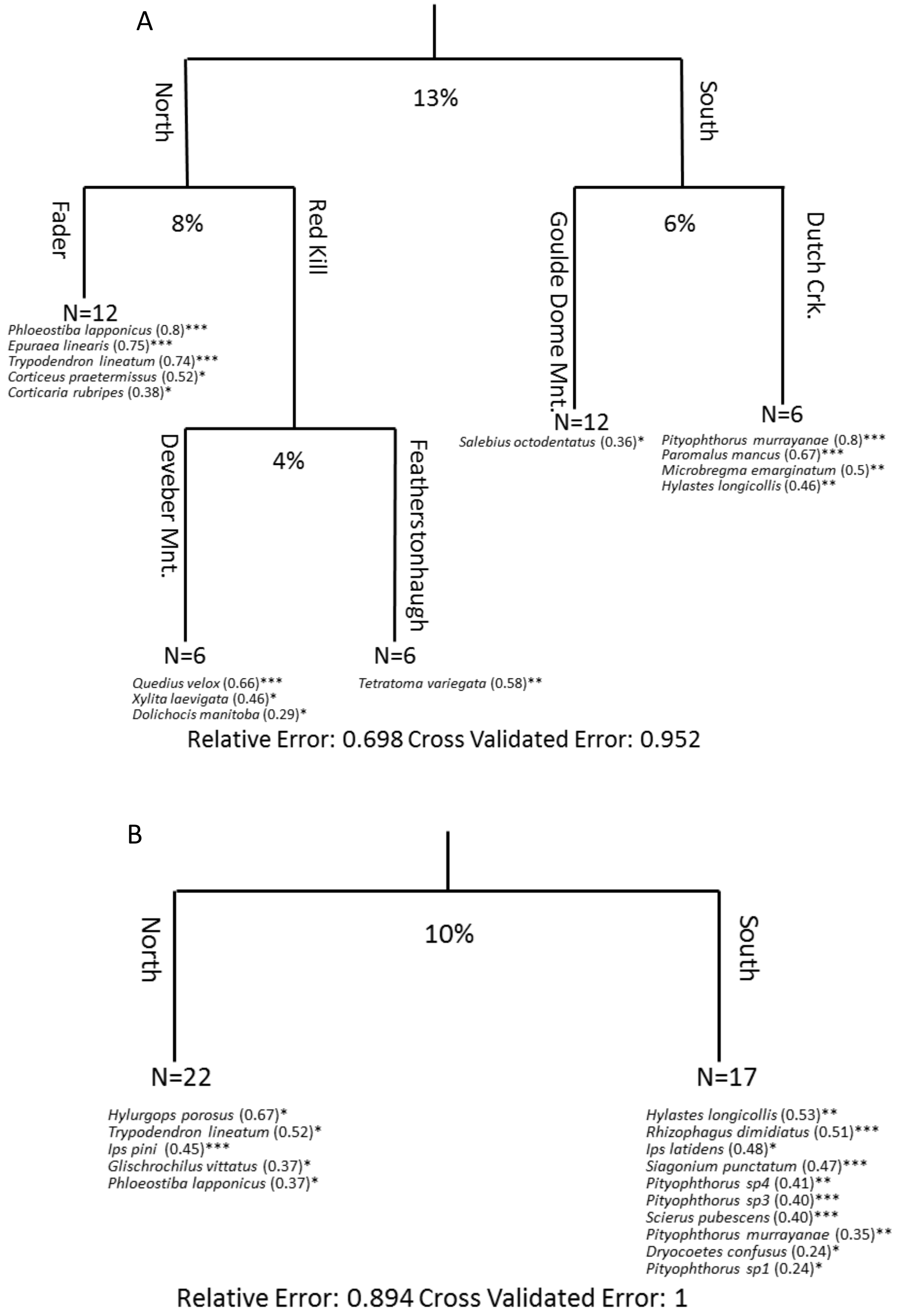


Figure 4.1: Species accumulation curves of beetles collected on two pine hosts across different snag age classes of MPB killed trees. Curves were computed by sample-based rarefaction for: (A) emergence traps; and (B) flight intercept trap catches. Estimates of species richness (Mao-Tao function) and 95% confidence intervals are presented.



Figures 4.2: MRT of saproxylic beetles collected in: emergence (A) and flight intercept traps (B). Explanatory variables inclue: snag age class, tree species, region and site. The factor determining and variance explained at each split are presented on the figures. ISA results and number of traps (N) for the terminal nodes of each tree are presented. Only species with indicator values (in parenthesis) >0.60 are presented. Significance codes: $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***.

high (0.95 and 1.0, respectively). Region was the most important explanatory variable, accounting for 13% of the variation in emergence trap catches and 10% of the variation in flight intercept trap catches. No further explanatory variables were identified as important in flight intercept trap catches. The variable snag age was important only in Willmore Wilderness Park, with the difference between *fading* and *red kill* trees explaining 8% of the overall variation in emergence trap catches. Differences among sites explained 6% of the variation in the in the Crowsnest Pass and a further 4% in the *red kill* snags in Willmore Wilderness Park (Figures 4.2 A, B).

Six species served as good indicators of the terminal nodes of the MRT for emergence trap data, but only one species qualified as a good indicator of flight intercept trap catches. *Phloeostiba lapponicus* ($I_{nd}V_{al} = 0.8$, $p<0.001$), *T. lineatum* ($I_{nd}V_{al} = 0.74$, $p = 0.004$), and *E. linearis* ($I_{nd}V_{al} = 0.75$, $p = 0.002$) were good indicators of *fader* snags. The staphylinid, *Quedius velox* Smetana ($I_{nd}V_{al} = 0.66$, $p = 0.002$), was a good indicator of *red kill* snags at Deveber Creek. *Pityophthorus murrayanae* ($I_{nd}V_{al} =0.80$, $p < 0.001$) and the histerid, *Paromalus mancus* Casey ($I_{nd}V_{al} = 0.67$, $p < 0.001$), were good indicators of the Dutch Creek site. *Hylurgops porosus* ($I_{nd}V_{al} = 0.67$, $p = 0.021$) was a good indicator of flight intercept trap catches in Willmore Wilderness Park (Figures 4.2 A, B).

RDAs of emergence trap catches (Figures 4.3 A, B) showed that, except for the differences between *fader* and *red kill* snags, the variables host species and snag age had relatively small effects on the beetle assemblages. In Willmore Wilderness Park, the variables site and accumulated trap days together explained 15% of the variation in emergence trap catches, while host species and snag age together explained 18%. In Wilmore Wilderness Park, beetle assemblages were strongly influenced by the variable snag age (df = 1, F = 4.02, $p < 0.001$) but did not differ significantly between host species (df = 1, F = 1.22, $p > 0.1$). In the Crowsnest Pass, the variables site and accumulated trap days together explained 15% of the variation in emergence trap catch but the variables host species and snag age together explained only 11%. In the Crowsnest Pass region, neither of

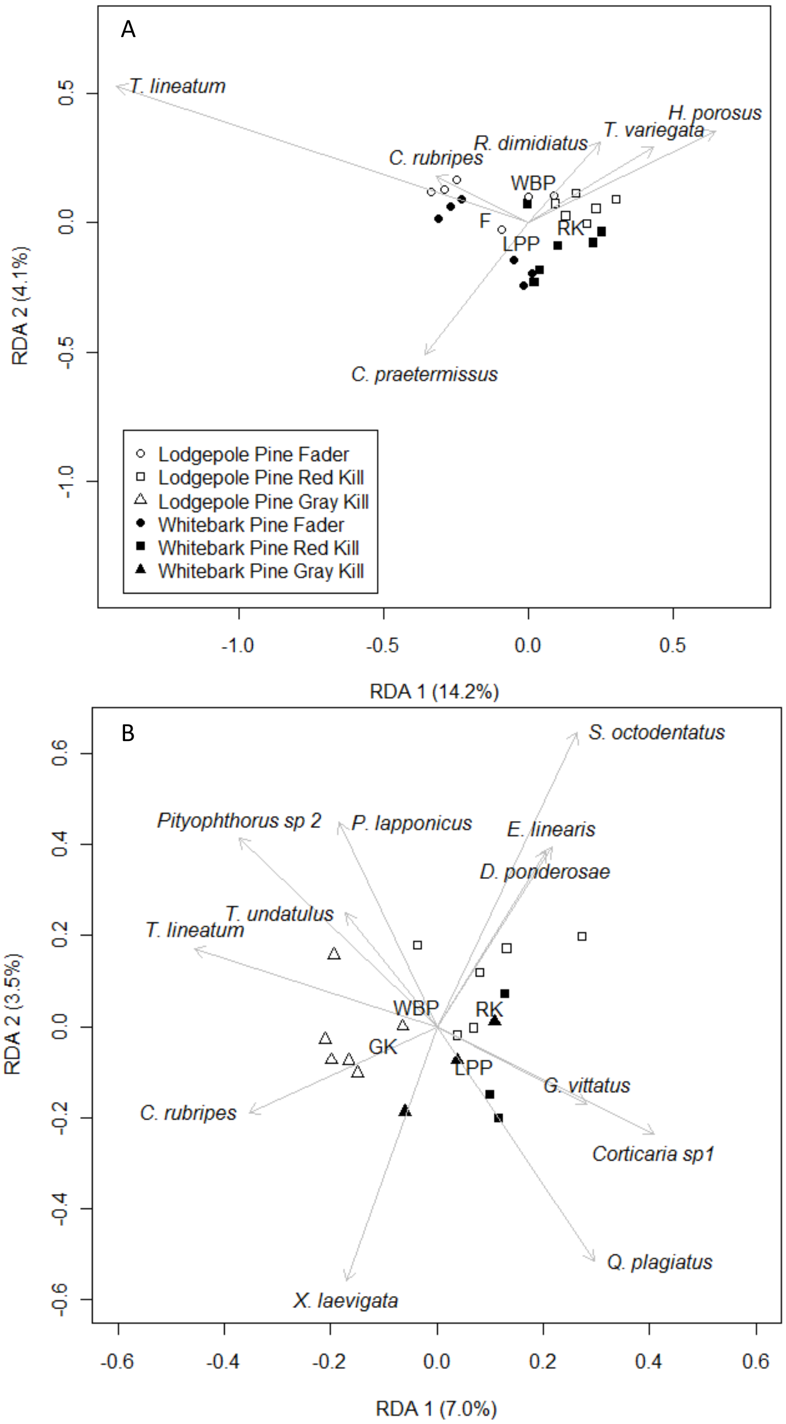


Figure 4.3: Redundancy analysis (RDA) of beetles collected in: (A) emergence traps in Willmore Wilderness Park; (B) emergence traps in Crowsnest Pass; (C) flight intercept traps in Willmore Wilderness Park; and (D) flight intercept traps in Crowsnest Pass. Variation explained by the first and second RDA axis presented on the figure. Ordination scaling focused on site scores. Only vectors of species scores extended beyond the circle of equilibrium are plotted. Vector labels are the first initial of the genus and the full species name. Factor centroids for the constraining variables tree species lodgepole pine (LPP) and whitebark pine (WBP); and snag age classes, yellow fader (F), red kill (RK), and gray kill (GK) indicated by bold text in the plot.

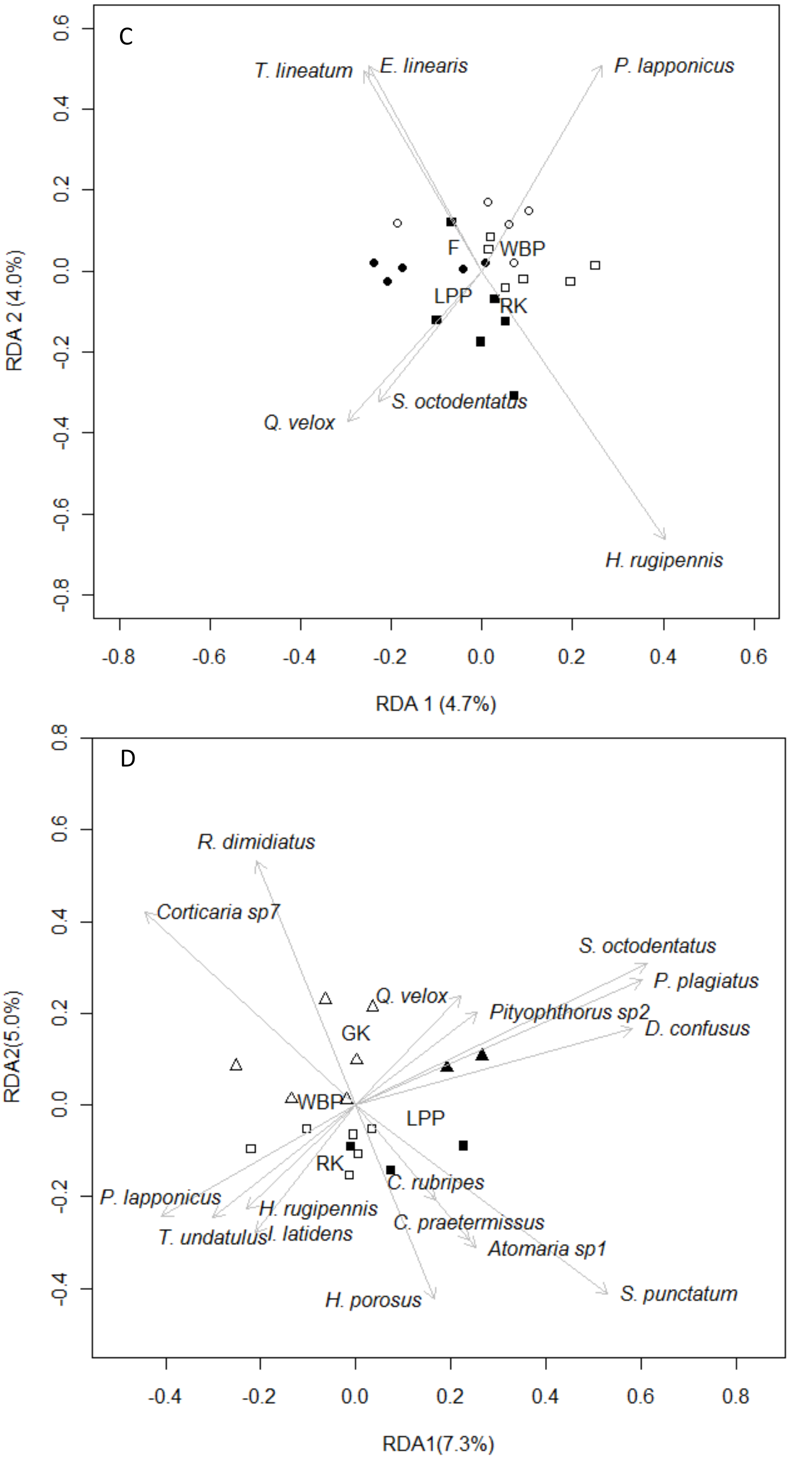


Figure 4.3: (*Continued*)

the variables snag age (df = 1, F = 1.07, p > 0.1) or host species (df = 1, F = 0.77, p > 0.1) had strong effects on beetle assemblages. The ordinations produced by RDA suggested some similarity of the fauna within snags of the same host species and age class; however, overlap among these groups was substantial and the variation explained by each RDA axis small (Figures 4.3 A, B).

RDAs showed that host species and snag age had relatively small effects on the beetle assemblages sampled by flight intercept traps (Figures 4.3 C, D). In Willmore Wilderness Park, the variables site and accumulated trap day together explained 19% of the variation in flight intercept trap catch while the variables host species and snag age together explained only 9%. In the Crowsnest Pass, the variables site and accumulated trap days together explained 19% of the variation in flight intercept trap catch and host species and snag age together explained 12%. Beetle assemblages were not significantly influenced by the variables host species ($df = 1$, $F = 1.02$, $p > 0.1$; $df = 1$, $F = 1.25$, $p > 0.1$) or snag age ($df = 1$, $F = 1.03$, $p > 0.1$; $df = 1$, $F = 0.90$, $p >0.1$) in either Willmore Wilderness Park or the Crowsnest Pass, respectively (Figure 4.3 C, D).

The more circumscribed assemblage including the MPB and its competitors and predators were, in contrast to the results above, influenced by the variables host species and snag age (Figure 4.4). The variables region, site, and accumulated trap days together explained 24% of the variation among emergence trap catches of this group, and host species and snag age together explained an additional 10%. Both host species ($df = 1$, $F = 1.95$, $p < 0.01$) and snag age ($df = 1$, $F = 1.90$, $p < 0.01$) significantly influenced this assemblage. Species by site biplots indicate that catches of five species most influenced this pattern: *I. pini* and *C. praetermissus* were strongly associated with *fader* lodgepole pines; *H. porosus* was more closely related with *red kill* whitebark pines; the predaceous clerid, *Thanasimus undulatus* (Say), was most commonly associated with *fader* snags; and *Q. velox* was most commonly associated with *red kill* snags (Figure 4.4).

4.3.2 *Individual species responses*

There were nine good indicators among the six different combinations of host species and snag age classes, five based on emergence trap data and four based on

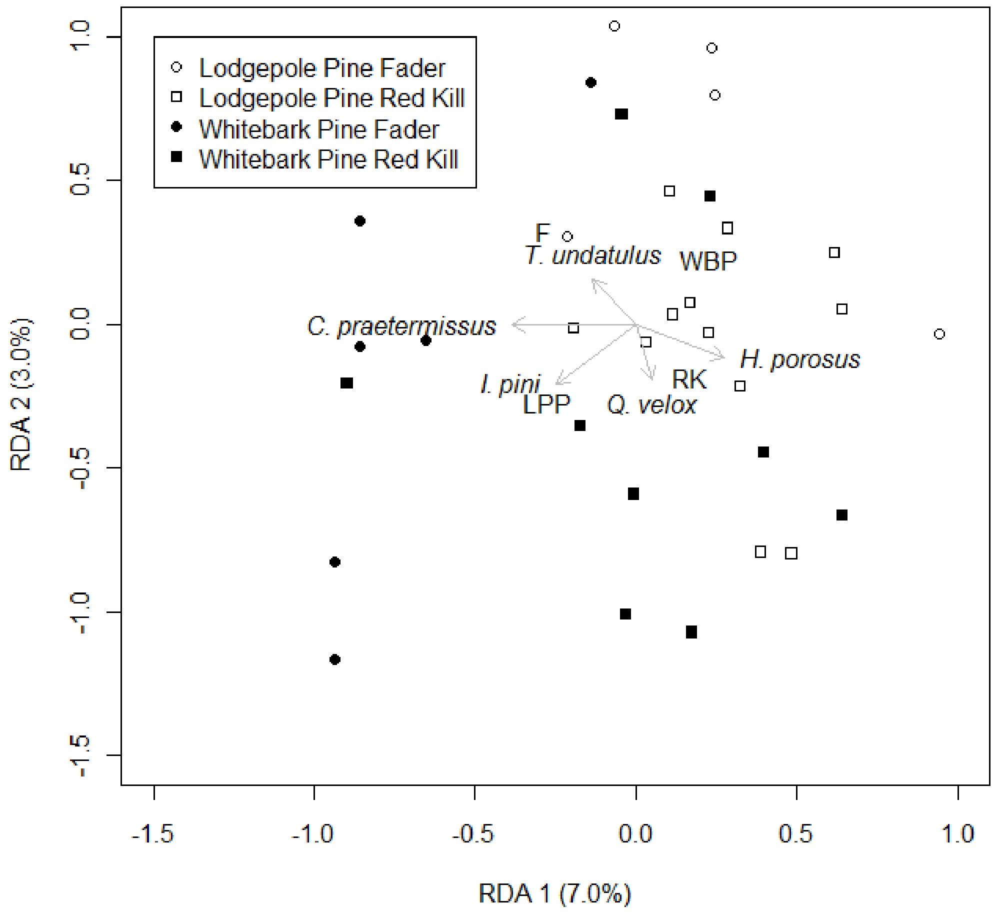


Figure 4.4: Redundancy analysis (RDA) of beetles collected in emergence traps from Willmore Wilderness Park and the Crowsnest Pass. This set of data includes 28 species known or likely to be associated with the mountain pine beetle. Variation explained by the first and second RDA axis presented on the figure. Ordination scaling focused on species scores. Only the longest five vectors were presented. Vector labels are species names shortened to the first four letters of genus and species names. Factor centroids for the constraining variables tree species lodgepole pine (LPP) and whitebark pine (WBP); and snag age classes, yellow fader (F) and red kill (RK) indicated by bold text in the plot.

flight intercept trap catches (Table 4.2). *Ips pini* was a good indicator of *fader* lodgepole pine based on both emergence trap data ($I_{nd}V_{al}$ = 0.61, p = 0.009) and flight intercept trap data ($I_{nd}V_{al}$ = 0.62, p = 0.015). *Corticeus praetermissus* ($I_{nd}V_{al}$ = 0.71, p = 0.010), *E. linearis* ($I_{nd}V_{al}$ = 0.65, p = 0.002) and *P. lapponicus* ($I_{nd}V_{al}$ = 0.60, p = 0.01) were also good indicators of *fader* lodgepole pines, based on emergence trap data. There were four good indicators of *gray kill* lodgepole pine, including the lathridiid, *Enicmus tenuicornis* LeConte ($I_{nd}V_{al}$ = 0.63, p = 0.001), based on emergence trap data, and the bark beetles, *Pityogenes plagiatus knechteli* Swaine ($I_{nd}V_{al}$ =0.93, p = 0.004), *Dryocoetes confusus* Swaine ($I_{nd}V_{al}$ = 0.90, p = 0.002) and *Pityophthorus* species 2 ($I_{nd}V_{al}$ = 1.0, p = 0.001), all based on flight intercept trap data. There was only one significant indicator of whitebark pine, *P. murrayanae* ($I_{nd}V_{al}$ = 0.89, p = 0.001), based on emergence trap data from *gray kill* snags.

Table 4.2: Summary of indicator species analysis of saproxylic beetles collected on whitebark pine (WB) and lodgepole (LP) pine snags. *Fader, red kill* and *gray kill* describe the canopy condition used to estimate snag age class. Only species with p values < 0.05 are shown. Significant indicators collected in emergence and window traps are presented separately in the upper and lower panels of the table.

Species	Snag Type	Indicator Value	P-Value
Emergence raps			
Corticeus praetermissus	LPP *fader*	0.71	0.01
Epuraea linearis	LPP *fader*	0.65	0.002
Ips pini	LPP *fader*	0.61	0.009
Phloeonomus lapponicus	LPP *fader*	0.60	0.01
Enicmus tenuicornis	LPP *gray kill*	0.63	0.001
Siagonium punctatum	LPP *gray kill*	0.47	0.012
Pityophthorus murrayanae	WBP *gray kill*	0.89	0.001
Microbregma emarginatum	WBP *gray kill*	0.50	0.021
Hylastes longicollis	WBP *gray kill*	0.43	0.011
Pityophthorus species *2*	WBP *gray kill*	0.30	0.042
Paromalus mancus	WBP *gray kill*	0.23	0.042
Window traps			
Ips pini	LPP *fader*	0.62	0.015

There was some evidence suggesting competitive exclusion between the MPB and *I. pini*. These two species were only collected together once in the same snag in similar abundances. In all other instances, when one species was present the other species was either absent of at least an order of magnitude less abundant. The MPB was 'dominant' in eight snags (whitebark: 6; lodgepole: 2) while *I. pini* was 'dominant' in eight different snags (whitebark: 1; lodgepole: 7).

Forty six of the species found in this study (30%) were collected in emergence traps on both hosts. Fourteen of the 20 most abundant species collected in emergence traps on each host were the same; however, their rank order differed between the two host species. Thirty-eight species were collected only in emergence traps on whitebark pines; however, the majority of these were also collected outside the known distribution of whitebark pine or on other hosts, making it clear that they do not exclusively inhabit whitebark pine. Nonetheless, two fungivores included in this group from emergence traps, *Microstagetus parvales* (Corylophidae) and *Agathidium fenderi* (Leiodidae), have only been collected within the distribution of whitebark pine. Four species of *Pityophthorus* and one species of *Corticaria*, which could not be confidently identified to species, were also collected only on whitebark pines. The likelihood that these species are associated exclusively with whitebark pine is discussed later.

4.3.3 Trap types

The beetle assemblages represented in the catches of emergence traps and flight intercept traps were quite similar overall. Interestingly, emergence traps collected more specimens (8942) than flight intercept traps (1240), even when *T. lineatum* was excluded (emergence, 3007; flight intercept, 1126). Emergence traps and flight intercept trap types also collected similar numbers of species, 104 and 98 species, respectively. Specimens that were abundant in emergence traps also tended to be abundant in flight intercept traps. A number of rarely encountered species were collected in only one trap type; some from flight intercept traps were likely not saproxylic, *e.g.*, the dung beetles, *Aphodius* spp., and the leaf beetles, *Syneta* spp., while other species that have saproxylic habits are not known to feed on *Pinus*, *e.g.*, the bark beetle, *Scierus pubescens* Swaine.

4.4 Discussion

4.4.1 *Host effects*

I did not find conclusive evidence of beetle species exclusively associated with whitebark pine snags. Two fungivorus species (*M. parvales* and *A. fenderi*) were collected emerging only from whitebark pine but these are poorly known ecologically, so it is risky to classify these as host specific. These observations from emergence traps, however, represented only single specimens for each species. It seems more likely that these species are associated with specific fungi

(Stehr 1991, Wheeler and Miller 2005a, 2005b) rather than with a specific tree species, and these associations can only be clarified with additional ecological study. It is also possible that species unique to whitebark pine may exist among a few taxa that I could not identify, such as beetle larvae, the genera *Corticaria* and *Pityophthorus* or species of Aleocharinae.

Although *P. murrayanae* was a good indicator of *gray kill* whitebark pine at the study sites, it has a transcontinental distribution and is associated with numberous species within the Pinaceae (Wood 1982). The several other unidentified species of *Pityophthorus*, however, are good candidates for having unique host associations with whitebark pine but this cannot be determined until these species are identified and known host associations determined. If there are beetle species that are exclusively associated with whitebark pine, they will likely be xylophagous or phloeophagous and in a group where gaps in our knowledge of host associations and distributions are prevalent (like *Pityopthorus*), or among undescribed species. We collected one unknown species of the genus *Corticaria* exclusively from whitebark pines, but this genus is largely unstudied and in need of taxonomic revision. It is known that *Corticaria* species are fungivores, so it is likely that the species collected exclusively on whitebark pine is associated with certain fungi rather than with the pine. Of course it is also possible that whitebark pine supports a different community of microorganisms than lodgepole pine, and so associations with fungivores could still be quite specific. In fact, differences in communities of microoganisms may account for some of the observed differences in beetle assemblage structure between whitebark and lodgepole pine. For example, preliminary work with ophiostomoid fungi associated with mountain pine beetle shows that success of some fungus species can vary among host species (Esch, unpublished data). In summary, saproxlyic beetle host specificity is likely rare when compared among hosts in the same genera. Instead host preferences are likely more common at the genus level (Bright 1976, Wood 1982, Siitonen 2001, Wu *et al.* 2008) or at higher taxonomic groupings, such as broad-leaved vs. conifer species (Irmler *et al.* 1996, Jacobs *et al.* 2007, Ulyshen and Hanula 2009).

My results do not preclude the possibility of exclusive host associations like the one observed between *Pinus flexilis* and *Ips woodi.* Saproxylic beetle assemblages vary with the cause of tree death (Langor *et al.* 2008), order of host colonization (Paine *et al.* 1981, Amezaga and Rodriguez 1997), part of tree utilized (*e.g*., bole, branches or root collar) (Wood 1982, Vodka *et al.* 2009, Foit 2010), exposure to sunlight (Vodka *et al.* 2009), decay class and position (Savely 1939, Howden and Vogt 1951, Wallace 1953, Irmler *et al.* 1996, Hammond *et al.* 2004, Vanderwel *et al.* 2005, Jacobs *et al.* 2007, Ulyshen and Hanula 2009, 2010). Had I included a broader range of such factors into this experiment, or identified other diverse taxa associated with dead wood (*e.g*., Diptera, Acari), I may have found more evidence for exclusive associations.

Although I did not find beetle species unique to whitebark pines or differences in species richness between the two hosts, there were differences in assemblage structure. These differences were most evident among the MPB and its competitors and predators, particularly so among the Scolytinae, with *I. pini* being a significant indicator of lodgepole pines and *I. latidens*, *D. ponderosae* and a number of *Pityophthorus* more common in whitebark pines. This is noteworthy from a pest management perspective because *I. pini* decreases MPB attack density and brood production through interspecific competition (Safranyik *et al*. 1999). Furthermore, these data suggest that *I. pini* may have a competitive advantage over *D. ponderosae* in lodgepole pine and that *D. ponderosae* may have a competitive advantage over *I. pini* in whitebark pine. I also observed a similar pattern of greater abundance of *I. pini* in lodgepole pines and absence from whitebark pines in MPB pheromone baited trees 1-2 months after attacked by the MPB (Chapter 3). Interestingly, Seybert and Gara (1970) also reported *I. pini* preferentially attacking hard pines over soft pines. Possible explanations for this pattern are differences in the chemical composition of the subcortical tissues of the host (Smith 2000) or other less studied aspects of host quality, such as the community of microorganisms inhabiting the snags. All await further study.

4.4.2 *Age effects*

Savely (1939) established three decay classes for dead pines in North America: *i*) phloem phase, *ii*) subcortical space phase, and *iii*) rot phase. Species richness is generally believed to decrease with advancing decay class in coniferous dead wood (Savely 1939, Howden and Vogt 1951, Siitonen 2001, Ulyshen and Hanula 2010). Although beetle species richness did not differ significantly between snag age classes in our study, I explored a relatively short period of decay, and because the bark was still intact on *gray killed* trees. I likely only captured the Savely's phase *i)*. I may have seen more marked differences in species richness and species composition had a broader range of decay classes been available to sample.

Beetle species composition, however, did change with snag age class, with differences between *fader* and *red kill* snags greater than those between *red kill* and *gray kill* trees. This pattern was mainly reflected by the fact that species specialized in utilizing freshly killed trees, such as ambrosia beetles, bark beetles and their predators, occurred in high numbers in *fader* snags. This rapid colonization and turnover of specialized fauna has been observed in other systems of saproxylic beetles (Howden and Vogt 1951, Hammond *et al.* 2001, Siitonen 2001, Hammond *et al.* 2004, Jacobs *et al*. 2007). Species turnover was likely relatively slow in the present experiment due to the cool temperatures at the high elevations of the study sites (Amman 1973, Bentz *et al.* 1991). For example, we observed MPBs emerging from *red kill* snags, possibly indicating that their development took > 1 year. This protracted emergence may have created greater overlap in the fauna than is observed at lower elevations, and it likely reduced faunal differences between snag age classes observed in this study.

4.4.3 Spatial effects

Variation between regions and sites had the greatest effects on beetle composition but these are not easily understood from the results of this study. Saproxylic assemblages exhibit high spatial variability, because many species have specific microhabitat requirements, and these microhabitats are not distributed evenly on the landscape (Siitonen 2001, Hammond *et al.* 2004, Langor *et al*. 2008). Factors that could have influenced the spatial variation observed in beetle assemblage composition include stand age/succession stage, stand structure, quantity/quality of dead wood in the stand, climatic/topographic factors, and the historic/ongoing anthropogenic activities in and around the study sites (Savely 1939, Okland *et al.* 1996, Vodka *et al.* 2009, Foit 2010, reviews by Siitonen 2001 and Langor *et al.* 2008). Unfortunately, temporal and spatial effects were confounded in this study. Both trapping period and year of collection differed between the two study regions, likely introducing substantial variation and biasing samples. This bias was likely compounded by trap disturbance.

4.4.5 *Conclusions and Management Recommendations*

This study showed that the assemblage of dead wood associated beetles differed only subtly between two sympatric, distantly related pine species. These differences occurred predominantly among scolytine bark beetles, which are species that generally require fresh or recently killed phloem to complete their development. We did not identify any species that we could confidently associate exclusively with whitebark pine. However, seven rarely encountered species, most of which could not be identified and may be undescribed, may have such exclusive associations with whitebark pine. These candidates deserve additional study to ascertain host range. Species exclusively associated with whitebark pine deserve some attention to ascertain whether conservation measures are warranted.

This project is the first systematic study of invertebrates associated with whitebark pine and the first for any subalpine tree species in Canada. It contributed new host associations and localities to the growing body of knowledge about saproxylic beetles in western Canada and broadened our understanding of the spatial and temporal patterns of variation of beetle assemblages in a little studied habitat. This study also produced a large number of non-beetle insect specimens that provide the basis for further research of subalpine insect ecology. Such baseline work is essential in order to track future changes in subalpine ecosystems associated with climate change or other disturbances.

Based on evidence compiled here, falling and burning MPB infested whitebark pine will not threaten saproxylic species esclusively associated with whitebark pines. Although, when beetle idenfications are completed, exclusive associations may become evident. Admittedly this study was limited to a short period after tree death 1-5 years; however, beetle affinities for particular host species decreases with time after death (Langor *et al.* 2008, Wu *et al.* 2010). Altering the amount or quality of dead wood on a landscape, as occurs through felling and burning, can lead to long-term declines in saproxylic species (Siitonen 2001). Given my results, however, I believe that the risks of allowing MPB populations to spread unchecked through whitebark pines and subalpine forests in general, are far greater than the possible impacts associated with altering dead wood dynamics. The best approach for saproxylic beetle conservation, in my view, is to ensure that subalpine whitebark pine stands are conserved to the extent possible and re-established in the wake of natural mortality and management activities so that a supply of habitat for saproxylic insects is ensured in the long term.

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Table 4.1: Beetles collected from emergence and flight intercept (window) traps on two host species, whitebark pine (WB) and lodgepole pine (LP). Beetles were collected from two regions of Alberta, north (N) and south (S), and from three ages of snags, yellow fader (F), red kill (RK) and gray kill (GK). The subscripts $_e$ and $_w$ indicate trap type for each age class, emergence traps and window traps, respectively. The superscript [a] indicates new provincial record, [b] indicates inclusion into a subset of known/probable mountain pine beetle associates, and[?] indicates tentative identification.

Family and Species	Total	Emergence		Window		Snag Age	Region
		LPP	WBP	LPP	WBP		
Agyrtidae							
Ipelates latus (Mannerheim)	4			1	3	$\mathrm{F_w/RK_w}$	N
Anobiidae							
Episenrus trapezoideus (Fall)[a]	1			1		$\mathrm{RK_w}$	S
Ernobius gentilis Fall	1				1	$\mathrm{RK_w}$	S
Microbregma emarginatum (Duftschmid)	8		3		5	$\mathrm{F_w,RK_w,GK_{ew}}$	N,S
Cantharidae							
Cantharidae species 1	1	1				$\mathrm{GK_e}$	S
Podabrus extremus LeConte	1			1		$\mathrm{RK_w}$	S
Podabrus ochocensis Fend[a]	1		1			$\mathrm{F_e}$	N
Podabrus piniphilus (Eschscholtz)	1	1				$\mathrm{RK_e}$	N
Podabrus species 1	2	2				$\mathrm{RK_e}$	N,S
Carabidae							
Calathus advena (LeConte)[b]	31	13	10	2	6	$\mathrm{F_{ew},RK_{ew},GK_e}$	N,S
Cerambycidae							
Acmaeops proteus proteus (Kirby)	6		2		4	$\mathrm{F_e,RK_e,GK_w}$	N,S
Asemum striatum (Linné)	1	1				$\mathrm{F_e}$	N
Cortodera coniferae Hopping & Hopping	1	1				$\mathrm{GK_e}$	S
Gnathacmaeops pratensis (Laicharting)	1		1			$\mathrm{F_e}$	N

Table 4.1: (*Continued*)

Family and Species	Total	Emergence		Window		Snag Age	Region
		LPP	WBP	LPP	WBP		
Judolia montivagans montivagans (Couper)	1				1	RK$_w$	S
Monochamus scutellatus (Say)	1		1			GK$_e$	S
Neospondylis upiformis Mannerheim	1			1		RK$_e$	N
Phymatodes dimidiatus (Kirby)	1				1	RK$_w$	S
Pygoleptura nigrella nigrella (Say)	1				1	RK$_w$	S
Rhagium inquisitor inquisitor (Linné)	2		1		1	GK$_{ew}$	S
Chrysomelidae							
Syneta carinata Mannerheim	2		1	1		RK$_w$, Gk$_e$	N,S
Syneta pilosa Brown	4	1	1	1	1	F$_e$, RK$_w$,GK$_{ew}$	N,S
Ciidae							
Dolichocis manitoba Dury	5	3	1	1		RK$_e$	N,S
Orthocis punctatus (Mellie)	1	1				GK$_e$	S
Clambidae							
Calyptomerus oblongulus Mannerheim	2		1		1	RK$_e$,GK$_w$	S
Cleridae							
Thanasimus undatulus (Say)	34	5	22	1	6	All	N,S
Coccinellidae							
Didion longulum Casey[b]	1		1			RK$_e$	S
Colydiidae							
Lasconotus intricatus Kraus	4		1	2	1	F$_w$,GK$_e$	N,S
Corylophidae							
Clypastraea obesa Casey	2		1	1		F$_e$,GK$_w$	N,S
Microstagetus parvulus Wollaston[a]	1		1			GK$_e$	S
Cryptophagidae							
Atomaria species 1	6		3	3		F$_e$,RK$_{ew}$,GK$_e$	N,S

Table 4.1: (*Continued*)

Family and Species	Total	Emergence		Window		Snag Age	Region
		LPP	WBP	LPP	WBP		
Caenoscelis ferruginea (C. R. Sahlberg)[a]	4		1		3	F_w,GK_{ew}	N,S
Cryptophagus laticollis Lucas	2		1		1	RK_e,GK_w	S
Cryptophagus peregrinus Wood. & Coom.[a]	5	1	1	3		RK_{ew},GK_{ew}	S
Cryptophagus pilosus Gyllenhal	1			1		GK_w	S
Cryptophagus tuberculosus Mäklin	7			3	4	F_w,RK_w,GK_w	N,S
Cryptophagus varus Woodroffe & Coombs	2	1	1			RK_e,GK_e	S
Henotiderus species 1	1		1			RK_e	S
Salebius octodentatus Mäklin	74	24	19	28	3	All	N,S
Curculionidae							
Carphonotus testaceus Casey	2	1	1			RK_e,GK_e	S
Pissodes rotundatus Leconte	2	1			1	RK_{ew}	N,S
Rhyncolus brunneus Mannerheim	2	1	1			F_e	N
(Scolytinae)							
Cryphalus ruficollis Hopkins[b]	5		2	1	2	F_e,RK_{ew},GK_w	N,S
Crypturgus borealis Swaine	1		1			F_e	N
Dendroctonus ponderosae Hopkins[b]	49	12	35		2	F_e, RK_{ew},GK_w	N,S
Dryocoetes autographus (Ratzeburg)	12		5	2	5	F_w, RK_w,GK_{ew}	N,S
Dryocoetes caryi Hopkinsb	5		2	1	2	RK_{ew},GK_{ew}	S
Dryocoetes confusus Swaine	10	2	1	6	1	RK_w,GK_{ew}	S
Hylastes longicollis Swaine[b]	53	2	6	12	33	All	N,S
Hylastes nigrinus (Mannerheim)	9		1		8	GK_{ew}	S
Hylurgops porosus (LeConte)[b]	372	34	27	107	204	all	N,S
Hylurgops rugipennis (Mannerheim)[b]	71	7	12	7	45	F_{ew},RK_w,Gk_{ew}	N,S
Ips latidens (LeConte)[b]	145	51	49	3	42	All	N,S
Ips mexicanus (Hopkins)[b]	1	1				F_e	N

Table 4.1: (*Continued*)

Family and Species	Total	Emergence		Window		Snag Age	Region
		LPP	WBP	LPP	WBP		
Ips pini (Say)[b]	126	82	6	26	12	F_{ew},RK_{ew}, GK_{e}	N,S
Phloeosinus hoferi Blackman[a]	3	1			2	F_{ew}	N
Pityogenes plagiatus knechteli Swaine	25	7	3	14	1	All	N,S
Pityokteines ornatus (Swaine)[a]	6	1	1	2	2	F_{ew}, RK_{e},GK_{w}	N,S
Pityophthorus murrayanae Blackman[b]	203	3	177	1	22	RK_{ew},GK_{ew}	S
Pityophthorus species 1	10		1	4	5	RK_{w},GK_{ew}	S
Pityophthorus species 2[b]	7		5	2		RK_{e},GK_{ew}	S
Pityophthorus species 3	21		1	11	9	F_{w}, RK_{w},GK_{ew}	N,S
Pityophthorus species 4	12		2	1	9	RK_{w}, GK_{ew}	S
Polygraphus rufipennis (Kirby)	1				1	GK_{w}	S
Scierus annectans LeConte	4		1	2	1	RK_{w}, GK_{ew}	S
Scierus pubescens Swaine	12			2	10	RK_{w}, GK_{w}	N,S
Trypodendron lineatum (Olivier)	6049	4144	1791	43	71	All	N,S
Xylechinus montanus Blackman	8				8	RK_{w},GK_{w}	S
Dermestidae							
Megatoma pubescens (Zetterstedt)	1	1				RK_{e}	N
Elateridae							
Ctenicera nigricollis (Bland)	2			2		F_{w}, RK_{w}	N
Ctenicera umbricola (Eschscholtz)	1			1		GK_{w}	S
Ctenicera volitans (Eschscholtz)[a]	1		1			F_{e}	N
Eanus albertanus W J Brown	1	1				F_{e}	N
Negastrius tumescens LeConte	1		1			RK_{e}	S
Endomychidae							
Endomychus limbatus (Horn)	1				1	GK_{w}	S
Mycetina idahoensis Fall[a]	1		1			GK_{e}	S

Table 4.1: (*Continued*)

Family and Species	Total	Emergence		Window		Snag Age	Region
		LPP	WBP	LPP	WBP		
Histeridae							
Paromalus mancus Casey	4		4			RK_e,GK_e	S
Laemophloeidae							
Leptophloeus species 1	17	7	6	4		F_e,RK_{ew},GK_e	N,S
Lathridiidae							
Corticaria rubripes [a]	37	15	12	4	6	F_{ew},RK_{ew},GK_e	N,S
Corticaria species 1	25	12	7	3	3	All	N,S
Corticaria species 2	2		2			F_e	N
Corticaria species 3	3	1	2			F_e,GK_e	N,S
Corticaria species 4	7	2	5			F_e,RK_e,GK_e	N,S
Corticaria species 5	2	1		1		F_w,RK_e	N
Corticaria species 6	5	1	2		2	RK_{ew},GK_e	S
Corticaria species 7	3	1	1		1	F_e,RK_e,GK_w	N,S
Corticaria unknown	138	78	45	9	6	All	N,S
Enicmus tenuicornis LeConte	4	2	1	1		RK_e,GK_{ew}	S
Leiodidae							
Agathidium estriatum$^{?}$ Horn [a]	2	1	1			F_e,GK_e	N,S
Agathidium fenderi Hatch [a]	3		1		2	RK_e	N,S
Agathidium angulare Mannerheim	1				1	GK_w	S
Catoptrichus frankenhaeuseri (Mannerheim)[a]	1				1	RK_w	N
Liocyrtusa luggeri (Hatch)	2		1		1	GK_{ew}	S
Lycidae							
Dictyopterus aurora (Herbst)	1		1			RK_e	N
Melandryidae							

Table 4.1: (*Continued*)

Family & Species	Total	Emergence		Window		Snag Age	Region
		LPP	WBP	LPP	WBP		
Xylita laevigata (Hellenius)	29	10	18		1	RK_{ew},GK_{e}	N,S
Zilora hispida LeConte	1	1				GK_{e}	S
Melyridae							
Hoppingiana hudsonica (LeConte)	1			1		RK_{w}	S
Monotomidae							
Rhizophagus dimidiatus Mannerheim	73	15	28	8	22	All	N,S
Rhizophagus minutus minutus Mannerheim	2	1	1			F_{e}, GK_{e}	N,S
Rhizophagus remotus Leconte	1		1			GK_{e}	S
Nitidulidae							
Epuraea flavomaculata Mäklin	1				1	GK_{w}	S
Epuraea linearis Mäklin	254	164	37	21	32	All	N
Epuraea planulata Erichson	12	8	3	1		F_{e},RK_{ew}	N
Epuraea rufida (Melsheimer)[a]	5	1		2	2	F_{w},RK_{ew},GK_{w}	N,S
Epuraea truncatella Mannerheim	386	303	19	14	50	All	N,S
Epuraea species 1	37	33	4			F_{e}, RK_{e}	N
Glischrochilus vittatus (Say)	43	11	6	13	13	F_{ew},RK_{ew},GK_{w}	N,S
Pityophagus rufipennis Horn[a]	1				1	GK_{w}	S
Oedemeridae							
Calopus angustus LeConte	2				2	RK_{w}	S
Ptiliidae							
Acrotrichis species 1	1				1	RK_{w}	S
Scarabaeidae							
Aphodius species 1	1			1		RK_{w}	N
Aphodius species 2	1				1	RK_{w}	S
Aphodius species 3	1			1		RK_{w}	S

Table 4.1: (*Continued*)

Family & Species	Total	Emergence		Window		Snag Age	Region
		LPP	WBP	LPP	WBP		
Scraptiidae							
Anaspis rufa Say	3		1		2	GK$_{ew}$	S
Canifa species 1	1				1	GK$_{w}$	S
Pectotoma hoppingi Hatch	2	1			1	RK$_{w}$,GK$_{e}$	S
Scydmaenidae							
Veraphis lacuna Marsh[a]	2	2				F$_{e}$,GK$_{e}$	N,S
Staphylinidae							
Acidota crenata (Fabricius)[b]	2		2			F$_{e}$,RK$_{e}$	N
Aleocharinae	772	641	62	28	41	All	N,S
Anthophagini species 1	2	2				F$_{e}$	N
Atrecus macrocephalus (Nordmann)	1				1	RK$_{w}$	S
Bisnius tereus Smetana	2	1	1			RK$_{e}$	S
Bryophacis canadensis Campbell	2			1	1	RK$_{w}$	N
Eusphalerum fenyesi (Bernhauer)	10	2	1		7	F$_{e}$,RK$_{w}$	N
Lordithon fungicola Campbell	1				1	GK$_{w}$	S
Phlaeopterus cavicollis (Fauvel)	3	1	2			F$_{e}$,RK$_{e}$	N
Phloeonomus suffusus (Casey)[a]	2			1	1	F$_{w}$	N
Phloeostiba lapponicus (Zetterstedt)	281	198	61	6	16	All	N,S
Pselaphinae	1			1		GK$_{w}$	S
Quedius criddlei (Casey)	1		1			GK$_{e}$	S
Quedius plagiatus Mannerheim	4	3	1			F$_{e}$,RK$_{e}$,GK$_{e}$	N,S
Quedius velox Smetana	82	28	32	13	9	All	N,S
Rabigus laxellus (Casey)	1				1	GK$_{w}$	S
Siagonium punctatum LeConte	18	3	3	7	5	RK$_{ew}$,GK$_{ew}$	S
Xylodromus concinnus (Marsham)	1				1	GK$_{w}$	S

Table 4.1: (*Continued*)

Family & Species	Total	Emergence		Window		Snag Age	Region
		LPP	WBP	LPP	WBP		
Xylodromus depressus (Gravenhorst)	16	2	2	1	11	F_{ew},RK_{ew}	N,S
Stenotrachelidae							
Cephaloon tenuicorne LeConte	2				2	RK_{w}	S
Tenebrionidae							
Corticeus praetermissus (Fall)[b]	364	342	18	2	2	F_{e}, RK_{ew},GK_{e}	N,S
Corticeus tenuis (LeConte)[b]	2		2			RK_{e},GK_{e}	N,S
Tribolium castaneum (Herbst)	1		1			F_{e}	N
Tetratomidae							
Tetratoma concolor LeConte	1		1			F_{e}	N
Tetratoma variegata Casey[a]	33	12	20		1	F_{e}, RK_{e},GK_{e}	N,S
Totals	10182	6313	2629	445	795		

Chapter 5: General Discussion

5.1 Conclusions

5.1.1 Host defenses

Results presented in this thesis demonstrate that host species identity affects both mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) life history traits and the composition of saproxylic beetle assemblages. Before discussion of the effects on MPB life-history traits, it is worthwhile to note the distinction between host *quality* and host *susceptibility*. In the present context, host quality refers to the favorability of the sub-cortical environment of a host for reproduction of MPB parents and development of their progeny. Susceptibility refers to how amenable a host is to colonization by the beetle and its associated blue-stain fungi, a feature that can be measured practically by the density of mass-attacking beetles required to overwhelm the defenses of the host tree (the trees response to associated blue-stain fungi is another way to measure susceptibility). This distinction is important because factors that are positively correlated with host quality, such as phloem thickness, are also related to vigor. Furthermore, they also may be negatively related to susceptibility, as more vigorous trees require greater attack densities to overwhelm host defenses (Shrimpton 1972, 1978, Cabrera 1978, Raffa and Berryman 1983, Waring and Pitman 1983, 1985, Christiansen *et al*. 1987 and references therein). With respect to these topics, I focused on host quality in Chapter 2, as the use of cut bolts negated the pitchout (primary) and hypersensitive (secondary) defense reactions (although not the defensive compounds found in resin blisters) that occur in a live host (Christiansen and Ericsson 1985, Miller and Berryman 1986). In Chapter 3, however, I approached a more natural examination of host susceptibility and quality, although climatic effects and the use of pheromones may have obscured these patterns to some degree.

Differences in life history traits that I observed between MPB in lodgepole and whitebark pine likely reflect differences in the constitutive (primary) and/or induced (secondary) defenses of these two hosts. Median attack densities were lower on average in successfully attacked whitebark than lodgepole pines, although differences were not statistically significant. The standard interpretation of this result would be that lodgepole pines are more vigorously defended than whitebark pines (Raffa and Berryman 1983, Waring and Pitman 1983, 1985). However, attack densities were strongly and significantly associated with gallery and brood characteristics, suggesting that egg survival was lower when attack densities were low. This is particularly poignant because data from Chapter 2 suggest that more eggs were laid per cm of egg gallery in whitebark than lodgepole pines, meaning that actual egg mortality would be even higher in whitebark pines. In cut bolts, where no active defense response should have occurred, MPBs were significantly less likely to establish “successful” galleries on whitebark pine than on lodgepole. I attributed this pattern in Chapter 2 to differences in constitutive levels of defensive compounds in the two hosts (Smith 2000). Therefore, I propose a different conclusion for the interaction of MPB and whitebark pine than did Logan *et al.* (2010) for those in the Greater Yellowstone ecosystem (GYE). They reported that whitebark pines in the GYE support similar reproductive rates to lodgepole pines under lower attack densities. It is possible that MPBs were attracted to the pheromone baits on the trees (Pitman and Vite 1969, Ryker and Rudinsky 1982, Borden *et al.* 1987), but were less likely to construct galleries because of unfavorable gustatory feedback (Raffa and Berryman 1982a). This could explain why I observed the lower attack densities, apparently higher egg mortality and lower brood densities on whitebark pines.

Ultimately, number of eggs surviving and number of live brood present prior to the onset of winter tended to be lower in baited whitebark than lodgepole pines and this pattern was most pronounced in Willmore Wilderness Park. Similarly, larval survival was significantly lower in cut whitebark than lodgepole pine bolts, something correlated with my observation that whitebark pines had significantly more radial resin ducts than did lodgepole pines. These data suggest that some aspect of host defense against the MPB is greater on whitebark pine than lodgepole pine. It may be that differences in monoterpene composition between the two hosts (Smith 2000) is enough to explain these patterns or there may be further differences in the strength and nature of the active defense responses that contribute to the patterns I observed. However, differentiating between the effects of primary and secondary defense responses is challenging and not essential for predicting overall patterns of reproductive rates (Franceschi *et al.* 2005, Bonello *et al.* 2006).

In a parallel study, not included as part of this thesis, ten living whitebark and lodgepole pines were inoculated in situ with three species of MPB-associated blue-stain fungi, *Leptographium longiclavatum* Lee, *Ophiostoma montium* (Rumbold), *Grosmannia clavigerum* (Robinson-Jeffrey and Davids) and an agar control. The size of lesions formed in response to these inoculations was then measured six weeks after their application. I found that one of the three fungal species (*O. montium*) produced significantly shorter lesions in whitebark than lodgepole pines. Though the classic paradigm of phytopathogenicicty of blue-stain fungi faces legitimate criticism (Lieutier *et al.* 2009, Six and Wingfield 2011), our changing understanding of this symbiotic relationship does not alter the weight of evidence suggesting that shorter lesions are correlated with greater tree resistance to the MPB (Raffa and Berryman 1982b). From my experiment, there is some reason to believe that whitebark pines are in some aspect, more resistant to the MPB-fungal complex than lodgepole pine, supporting conclusions drawn in Chapters 2 and 3.

I did not see in the field complex patterns of variation in brood production with respect to phloem thickness and host species similar to those observed in the laboratory. However, given the small number of trees where brood survived after winter (4 of each species) such complex patterns could easily have been missed. Consequently, the hypothesis proposed in Chapter 2 to explain this complex pattern of variation, namely that these differences are related to different life-history strategies of the two pines, remains tenable.

5.1.2 Phenology

As discussed in Chapter 3, the appearance of a 1-year (univoltine) life cycle at the latitudes and elevations of the sites selected for this thesis is outside the range of historic norms for the MPB (Amman 1973, Safranyik and Carroll

2006). However, these data clearly show that the entire cohort of MPB progeny would not reach maturity by the typical MPB flight period in July and August. Furthermore, in chapter 4, I collected MPBs emerging from 1- (*fader*) and 2-year dead (*red kill*) pines in the fall and spring/summer collections in all sites. Though the full period of emergence phenology was not observed nor what proportion of the total brood emerging these records represent, this indicates some component of the cohort require > 1 year (and in some cases almost 3 years) to complete their development and that emergence is protracted for many of these individuals. Similar patterns of protracted emergence and multi-year life cycles within the same cohort of attacking beetles have been observed in stands 43-45°N latitude and 2650-2290 m elevation (Bentz and Schen-Langenheim 2007). These multi-year life cycles and protracted emergence periods should increase MPB mortality and slow the spread of the MPB on the east slopes of the Rockies of Alberta (Amman 1973, Cole 1981, Raffa and Berryman 1983, Bentz *et al.* 1991, Bentz and Mullins 1999). Given the low reproductive rates observed in Chapter 3 it appears unlikely that MPB eruptions would occur in these study sites; however, MPB outbreaks have been observed at high elevation stands in the absence of a synchronous, univoltine life cycle (Bentz *et al.* 2011), suggesting extreme vigilance of MPB populations is warranted.

5.1.3 MPB competition

Ips pini (Say) were less commonly collected from lodgepole pines than whitebark pines in Chapters 3 and 4 and tended to be only collected in low abundances on whitebark pines when MPBs were also present (Chapter 4). This could mean that the MPB has a competitive advantage over *I. pini* in whitebark pine or that *I. pini* preferentially attack hard pines like lodgepole over soft pines whitebark (Seybert and Gara 1970). Either way, these data suggest that MPBs will experience less interspecific competition from their main competitor, *I. pini*, in whitebark pine than in lodgepole pine. This will likely encourage the spread of MPB through whitebark pine containing stands in Alberta.

5.1.4 Synthesis

One host species was not better, in terms of quality or susceptibility, for the MPB in all situations. Greater mortality of early MPB life stages in whitebark pine suggest that MPB will spread less quickly through whitebark pine containing subalpine stands than pure lodgepole pines stands, while reduced competition fom *I. pini* suggest the opposite. Host quality also varied with the individual tree quality (phloem thickness) and different patterns of quality were observed depending on which life history traits were considered. Data from this thesis, and observations from forest health officers (Brooks Horne, ASRD, personal communication) suggest that the largest diameter whitebark pines with thick phloem will contribute most to the spread of the MPB in Alberta, and that such large whitebark pines may contribute more to local population growth of MPB than similar diameter lodgepole pines. Given that I did not observe that whitebark pine was an obviously superior host to lodgepole pine, as was the case in limber pine (Langor 1989; Langor *et al.* 1990), it is likely that MPB will not spread through stands with whitebark pine, as rapidly as for those with limber pine.

Climatic effects will be more influential on MPB population dynamics than host mediated mortality related to tree defenses or interspecific competition (Cole 1981). The results presented here show that a MPB cohort in whitebark pine containing stands will not exhibit a completely univoltine life cycle with >90% of the population synchronously emerging in July-August as is typical in lower elevation lodgepole pine forests. However, the climate is becoming more favorable for the MPB at the elevations and latitudes studied, as evidenced by approximately one third of the MPB cohort exhibiting univoltinism. The degree to which whitebark pines will contribute to MPB eruptions in the sub-alpine forests of the east slopes of the Rockies in Alberta is will depend on heavily on climatic factors.

MPB populations have largely collapsed on the east slopes due to aggressive MPB control and unfavorable climate for the beetle. Unfortunately, regardless of whether or not local MPB populations erupt in whitebark pine containing stands, these trees will still be challenged by MPB caused mortality, as in-flights from massive the eruption in BC will likely continue for several more years (Alberta Sustainable Resource Development, 2011). For example, I observed MPB caused mortality in whitebark pine in Nelson, BC in 2010 from long distance MPB in-flights. Although MPB populations did not become established in these stands, they killed a number of large, cone bearing trees. The fact that the largest diameter trees are typically attacked first by MPBs (Amman 1984) and that these largest trees are typically those bearing cones (Arno and Hoff 1989), will have consequences for regeneration of whitebark pines. This problem will be further compounded by the impacts of white pine blister rust (*Cronartuim ribicola* Ficher) (WPBR), a non-native pathogen particularly damaging to five needle pine seedlings and saplings (Burns *et al.* 2008). These observations suggest that proactive prevention of MPB mortality will be an important tool, especially in high-value whitebark pines where resistance to WPBR has been identified.

5.2 Future research

Much remains to be learned if we are to effectively predict how the MPB will impact stands containing whitebark pine. With respect to making significant contributions toward that end, the results from Chapter 3 were disappointing, given the low survival of MPB after severe winters. A multi-year study that relates tree and stand characteristics (*e.g.*, host species, phloem thickness, tree vigor, stand density, soil moisture, drought stress, tree chemistry) to MPB host selection and net-reproductive rates under natural conditions (*i.e.* without baiting trees with pheromone) would be informative. Furthermore, discrepancies between the results of laboratory experiments (Amman 1982, Gross 2008, Chapter 2) and field observations (Logan *et al.* 2010, Chapter 3) might be explained simply as regional differences in genotype and/or phenotype that influence MPB life-history traits. Recognizing these differences is essential for effective planning and management.

Whitebark pine can be found in a number of different forest types in western North America. It ranges from a dominant, sometimes self-replacing, canopy species on the unique volcanic soils of the GYE, to a major or minor seral species, apparently associated with siliceous soils, across much of its Canadian distribution (Arno and Hoff 1989, Joyce Gould, Alberta Parks, personal communication). It is likely that tree vigor and susceptibility/quality to/for the MPB will vary in these different situations. Tree vigor (often measured as growth efficiency: woody biomass increase/area foliage), closely related to stand density, is one of the most important conditions making trees susceptible to the MPB (Waring and Pitman 1983, 1985, Smith *et al.* 2002, MacQuarrie and Cooke 2011). This pattern has been confirmed for whitebark pines, with the added effect on susceptibility of the number of stems per tree cluster (a consequence of animal seed dispersal not observed in lodgpole pines) (Perkins and Roberts 2001). Understanding how stand density influences susceptibility in these different geographic/climatic situations would help identify the stands most vulnerable to MPB attack and would provide a starting point to prioritize management actions.

The other major factor predisposing a stand to MPB attack is drought stress (Waring and Pitman 1983, Christainsen *et al.* 1987). Six and Adams (2007) suggest that whitebark bark pine is less tolerant to drought than lodgepole pine, though the evidence is inconclusive. Analysis of forest inventory and climate data from the American Inland Northwest indicate that whitebark pines is more commonly found in cooler, wetter sites in which moisture would ordinarily not be a limiting factor, while lodgepole pines were associated with warmer, dryer sites, suggesting whitebark pine may in fact be less tolerate to drought stress than lodgepole pine (Brunelle *et al.* 2008). Montane vegetation community types are controlled primarily by temperature and drought (Daubenmire 1943). Although variation through the North American Cordillera is great and relationships between altitude and latitude are not strictly linear, there are general patterns for cooler, wetter climates farther north and warmer dryer climates to the south (Daubenmire 1943). If the GYE, Crowsnest Pass and Willmore Wilderness Park represent points along a warm, dry, southern to cool, wet, northern gradient, then greater drought stress in whitebark pine compared to lodgepole pine may explain why whitebark pines were more susceptible to the MPB than lodgepole pine in the GYE, similairly susceptible in the Crowsnest Pass and slightly less susceptible in Willmore Wilderness Park. Experimentally testing this hypothesis, as well as examining soil drainage, precipitation patterns and periods of maximal drought stress on whitebark pine across its distribution would further our understanding of whitebark pine susceptibility to the MPB. Climate change models suggest that conditions will become less favorable for whitebark in parts of Canada and the GYE (Romme and Turner 1991, Hamann and Wang 2006). Expanding work on whitebark pine drought stress explore the effects of changing climate would also be a worthwhile avenue of research.

Adapting stand susceptibility models and stand thinning management recommendations from the MPB's primary hosts, lodgepole pine and ponderosa pine, to whitebark pine and other five-needle stone pines is complicated by a number of issues. Adequate stand inventories do not exist for much of this species range. Furthermore, whitebark pines, and other five-needle stone pines, produce large animal dispersed seeds, instead of the semi-serotonous seed set produced by lodgepole pines (Arno and Hoff 1998). According the to the growth-differentiation balance hypothesis, the energetic costs of producing a large seed set in mast years will alter the availability of non-structural carbohydrates available for defense, and potentially impact susceptibility of these trees to the MPB (Lorio 1986, Herms and Mattson 1992). Research into how the energetic demands of masting influence tree vigor, defense and susceptibility to the MPB will improve the understanding of how the MPB will impact whitebark pine populations.

The other major unknown in understanding how the MPB will impact whitebark pine relates to how WPBR will affect host quality and susceptibility. Trees infected with other diseases, such as dwarf mistletoe (*Arceuthobium americanum* (Nutt. ex Engelm.)), comandra blister rust (*Cronartium comandrae* Pk.) or armillaria root disease (*Armillaria mellea* (Vahl. *ex.* Fr.) are typically more susceptible to MPB attack (Rasmussen 1987, Tkacz and Schmitz 1986, Schowalter and Filip 1993). However, Bonello *et al.* (2006) suggested that these relationships can be complicated, and that low levels of infection may actually increase resistance to attacks by other pathogens or herbivores. Six and Adams (2007), suggested that WPBR predisposes whitebark pines to attack by MPB, though their data were not conclusive. Bockino (2008) reported a similar pattern, and suggested that whitebark pines with severe WPBR infections were points of origin for MPB eruptions in the subalpine stands studied. Research into how WPBR effects whitebark pine susceptibility and quality would further our understanding of the MPB's spread through whitebark pine containing stands as well as provide a system where one could test Bonello *et al.'s* (2006) hypothesis of systemic induced resistance.

It is perhaps worthwhile to note here that attack and brood density were very low in the whitebark pine infected with white pocket rot (*Phellinus pini* (Thore: Fr.) A. Ames). This may have been because white pocket rot, unlike the aforementioned pathogens, infects the same part of the tree utilized by the beetle, i.e. the phloem of the bole, and ergo is in direct competition with the MPB/blue-stain complex. The pocket rot infection on the baited tree was extensive, with fungi present throughout the sapwood and inner layers of phloem on the bole. The phloem of this tree was extremely dry, and possibly altered chemically (Nebeker *et al*. 1994), likely explaining why this tree was unsuitable for the MPB.

A great deal more work could be done exploring the relationships between whitebark pines and invertebrates. Similar surveys in different regions, studies of different taxa and studies of invertebrates associated with live whitebark pines would all increase our understanding of the natural history of sub-alpine forests. One functional group of particular interest are the cone feeding insects *Dioryctria* spp., *Eucosma* spp. and *Conophthorus* spp. that inhabit whitebark pines (Bartos and Gibson 1990). Determining if changing climate will increase damage caused by these insects, as is the case for the MPB, would be a valuable avenue of research, given that cone production is such an important part of the ecological role of whitebark pine in subalpine ecosystems.

5.3 Management Recommendations

Attempting to simultaneously manage threats from the MPB and WPBR creates a serious dilemma. Currently, WPBR management programs have two objectives: 1) identifying, collecting seeds from and protecting trees and populations with natural genetic resistance to WPBR; and 2) Conserving as much genetic diversity on the landscape as possible (reviewed in Burns *et al.* 2008). The only practicable, long-term strategy in MPB management (other than ensuring a heterogeneous mixture of species and age-classes on the landscape) is stand thinning (Waring and Pitman 1983, 1985, Smith *et al.* 2002, MacQuarrie and Cooke 2011). From a WPBR perspective, stand thinning is undesirable for 3 reasons: 1) Opening the canopy will increase rates of transmission of aerially dispersed WPBR spores; 2) Increased light improves conditions for *Ribes* spp., the alternate hosts of WPBR; and 3) When thinning involves removal of healthy whitebark pines, genetic diversity and potential resistance will be lost (Burns *et al.* 2008). Thus, the challenges facing land managers are great.

Much of whitebark pine's distribution is within protected areas, meaning that management options will be limited by park mandates and directives. Outside of these areas, there will be more freedom to implement intensive management strategies. However, outside protected areas whitebark pines face other challenges. My own observations in the Crowsnest Pass region of Alberta, (inside the C-5 Forest Management Unit, harvested by Spray Lakes) suggested harvesting activities are likely directly and indirectly impacting whitebark pines. Cutblocks extend into the sub-alpine zones where whitebark pines grow, and though Alberta Sustainable Resource Development directives prohibit cutting of this species, these trees are not always easily distinguishable from lodgepole pines at close quarters (Day 1967). Furthermore, clear cutting greatly increases populations of alternate hosts for WPBR (*Ribes, Castilleja* and *Pedicularis*). Therefore, involving logging companies in Alberta and other forestry companies throughout western North America will be essential for the protection of this species outside protected areas. Getting these companies involved in identifying whitebark pines on the landscape, identifying rust resistant trees, and replanting subalpine cut-blocks with some component of rust-resistant seedlings would all be valuable activities.

Ensuring the persistence of whitebark pine on the landscape will take dedication, ingenuity and a substantial investment of resources. Developing rust resistant breeding programs will be costly, although likely essential for effective management of this species. However, relying solely on cultivated stock for out-planting raises a number of serious concerns about the ‘naturalness’ of our forests, and such concerns should not be overlooked. Encouraging both natural regeneration of whitebark pines and historic patterns of fire on the landscape will be essential. Managing threats from the MPB will be challenging and will require both long term and large scale planning. Returning pine age-class distributions to historic norms (Taylor and Carroll 2004) at national scales will be important, though challenging to implement. Stand thinning may be a viable option to create buffers around susceptible whitebark pine containing stands, although this likely will not be a suitable approach within susceptible whitebark pine containing stands. Aggressive control, via falling and burning, should be employed in high value stands where evidence of genetic resistance exists and these efforts should focus on removing the largest diameter MPB infested whitebark pines, where net reproductive rates will be highest. The use of verbanone to repel MPB from high value trees and stands is a valuable tool, but is often prohibitively expensive. Maximizing the return from limited resources will require careful planning and integration of the efforts of non-governmental organizations, forestry companies, provincial/state and federal governments in both Canada and United States.

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