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Mountain pine beetle outbreaks in high elevation whitebark pine forests: the effects of tree host species and blister rust infection severity on beetle productivity

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MOUNTAIN PINE BEETLE OUTBREAKS IN HIGH ELEVATION WHITEBARK PINE FORESTS: THE EFFECTS OF TREE HOST SPECIES AND

BLISTER RUST INFECTION SEVERITY ON BEETLE PRODUCTIVITY

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 In recent years, the mountain pine beetle (MPB, *Dendroctonus ponderosae*) has caused dramatic levels of mortality of whitebark pine (*Pinus albicaulis*). This keystone and foundation tree species is also being killed by the exotic fungus, *Cronartium ribicola*, which causes the disease white pine blister rust (WPBR). This study examines MPB productivity in whitebark pine compared to that in lodgepole pine, and also in whitebark pine of varying WPBR infection severities to determine if either of these host factors contributes to the current, dramatic MPB outbreaks in whitebark pine. To evaluate host tree effects on MPB, I tracked attack densities, emergence rates, size and sex ratio of MPB from lodgepole pine, and from healthy and WPBR-infected whitebark pine. Beetle emergence rate was higher from whitebark pine. I found no differences in beetle size between lodgepole and whitebark pine. The three populations I tracked declined precipitously during the period of study. This decline was likely caused by a cold snap in October 2009 as indicated by combined phenology/cold tolerance model results. MPB attack density was lowest on the most severely WPBR-infected trees, but emergence rates and size of beetles from these trees were greatest. Low attack rates in severely infected whitebark pine may indicate that these trees have lower defensive capabilities, while the greater emergence rates from these trees are likely due to low intraspecific competition afforded by low attack rates. Given that highly infected whitebark pine support high MPB productivity, these trees could support rapid MPB population growth when environmental conditions are favorable. It appears that whitebark pine is a better host for MPB than lodgepole pine, but whitebark pine of varying WPBR infection severity do not differ from each other in terms of beetle productivity. Therefore, the extensive MPB outbreaks in whitebark pine likely reflect the combination of both whitebark pine's superior host quality, as well as the favorable conditions for MPB development created by a warming climate in high elevation forests.

<u>Dedication</u>

      I dedicate this work to my parents, Dr.'s Patrick and Nora Dooley. Their love of learning and perpetual academism inspired me to pursue, and complete a Master's degree. Their constant love, encouragement and interest in my studies fueled my scholarship. I also dedicate this thesis to Dr. Gene Amman, a seminal entomologist who studied mountain pine beetles. Dr. Amman passed away during my final stages of writing when I was most dependent on, and grateful for, his comprehensive research on the mountain pine beetle.

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Chapter 1: Literature review of whitebark pine ecology and disturbance agents

<u>Introduction</u>

Whitebark pine (*Pinus albicaulis* Engelm.) is an ecologically important, high elevation, five-needle pine that warrants study because its survival is threatened by three interacting factors: mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins), white pine blister rust (WPBR) caused by the exotic fungus *Cronartium ribicola* J.C. Fisch.*,* and succession and replacement by shade tolerant conifer competitors (Keane and Arno 1993, Tomback et al. 2001). These three factors interact with climate change, which is also predicted to directly impact the range of whitebark pine (Warwell et al. 2007). Because of these combined threats, whitebark pine has been designated as "warranted but precluded" for listing as an endangered species (Federal Register 2011).

This tree is not typically valued for economic uses; instead its importance lies in its ecological roles (Tomback et al. 2001). Whitebark pine is considered both a foundation and a keystone species. A foundation species is defined as the dominant primary producer in an ecosystem (Ellison et al. 2005). A keystone species is one whose ecological impacts provide stability to the ecosystem it inhabits (Paine et al. 1969). Whitebark pine fits these descriptors well. Whitebark pine serves as a foundation species in locations where it grows as a climax species (Ellison 2007). The high fat content of whitebark pine seeds makes them an important food source for over 110 animal species (Keane and Parsons 2010). Without whitebark pine's provision of food, shelter, and microsites, many plant and animal species would not be able to exist in their subalpine habitats, indicating that whitebark pine is a keystone species in these ecosystems (Kendall and Arno 1990).

Whitebark pine is excellent model system to examine the effects of, and interactions between, mortality agents, as well as how climate change may act to influence these agents (Turner 2010). While WPBR and climate change affect whitebark pine ecosystems, they are not disturbances, per se, because they are not discrete in time (White and Pickett 1985). Regardless, these agents of mortality interact and can have similar effects as disturbances. In North America, the occurrence of natural disturbances such as fire (Ryan 2000), insect outbreaks (Bentz et al. 2010), and hurricanes (CCSP 2008) is expected to increase with climate change.   If the magnitude or frequency of these disturbances intensifies in the future, it is likely that more often, disturbances will interact in time and space (White and Pickett 1985). Co-occurring disturbances can sometimes have opposing effects, thereby limiting each other's impacts. Alternatively, interacting disturbances can amplify each other's effects and result in compounded perturbations (Paine et al. 1998). When disturbances acting across spatial scales work synergistically to create nonlinear, threshold responses, the ecological effects are often unpredictable. Tree declines are an example of how positive feedbacks between disturbance agents can lead to unpredictable ecological outcomes (Paine et al. 1998). Understanding the nature and role of these compounded disturbances will be critical for forest management in the future (Paine et al. 1998, Turner 2010).

Multiple disturbance and mortality agents may interact in an additive or synergistic fashion to lead to the functional collapse of whitebark pine ecosystems (Logan and Powell 2001, Kegley et al. 2004, Tomback and Achuff 2010, Larson 2011, Tomback 2011). Such interactions may be exacerbated by climate change. Climate change is a serious threat to the continued dominance of whitebark pine because the area that is bioclimatically suitable for whitebark pine habitat is expected to decrease considerably (Schrag et al. 2007, Warwell et al. 2007). Additionally, climate change influences the distribution and extent of the mortality agents that

are already contributing to the tree's decline, primarily MPB, WPBR and successional

replacement (Logan and Powell 2001, Carroll et al. 2004, Bentz et al. 2010, Kejunas 2011, Schrag

et al. 2007).

Whitebark pine ecology

Whitebark pine grows over a vast geographic range extending from the coastal

mountains of British Columbia, Canada, south through the Sierra Mountains in California, and

eastward through the Wind River Range in Wyoming (Figure 1). Throughout this range,

whitebark pine occurs at elevations ranging from 900 to 3,660 m (Arno and Hoff 1989,

McCaughey and Schmidt 2001).   Because of its large geographic and elevational ranges,

whitebark pine occurs in sites with a diversity of climates and topography. These span moist

subalpine habitats where the tree exists as an upright-growing, seral species, to cold, dry, tree-

line areas where it occurs as a climax species (Arno 2001). Whitebark pine is the climax tree

species in areas with snowy, rocky and windy environments, because it is better adapted to

these conditions than its competitors which are most often subalpine fir (*Abies lasiocarpa*

(Hook.) Nutt.), Engelmann spruce (*Picea engelmanii* Parry ex Engelm.) and mountain hemlock

(*Tsuga mertensiana* (Bong.) Carriére) (Arno 2001). At the harshest sites with respect to cold, dry

and wind, whitebark pine assumes a stunted, krummholz growth form (Tomback et al. 2001),

although upright whitebark pines can also be found on relatively dry and severe, windswept

sites at and near timberline (Arno and Hoff 1989).

Whitebark pine is a long-lived, slow growing tree species (Critchfield and Little 1966).

Individuals typically do not begin producing cones until 60 to 80 years of age (Day 1967, Arno

and Hoff 1989), although trees as young as 29 years can produce cones (Mahalovich 2012).

Cones are produced in large crops at irregular intervals (Tomback 2001). Cone scales, which

enclose wingless seeds, do not open upon ripening (indehiscent), but must be forced open. This

indehiscent cone characteristic is unique to stone pines (McCaughey and Schmidt 2001) of which whitebark pine is the only North American representative (Arno and Hoff 1990). Whitebark pine is dependent on its mutualist, the Clark's nutcracker for seed dispersal (Tomback 1982). Clark's nutcrackers remove seeds from cones, then either eat them, or fill their sublingual pouch with up to 150 seeds and cache them for later use (Tomback 1982). Nutcrackers cache seeds one to three cm below the soil surface (a depth suitable for germination) in sheltered microsites in forest openings (Tomback 1982). In good cone crop years, nutcrackers cache more seeds than they need to survive. The uneaten seeds germinate and the resulting seedlings ensure whitebark pine regeneration (Tomback 1982).

Whitebark pine seeds are also an important food source for two other major seed predators, the red squirrel (*Tamiasciurus hudsonicus*) and the grizzly bear (*Ursus arctos)*. The squirrels harvest whitebark cones, store them in middens, and then eat the stored seeds over time (Siepielski and Benkman 2007). Bears raid squirrel middens for the large, fatty seeds. The seeds support the weight gain needed for hibernation (Lanner and Gilbert 1994). For grizzly bears in the Greater Yellowstone Ecosystem (GYE), whitebark pine seeds are a crucial food source comprising an estimated one-quarter to two-thirds of their energy intake (Mattson and Reinhart 1994). In 2009, the grizzly bear in the GYE was relisted as an endangered species. The decline of whitebark pine was cited as a main reason for the bear's relisting (Greater Yellowstone Ecosystem Coalition vs. Servheen 2009). In addition to its importance in providing food for wildlife, whitebark pine is also important for stabilizing high elevation snowpack, and thus, regulating subsequent summer water runoff (Farnes 1990). Whitebark pine serves another important ecological service by acting as a nurse tree which facilites the establishment and survival of trees at treeline (Tomback 2001). Established whitebark pine shelter tree seedlings from harsh growing conditions (Holtmeier and Broll 1992, Resler and Tomback 2008).

Fire plays an integral role in whitebark pine ecology. Nutcrackers are attracted to open sites for seed caching, including burns of all sizes (Tomback 1978). Whitebark pine has an advantage in re-seeding large burns because Clark's nutcrackers can transport seeds up to ten times further than the dispersal distances of whitebark pine's wind dispersed competitors (Keane and Parsons 2010). Compared with recruitment in other forest successional stages, conditions for whitebark pine establishment are most favorable following a fire (Campbell and Antos 2003). Furthermore, the ability of whitebark pine seedlings to endure hot, dry, post-fire soil conditions gives them a competitive edge over other tree species during initial stand establishment (Tomback et al. 1993, Tomback 1995, Maher and Germino 2006).

Unfortunately, this natural regeneration process has been hampered by fire suppression and WPBR (McCaughey and Tomback 2001). Fire suppression has led to encroachment of subalpine fir and Engelmann spruce into whitebark pine stands in the more mesic portions of whitebark pine's range (Keane 2001). Crowding by these tree species eliminates the open areas required for nutcracker caching which could otherwise serve as arenas for natural regeneration of whitebark pine (Tomback 1978). Even with open areas, however, seed dispersal and regeneration may not occur. In low cone crop years, or in areas with high WPBR infection and mortality of whitebark pine, the number of cones produced can fall below the threshold amount needed to attract foraging nutcrackers to the area (McKinney et al. 2009). When this happens, the dispersal of seeds required for regeneration of whitebark pine is greatly reduced or stops, further exacerbating the decline of the tree at those sites (McKinney et al. 2009). Therefore, the combined effects of WPBR-caused mortality and fire suppression are decreasing whitebark pine regeneration and genetic diversity.

Mountain Pine Beetle

MPB is a principal biotic disturbance agent in western North American pine forests (Raffa 2008). The beetle can develop in almost any pine species (Wood 1982), but is most common in its most coevolved host, lodgepole pine (*Pinus contora* Douglas ex. Louden) (Cole and Amman 1980). To overwhelm a tree's defenses and successfully reproduce, MPB uses a pheromone-meditated mass attack to kill the host tree (Raffa and Berryman 1983, Safranyik and Carroll 2006). The more vigorous a tree is the greater number of attacking beetles are required to produce a successful mass attack. Females attack trees first, releasing pheromones manufactured from host monoterpenes that then attract both sexes to the tree (Pureswaran and Borden 2003). Males follow females into the same entrance holes. The males and females mate and then construct parent galleries in the phloem where females lay eggs (Amman and Cole 1983). Once eggs hatch, larvae develop by consuming phloem until cold initiates winter dormancy. Larvae resume feeding and development in spring and summer and pupate in individual chambers from which they emerge by chewing through the bark later that summer.

MPB are usually present in low numbers in a forest but can occasionally develop outbreaks. During non-outbreak phase, MPB are limited to stressed, or diseased hosts which have lowered defenses and thus require fewer beetles for a successful attack to occur (Safranyik and Carroll 2006). When beetle populations grow large enough, MPB can overcome the defenses of vigorous trees, and may develop an outbreak (Raffa and Berryman 1983, Raffa 2001). An outbreak of MPB requires both appropriate site conditions and a trigger (Bentz 2005). Appropriate stand conditions include large numbers of preferred hosts of a usable size (typically 13 cm in diameter at breast height or greater) (Cole and Amman 1969). Outbreak triggers include warm temperatures or drought. MPB, like all insects, are poikilothermic, so survival, activity, and reproductive rates are heightened with increasing temperatures. Therefore, extended warm temperatures can trigger an outbreak. Drought, which increases tree

physiological stress and results in lowered tree defenses (Safranyik and Carroll 2006) can also serve as a MPB outbreak trigger. Often, warm temperatures and drought co-occur further increasing the likelihood of an outbreak (Bentz 2005).

MPB outbreaks often occur in lodgepole pine (Carrol and Safranyik 2006). The extensive, even-aged stands typical of this species can support rapid MPB population growth if a trigger occurs supporting population expansion of the beetle. Additionally, in the elevations where lodgepole pine occurs, typically a univoltine (one year) life cycle of the beetle is supported. A one-year life cycle is most adaptive for the beetle because it supports adaptive seasonality and synchrony. Adaptive seasonality means that beetles develop and emerge on a timeframe which is timed correctly for overwintering (Logan and Bentz 1999). Synchronous development and emergence ensures that attack at the same time, which is required for the mass attack strategy (Raffa and Berryman 1983). Additionally, a one year life cycle means that beetles only have to survives harsh, wintertime conditions once.

In the past few years, whitebark pine has also supported outbreaks of MPB. Historically, whitebark pine has been mostly protected from MPB predation due to cold conditions in high elevations. In high elevations, the beetle suffered high levels of mortality and was constrained to a semivoltine (more than one year) life cycle which is highly maladaptive and results in high levels of mortality (Amman 1973). While whitebark pine has not been a common host for MPB, it has occurred in high numbers in the tree in the past. Outbreaks of MPB in whitebark pine occurred in the 1930's (Gibson 1939, Evenden 1944) and 1970's (Bartos and Gibson 1990). These outbreaks were driven by unusually hot dry periods (Perkins and Swetnam 1996). With increasing temperatures in high elevations due to climate change (IPCC 200 1), MPB will likely

continue to be prevalent in whitebark stands. Warmer temperature have allowed MPB

population expansion because overwintering survival is higher due to fewer hard freeze events

(Logan and Bentz 1999, Logan and Powell 2001), and their semivoltine life cycle (in this habitat)

has shifted to a univoltine life cycle (Bentz and Schen-Langenheim 2007, Bentz el al. 2011).

Whitebark pine's role as both a keystone and foundation species is currently threatened

by MPB outbreaks (Gibson 2008, MacFarlane et al. 2009, Bentz et al. 2011). Across the range of

whitebark pine (Figure 1), localized outbreaks of MPB started in 1999, and have increased

steadily in extent (Gibson 2008). In the year 2007 alone, approximately a half a million acres in

seven western states exhibited current MPB-caused whitebark pine mortally (Gibson 2008). By

2007, cumulative MPB caused whitebark pine mortality was most extensive in Wyoming

(approximately 182,000 ha), followed by Montana (approximately 125,000 ha), Idaho

(approximately 105,000 ha) and Washington (approximately 69,000 ha) (Gibson 2008). USDA

Forest Health Protection data suggested that some of the most severe MPB-caused whitebark

pine mortality has occurred within the GYE (Gibson 2008). A separate study confirmed this

finding: in 2009, 82% of whitebark pine forests within the GYE showed medium to high

whitebark pine mortality due to MPB (MacFarlane et al. 2009).

The ongoing MPB outbreak in whitebark pine has been attributed to climate change

creating favorable, warmer temperatures in high elevations sites containing whitebark pine of

suitable size for MPB attack (Logan and Powell 2001) (Larson 2011). However, it is unclear

whether temperature alone has allowed the development of outbreaks of MPB in whitebark

pine, or if the quality of whitebark pine as a host has contributed. It has been speculated that

whitebark pine may be superior to lodgepole pine since MPB prefer to attack whitebark pine

over lodgepole pine (Six and Adams 2006, Bokino 2008). Additionally, WPBR infection has been

found to increase the likelihood of MPB attack (Six and Adams 2006, Bokino and Tinker 2012). It is unknown, however, if MPB productivity is related to host tree species or infection severity.

Host tree species, condition and defenses affect MPB attack behavior and productivity (Lieutier 2002 and references therein). Differences in productivity of MPB in different host tree species may not be pertinent during outbreaks (Safranyik and Carroll 2006, Cole and Amman 1980); however, differences in MPB productivity or size in different hosts could translate into critical tipping points in building populations (Raffa et al. 2008). Two measures of beetle productivity are number of beetles produced and beetle size. Greater numbers of beetles increase the probability of successful attacks and can initiate more mass attacks. Bigger beetles can support more rapid population increases because larger beetles display higher survival rates in cold temperatures (Atkins 1967), and are known to lay more, and larger eggs (McGhehey 1971).

In laboratory studies using logs to rear beetles, beetle size, numbers of eggs laid, and numbers of MPB emerging have been used as metrics to evaluate the productivity of MPB in whitebark pine compared with other pine species. An experiment testing the effects of host species on MPB productivity indicated that whitebark pine might be a more nutritious host for MPB than lodgepole pine (Amman 1982). In this experiment, lodgepole pine was found to be the poorest host, producing the lowest number of beetle offspring compared with ponderosa, whitebark and western white pine (Amman 1982). Overall, the five-needle white pines were the best hosts for MPB (Amman 1982). In this same study, whitebark pine had the thickest phloem, a variable that has previously been shown to positively influence beetle brood production in other pines (Amman 1972, Amman 1982). A recent lab study comparing MPB productivity in whitebark and lodgepole pine bolts found that MPB fecundity was higher in lodgepole pine, but that MPB emerging from whitebark pine were larger than those emerging from lodgepole pine

(Gross 2008). Therefore, it is still unclear how host tree affects MPB productivity. Furthermore, it is likely that to truly understand host effects, measurements of productivity will need to be conducted under field conditions.

White Pine Blister Rust

WPBR was introduced from Europe to western North America in approximately 1910 (Mielke 1943). This disease has caused widespread mortality of whitebark pine. Between 1971 and 1991, 65% of surveyed whitebark pine in western Montana had been killed by WPBR (Keane and Arno 1993). Additionally, this disease infected an average of 89% of the living overstory whitebark pine trees sampled (Keane and Arno 1993). A later study revealed that 83% of sampled trees in the Bob Marshal Wilderness Complex in Montana were infected with WPBR (Keane et al. 1994). Currently, most whitebark pine stands –including the cold, dry areas in Yellowstone National Park that were previously though to be incapable of supporting WPBR (Hendrickson 1970)- show some level of WPBR infection (Tomback and Achuff 2010). The current level of WPBR infection in whitebark pine in the GYE is approximately 20% (Jean et al. 2011).

The causal agent of WPBR is *Cronaritium ribicola*, a fungus in the order Uredinales (Kendrick 2000). This fungus has five spore stages, and is heteroecious with two primary alternate hosts types: pines in the subsection *Strobus* (bearing five needles per fascile) and *Ribes* (gooseberries and currents) (Mielke 1943). In addition to these hosts, *C. ribicola* has also been found infecting *Pedicularis* (paintbrush) and *Castilleja* (lousewort) (Geils 2010). During the summer, basidiospores are produced on telial columns growing on the undersides of *Ribes*, *Pedicularis*, and *Castilleja* leaves. These spores are wind dispersed and infect pine stomata.

On pines, WPBR infections grow from the needle to twig, then to branches, and finally form cankers on the bole of the tree. *C. ribicola* hyphae occur primarily in the phloem and cambium, but can sometimes extend into and around tracheids running through multiple annual layers of xylem tissue (Hudgins et al. 2005). The canker grows out concentrically causing swelling of the bark beyond its edge. This fusiform bark swelling occurs because the presence of *C. ribicola* hyphae induces cortical and phloem polyphenolic parenchyma cell division, cell enlargement and an increased concentration of phenolic compounds (Hudgins et al. 2005). The center of the canker dries and cracks after aecial formation kills host cells (Hudgings et al. 2005). These cankers eventually cause tree death by girdling (Mielke 1943, Geils 2010). In large trees, death by girdling a slow process; WPBR infected trees can live with an infection for more than ten years (Tomback et al. 2001). However, small trees have a smaller circumference of cambium to girdle, so bole cankers cause death much faster is these trees (Geils 2010). In mature trees, bole cankers in the upper stem, or multiple branch cankers, often reduce a tree's reproductive output long before the pathogen actually kills the tree (McKinney and Tomback 2007, McKinney et al. 2009).

Mammal-chewed cankers (which hasten girdling) are a diagnostic symptom of WPBR infection (GYNWPMWP 2011). In one study, squirrels, hares and bears damaged 11.5% of whitebark pine by stripping away bark to feed on WPBR–infected tissue (Zeglen 2002). Mammals most likely eat the cankers because parenchyma cells in WPBR-infected tissue contain dramatically more starch granules than uninfected tissues (Hudgins et al. 2005). Both *C. ribicola* and MPB utilize the phloem layer of trees. Since mammals key into nutritional changes in WPBR-infected phloem, it is likely that MPB, who are highly sensitive to phloem quality, would also detect and respond to WPBR-altered phloem quality. Six and Adams (2006) found that WPBR infection severity in whitebark pine was significantly positively correlated with the

likelihood of MPB attack, and negatively correlated with sapwood moisture content. They hypothesized that these trees were stressed by moisture availability due to WPBR, and that this stress reduced tree defenses causing the infected trees to be preferred by beetles (Six and Adams 2006). Therefore, WPBR-induced changes in phloem cell structure, chemical composition, and tree water relations could affect beetle attack behavior, as well as phloem nutrition for beetles habiting WPBR-infected trees.

Need for present research

Compared with the abundance of research on MPB in lodgepole pine, little is known about MPB in high elevation systems. The rapid and devastating response of this beetle to warming temperatures indicates an acute need for research on the dynamics of this beetle in whitebark pine. Laboratory studies indicate that MPB may be more productive in whitebark pine (Amman 1982, Gross 2008), so this tree may be a better host than lodgepole pine. This possibility has not been tested in the field. Besides host species effects, WPBR infection severity may also affect MPB productivity. The incidence of WPBR is increasing in the GYE, where this research was conducted (Jean 2011), as well as across the range of the tree. Therefore, an understanding of how beetle productivity is affected in WPBR-infected trees will better inform us of the potential of these trees to impact MPB population dynamics in high elevation forests. While many studies have examined either the effects of WPBR (Tomback et al. 1995, McKinney and Tomback 2007, Tomback and Resler 2007, Resler and Tomback 2008, McKinney et al. 2009), or MPB (Logan and Powell 2001, Perkins and Roberts 2003, Waring and Six 2005, Bentz and Schen-Langenheim 2007) on whitebark pine, only two published studies have examined the interactions of these two disturbance agents in whitebark pine (Six and Adams 2006, Bokino and Tinker 2012). Both of these studies examined how WPBR infection influences likelihood of attack by MPB, but neither study examined how beetles actually fare in diseased trees.

There is no evidence that the threat of either MPB or WPBR will diminish in the future, so it will be important to better understand how MPB and WPBR interact since both agents will be challenges to whitebark pine survival and restoration efforts. A better understanding of how MPB outbreaks will progress in healthy and WPBR-infected whitebark pine stands will allow managers to prioritize areas in need of restoration efforts such as cone collection. Additionally, as invasion of exotic species is increasingly common with global trade (Mack et al. 2000), and forest pests are expected to intensify with climate change (Logan et al. 2003), an understanding of how a native insect pest and an exotic pathogen interact when simultaneously affecting an ecosystem will become critical ecological knowledge.

My objectives for my thesis research were to determine if the severity and magnitude of current MPB outbreaks in whitebark pine are due, at least in part, to increased productivity in whitebark pine relative to lodgepole pine, and whether WPBR severity affects beetle productivity. I conducted two field studies (described in Chapters 2 and 3). The study presented in Chapter 2 tested the hypothesis that whitebark pine is superior to lodgepole pine as host for MPB by comparing MPB attack density, emergence rate and body size between the two species. This study also investigated the possible causes of a sharp decline in the MPB study population that I tracked by using field observations and MPB phenology modeling. The work in Chapter 3 examined whether WPBR infection in whitebark pine affects beetle productivity by testing for the effects of a range of WPBR infection severities on MPB attack density, emergence rate, body size and sex ratio.

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Figure 1. Distribution of whitebark pine from Arno and Hoff 1989.

Chapter 2: A comparison of mountain pine beetle attack density, emergence rate and size in lodgepole and whitebark pine after a region-wide cold weather event

Abstract

In recent years, mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) has caused dramatic levels of mortality of high elevation whitebark pine (*Pinus albicaulis* Engelm.) within the Greater Yellowstone Ecosystem (GYE) and elsewhere. While warming has allowed the beetle to move up in elevation into whitebark pine forests, temperature alone may not explain the current severity and magnitude of MPB outbreak. The dramatic and rapidly spreading outbreaks of MPB in whitebark pine may be supported by a superior nutritional content in whitebark compared with lodgepole pine resulting in the production of more and/or larger beetles. To test this hypothesis, I undertook a field study monitoring numbers of beetles attacking and emerging from whitebark and lodgepole pines growing in mixed stands. I also measured size of beetles emerging from both tree species. I found that MPB had a significantly higher emergence rate from whitebark pine than lodgepole pine. This difference likely reflects the thicker phloem of whitebark than lodgepole pine at our sites. I found no difference in size of beetles emerging out of whitebark and lodgepole pine. However, beetle populations declined precipitously during the period of study, potentially influencing our results. Using a combined phenology/cold tolerance model, validated by field measurements, I determined that a cold weather event in October 2009 was responsible for the rapid decline in beetles. Survival of beetles developing trees affected by the cold weather event did not differ between host species. This study validates published phenology/cold tolerance models predicting MPB mortality in high elevations, and indicates that the integration of these models increases accuracy.

<u>Introduction</u>

Whitebark pine, (*Pinus albicaulis* Engelm.), a five-needle white pine, is considered a foundation and keystone species in the high elevation subalpine ecosystem of western North America (Tomback 2001). It is currently threatened by the mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins), white pine blister rust (caused by the exotic fungal pathogen *Cronartium ribicola* J.C. Fisch)*,* and successional replacement by shade tolerant firs that has occurred, in part, due to a century of fire suppression (Keane and Arno 1993, Tomback 2001). By 2001, mortality from these three factors has caused the functional extinction of this species across a third of its range (Tomback 2001). The recent decision that inclusion of whitebark pine on the endangered species list is 'warranted but precluded' recognizes the precarious state of the tree (Federal Register 2011).

 MPB-caused mortality of whitebark pine has increased dramatically within the Greater Yellowstone Ecosystem (GYE). A comprehensive aerial survey conducted in 2009 found that approximately 82% of whitebark pine forests in the GYE had mortality from recent and ongoing MPB outbreaks (Macfarlane et al. 2010). Such an extensive loss of whitebark pine in the subalpine ecosystem will have a multitude of effects including the loss of ecosystem services and functions such as snowpack retention and waterflow stability (Farnes 1990) and support for plant and wildlife communities (Tomback 2001).

MPB is in outbreak phase across much of western North America. In Canada alone, the current outbreak in is ten times larger than the next largest recorded outbreak (Safranyik et al. 2010) and continues to expand. The current MPB outbreak is also unprecedented in the extent of its expansion into higher latitudes and elevations which were previously too cold for beetle survival (Carroll et al. 2004, Safranyik et al. 2010). As part of this expansion, warmer

temperatures have brought this insect into contact with mature whitebark pine forests, with dramatic results.

Under thermal conditions optimal for the beetle, development is univoltine. To avoid mortality of vulnerable life stages (eggs, pupae and adults) caused by freezing, the timing of mass emergence and subsequent attack must be synchronized and occur at the correct time of the year. This is termed adaptive seasonality (Logan and Bentz 1999). Seasonally adaptive emergence occurs when the threat of freezing is low, yet early enough in summer to allow brood sufficient time to develop into larvae which are capable of overwintering (Logan and Bentz 1999, Powell and Logan 2005). While MPB development in lodgepole pine is typically univoltine, MPB historically has had a semivoltine life cycle (more than one year) in the higher elevations where whitebark pine is the dominant suitable host (Amman 1973, Safranyik 1978, Logan and Powell 2001).   This was because development of the beetle was slower due to cooler temperatures and an overall shorter growing season at these sites. A semivoltine life cycle is maladaptive in several ways. First, adaptive seasonality may be disrupted resulting in life cycles that are not timed correctly for overwintering. It also challenges beetles to survive mortality factors for a longer period of time (including two winters) in a resource which is constantly declining in moisture and nutritional content (Bleiker and Six 2008, Kim et al. 2005). Recently, because of warmer temperatures, most MPB have switched to a univoltine life cycle in whitebark pines (Gibson 2006, Bentz and Schen-Langenheim 2007, Logan et al. 2010) which supports adaptive seasonality (Logan and Powell 2001), and therefore, increased MPB survival rates. These factors have enabled MPB to reach outbreak levels in whitebark pine (Logan and Powell 2001).

MPB has likely been present in whitebark pine for thousands of years; paleoecological evidence supports the occurrence of *Dendroctonus*, most likely *Dendroctonus ponderosae*, in

whitebark pine forests as early as the Holocene (Brunelle et al. 2008). MPB outbreaks were

documented in whitebark pine in the 1930's and 1980's (Bartos and Gibson 1990, Perkins and

Swetnam 1996, Funiss and Renkin 2003). However, these historical outbreaks were limited to

periods of anomalous warm temperatures and drought that allowed the insect to prosper at

high elevations. When cooler, wetter weather returned, thermal conditions in the high

elevations were no longer conducive for a the beetle to complete a univoltine life cycle and

outbreaks ended (Bentz and Schen-Langenheim 2007, Bentz et al. 2011).

However, the current increase in temperatures alone may not explain the magnitude

and severity of MPB outbreaks in whitebark pine. MPB prefer to attack whitebark pine over

lodgepole pine (Six and Adams 2007, Bokino 2008). This preference could be caused by lower

innate defenses of whitebark pine which is suggested by the smaller size (or lack of) pitch tubes

at points of entry of attacking adults (ED, personal observation, Logan et al. 2010). Alternatively,

or additionally, beetles may be more productive in whitebark than lodgepole pine if whitebark

pine is a higher quality host. Lower defenses may account for the preference MPB exhibits

toward whitebark pine, but may also result in higher brood survival supporting more rapidly

expanding beetle populations. Likewise, a more nutritious host may support greater brood

productivity and/or larger beetles, and thus population expansion.

In a laboratory setting, Langor et al. (1990) found that MPB reared in bolts of limber

pine (*Pinus flexilis* James), another high elevation five-needle pine, laid a higher density of eggs

and produced heavier offspring than MPB reared in lodgepole pine. A lab experiment

comparing MPB fitness in ponderosa (*Pinus ponderosae* Lawson & C. Lawson), western white

(*Pinus monticola* Douglas ex D. Don), lodgepole and whitebark pine logs likewise indicated that

whitebark might be a more nutritious host than lodgepole pine; lodgepole pine was found to be

the poorest host, producing the lowest number of offspring of the four species (Amman 1982).

However, whitebark pine did not significantly differ from lodgepole pine in any MPB fecundity measure (1982). A laboratory study comparing fecundity and size of MPB brood emerging from bolts of whitebark and lodgepole pine found that MPB fecundity was higher out of lodgepole pine, but that MPB emerging from whitebark pine were larger than those emerging from lodgepole pine (Gross 2008). The conflicting results of these studies indicate a need to further investigate host effects on MPB productivity. Furthermore, such studies should be conducted under field conditions to best determine how host tree species affects beetle population dynamics.

The current western North American outbreak of MPB is more extensive than any known historical outbreak and is believed to be driven by anthropogenic climate change (Carroll et al. 2004, Gibson 2006, Hicke et al. 2006, Raffa et al. 2008, Bentz et al. 2010, Jewett et al. 2011). The extent of the current MPB outbreak in whitebark pine may simply be an expression of warmer temperatures in high elevations or, along with warmer temperatures, low host defenses and higher host quality may also be contributing to beetle success and outbreak intensity. To determine if the current rapid spread of MPB through whitebark pine forests is a result of whitebark pine being a higher quality host than lodgepole pine, I conducted a field study monitoring numbers of beetles attacking and emerging from whitebark and lodgepole pines of similar size growing in mixed stands. I also measured size of brood adults emerging from trees of both species. Size is a strong measure of fitness in MPB. Larger beetles fly further (Thompson and Bennett 1971), lay more and larger eggs (Amman and Cole 1983, McGhehey 1971), and are more likely to survive cold temperature (Atkins 1967). Larger beetles should, therefore, have higher fecundity and survival rates.   If whitebark pine is a better host than lodgepole pine, I would expect to find a greater emergence rate (number of brood produced per

parental adult pair) and/or larger brood beetles associated with this trees species relative to lodgepole pine.

While I was tracking a cohort of MPB for this study, a cold weather event occurred that resulted in the mortality of most beetles at our study sites. While this event affected my ability to acquire robust productivity data, it presented me with the unique opportunity to field validate published phenology (Powell and Logan 2005) and cold tolerance (Régnierè and Bentz 2007) models as part our investigation of the probable cause of the population decline.

Methods

Study sites

Three sites were selected that fit the following criteria: stands 1) were composed of both lodgepole and whitebark pine, 2) had an ongoing infestation of MPB in trees of typical size for MPB attack, and 3) had low overall white pine blister rust infection severity in whitebark pine. Two study sites, Fiddler's Lake (42°38.47 N, 108°52.03 W) in the Shoshone National Forest, Wyoming, and Palmer Creek (45°03.12 N, 110°35.51 W) in the Gallatin National Forest, Montana, were located within the GYE.   A third site, Vipond Park (45°42.31 N, 112°55.54 W), was located in the Beaverhead-Deerlodge National Forest, Montana, just northwest of the GYE.

The Fiddler's Lake site was located on a gentle, west-facing slope at the south-eastern end of the Wind River Mountain Range and was the highest site at 2903 m elevation. This site consisted of a mixed stand of whitebark and lodgepole pine with a very sparse understory.   At Fiddler's Lake, the MPB outbreak was in the early (incipient) stages and the landscape exhibited only occasional pockets of red trees killed by the beetles.   The Palmer Creek site was located on a south-facing slope at 2630 m and consisted of a mixed stand of lodgepole pine, whitebark pine, subalpine fir (*Abies lasiocarpa* Hook. Nutt.) and Engelmann spruce (*Picea engelmanni* Engelm.) with a diverse herbaceous understory. Vipond Park site was situated at the base of a

north-facing hill (2516 m) and was relatively flat. This site consisted of a mature stand of

lodgepole and whitebark pine with a younger cohort of subalpine fir and Engelmann spruce

regenerating in a sparse understory.   Vipond Park and Palmer Creek had ongoing, outbreak-

phase MPB infestations.

Estimates of MPB productivity

 This study relied on proper timing of sampling in relation to MPB life history events to

estimate productivity of the beetles. Mass attacks by univoltine MPB in high elevation whitebark

generally occur in late July through August. Females attack trees first, releasing pheromones

manufactured from host monoterpenes that then attract both sexes to the tree (Pureswaran

and Borden 2003).   Males follow females into the same entrance holes. The males and females

mate and then construct parent galleries in the phloem where females lay eggs (Amman and

Cole 1983). Once eggs hatch, larvae develop until cold initiates winter dormancy. Larvae resume

development in spring and summer and pupate in individual chambers from which they emerge

by chewing through the bark later that summer. Occasionally, parent beetles re-emerge to

attack new trees in the fall, or overwinter and attack new trees the following spring (Safranyik

and Linton 1985, Hansen and Bentz 2003). When brood densities are very high, pupal chambers

can coalesce and multiple beetles may emerge through a single emergence hole (Reid 1963). At

lower emergence densities (up to approx. 215 emergence holes/m^2), the ratio of emerging

beetles to emergence holes is typically 1:1 (Safranyik and Linton 1985). At high emergence

densities of 1075/m^2 or greater, the relationship of emerging beetles to emergence holes

becomes 2:1 (Amman and Cole 1983, Safranyik and Linton 1985).

At each site, I located 30 whitebark and 30 lodgepole pine trees that were 1) currently

infested with MPB, 2) had either no blister rust infection, or had no more than one flagged small

branch and no bole cankers, and 3) did not have top-kill or other obvious damaging pathogens

or insects. Trees ranged from 22 to 43 cm in diameter at breast height (DBH, 1.4 meters above the ground).   For each tree, I recorded location with a GPS, measured DBH, and marked it with a unique number. To capture possible variability in beetle attack and reproductive success within a tree, we drew two 40 cm wide by 60 cm tall rectangles on the bark with one centered on the north and the other on the south side of the bole at 1.4 m (occasionally the sampling area was shifted slightly to avoid scars or large branches). Within these subsamping areas, I counted and marked each MPB entrance hole, identified by the presence of frass, a pitch tube, or some combination thereof. Counts of entrance holes were conducted between 30 June 2010 and 22 July 2010. While I am confident that counts of entrance holes were conducted before the emergence of MPB brood adults, I did note the presence of some emergence holes while counting entrance holes. Because brood in nearby trees were still in the larval stage at the time of the initial counts, it is unlikely that these emergence holes were created by brood emergence, so they were recorded as holes made by re-emerging parents. After brood emergence was complete, I counted all new (unmarked) emergence holes within the sample areas (between 1 October and 25 October 2010).

At one site, Vipond Park, I collected emerging brood adults to assess whether beetles emerging from lodgepole and whitebark pine differed in size or sex ratio. Collection of MPB was accomplished by stapling emergence cages over north and south subsample areas on ten trees of each species prior to brood emergence. The cages were made of vinyl screen folded into a funnel at the bottom which emptied into a piece of surgical tubing with screen secured over the bottom of the tube (following the design of Bentz 2006). The tubes were attached with glue to the folded screen via the neck and cap of a plastic soda bottle. This design allowed for the tube to be easily removed to collect beetles approximately every two weeks. A piece of No Pest

Strip© (Hot Shot, Madison, WI) was placed in the bottom of each tube to kill insects that emerged into the traps.

Estimates of beetle size and sex ratio

All MPB emerging into cages were sexed using the gender distinct anatomy of the seventh abdominal tergite (Lyon 1958). To estimate size, I measured pronotum width, a standard single metric of beetle body size (McGhehey 1971, Amman 1982). Beetle pronota were photographed from above at 30x magnification using a Leica EZ4D dissecting microscope (Switzerland) and the Leica Application Suite v. 2.0.0. Pronotum width was then determined from the calibrated photos using Image J software (Rasband 2011).

Data analyses

Counts of entrance, adult re-emergence, brood emergence holes, and MPB adults collected from cages on north and south sampling areas on each tree were compared using non-parametric Mann-Whitney Rank Sum tests or paired t-tests (depending on whether data met the assumptions of a parametric test) to determine if the subsamples could be pooled. Because numbers of entrance holes, parent re-emergence holes, brood emergence holes, adult beetles, and beetle size were not significantly different between north and south subsamples in most cases, we pooled the subsample data for analyses. All three types of pooled hole counts for each study tree were converted to holes/m^2 and rounded to the nearest number. The number of parent re-emergence holes/m^2 between tree species at each site were compared using non-parametric Mann-Whitney rank sum tests because these data did not meet the assumptions of a parametric test. For each site, tree DBH between species was compared using non-parametric Mann-Whitney Rank Sum tests or paired t-tests (depending on whether data met the assumptions of a parametric test).

A generalized linear mixed effects model fit by maximum likelihood estimation was used to determine if tree species, and/or tree DBH significantly affected MPB entrance hole density. This entrance hole density model was fit using a Poisson error distribution with a logarithmic link function, with tree species and tree DBH as fixed factors, and study site as a random factor. We detected over-dispersion of the residuals in the Poisson model, so to correct the reported standard errors, the variance was defined as the mean multiplied by the dispersion parameter (Zuur et al. 2009).

Another generalized linear mixed effects model fit by maximum likelihood estimation was used to determine significant predictors of brood adult emergence rate (hereafter emergence rate). Emergence rate is defined as emergence holes/m^2 per entrance holes/m^2 and was modeled treating the number of entrance holes/m^2 as an offset variable. This model used log(entrance holes /m^2) (Berryman 1976), tree species, tree DBH, and the interaction of tree species and DBH as fixed factors; study site was included as a random factor. This generalized linear mixed effects model was also fit with Poisson error distribution with standard errors corrected for residual over-dispersion as described above.

To determine if brood productivity differed among sites and between tree species, we calculated a measure of MPB productivity by tree species at each site using the following equation:

productivity= # of emergence holes-2(# of entrance holes)

This simple model does not account for occasional parent re-emergence and male gallery abandonment and subsequent remating. Because each entrance hole represents a male/female parental pair, and each emergence hole is assumed to be created by one offspring beetle, two emergence holes per each entrance hole equals a productivity value of 0 (parental replacement). Values greater than zero would indicate more offspring are produced than

required to replace parents, while values less than zero would indicate that brood survival is lower than parental replacement (Berryman 1976). Differences between tree species in productivity and/or emergence rate within a site may indicate differences in tree host quality for the beetle. Differences among sites are likely due to environmental factors including weather, stand composition and structure, and outbreak stage. Productivity measures can also be used to roughly predict population trends (Berryman 1976). T-tests were used to compare productivity values between tree species within a site, and a Kruskal-Wallis one-way ANOVA on ranks was used to determine if differences in productivity existed between sites.

I used a linear mixed effects model fit by maximum likelihood estimation to test for the significant effects of tree species, tree DBH, number of entrance holes with caged area (a measure of intraspecific competition), and beetle sex on beetle size. Beetle size was modeled with a log-normal distribution (which provided the best approximation of the distribution of this data) and individual caged tree was used as a random factor in this model.

Data on tree diameter and phloem thickness measured at breast height on the north and south sides of whitebark and lodgepole pine were collected at Vipond Park and Palmer Creek in the summer of 2008 and 2009 (D. Six and T. Dahl, unpublished data). For each site, we used a linear model to test for differences in phloem thickness based on tree species, and tree DBH. To test for the effect of diameter on phloem thickness within each tree species, at each site, we ran linear regressions. Non-parametric Mann-Whitney rank sum tests and t-tests were conducted using Sigma Plot 11.0 (Sigmaplot 2008). R Statistical Software v. 2.12.1 was used for the linear regression, generalized linear mixed effects model and mixed effects models analysis (R Development Core Team 2011).

Analysis of weather as a potential cause of MPB mortality

Because of the very low number of beetles collected from cages and negative productivity values at all three sites, I investigated the potential role of cold weather as a cause of overwintering mortality. In order to estimate when mortality occurred, I peeled bark from south aspects of five randomly selected trees of each species that had been caged at Vipond Park. Within the sample area that had been used for hole counting and caging, we counted the number of parent galleries and classified each parent gallery into the following mutually exclusive categories: 1) no larval galleries present for the length of the parent gallery within the sample area (all brood died as eggs or no eggs were laid), 2) the most advanced brood stage was first or second larval instar, 3) the most advanced brood stage was a third or fourth larval instar, or 4) the most advanced stage was a pupal chamber or emergence hole. These classifications were based on gallery shape (larvae vs. pupae) and width, which reflects head capsule size that diagnostic of larval instar stage. I converted these counts into percentages of parent galleries in each of these categories for each tree.

Weather data

I examined weather patterns that occurred over the course of our study to determine if a cold-weather event coincided with when we estimated mortality had occurred from our bark samples. The weather data was used with cold tolerance and phenology models developed for MPB to further test our hypothesis that a cold weather event was responsible for low beetle productivity at our three sites. We accessed temperature and precipitation data from the closest SNOTEL stations to our sites for the period extending from June 2009 to September 2010 (SNOTEL Data and Products 2011). The weather data for Vipond Park was obtained from Mule Creek SNOTEL site (45°25'N, 112°58'W) located 29 km away at an elevation of 2530 m, which is 14 m higher than Vipond Park. Palmer Creek weather data was from the Monument Peak SNOTEL station (45°13' N, 110°14' W) located 33 km away and 67 m higher in elevation (2697

m) than the Palmer Creek site. Deer Park SNOTEL station (42°35'N, 108°54'W) was used for the Fiddler's Lake site. Deer Park SNOTEL is 7 km away from the Fiddler's lake site and is 55 m higher in elevation (2957 m).

Cold tolerance modeling

Population survival probabilities in response to temperature and LT_{50} (the median lethal temperature which kills 50% of MPB) for MPB larvae at Vipond park were estimated using the cold tolerance model developed by Régnierè and Bentz (2007) and the Mule Creek SNOTEL temperature data (J. Powell, personal communication).   The model captures dynamic adaptation of an individual beetle's supercooling point (the temperature at which larvae freeze solid) as a function of individual history of exposure to cold challenges as measured via daily mean temperatures and the daily swing between minimum and maximum temperatures.   Daily survival probabilities for each individual are predicted; seasonal survival of a cohort of individuals laid on the same day in the fall is the minimum survival probability predicted through the subsequent winter. Survival of eggs, pupae and teneral adults are not modeled; likewise, mortality due to other factors is not included. Accordingly, predictions of net survivorship likely overestimate real-world observations.

The model of Régnierè and Bentz (2007) assumes that the first step toward cold hardening is cessation of larval feeding and voiding of the gut.   In their model, this begins when an index tracking individual physiological "memory" of previous cold challenges passes a given threshold. Cessation of feeding can be reversed if the index does not pass a second threshold, but once the second threshold is passed, cessation of feeding becomes irreversible until spring. Feeding cessation is significant for predicting larval development because when larvae are not feeding, development should stop.

Integrated cold tolerance and phenology modeling using phloem temperature

MPB development is under direct temperature control, with no known diapause (Bentz et al. 1991, Logan and Bentz 1999). Development of 5individuals in seven life stages (egg, four larval instars, pupae and teneral adult) proceeds as a nonlinear function of phloem temperature (Powell and Logan 2005). Timing of oviposition, i.e. temperature-dependent rate of gallery production by burrowing adult females and distribution of eggs along the gallery, also depends directly on temperature (Logan and Bentz 1999). To model the long, drawn out attack period that occurred at Vipond during 2009, I chose a normal distribution of attacks centered on Julian d 215 (2 August 2009), with standard variation of 15 d. This attack period was chosen based on a combination of observations of beetle attacks in 2009, and days when the maximum air temperature (recorded at the Mule Creek SNOTEL) reached 19°C, the minimum temperature required for MPB flight (McCambridge 1971). Each attack generates a distribution of 64 eggs in an ovipositional gallery (Logan and Bentz 1999). Cold hardening was integrated with the models for ovipositional timing and median development by setting larval development rates to zero for each individual that had stopped feeding according to the Régnierè and Bentz cold tolerance model (2007). Survivorship for larvae, depending on cold exposure since egg hatch for each individual, was predicted separately.

Temperatures in the phloem of trees at Vipond Park were not measured in 2009/2010, but they were collected from five lodgepole pines at Vipond Park in 2010/2011 by the USDA Forest Service Rocky Mountain Research Station (Bentz and Vandygriff, personal communication). Hourly phloem temperatures at Vipond Park for 2009/2010 were generated using a matching method and the archive of phloem temperatures collected in 2010/2011. Each daily ambient min-max-min signal from the SNOTEL data was compared with all ambient min-max-min signals in the archive; the daily sequence of phloem temperatures associated with the archival signal having closest min-max-min (least sum square difference) was used to predict

phloem temperatures at Vipond Park. The matching method successfully recreates relevant developmental milestones for MPB and has been tested across a variety of altitudes and latitudes (Lewis 2011).

Results

Estimates of MPB entrance, parent re-emergence, and brood adult emergence rates

There was no difference in DBH between tree species at either Vipond Park (U = 400.0, df = 1, p = 0.461) or Fiddler's Lake (t = 1.86, df = 59, p = 0.067) (Table 1). However, at Palmer Creek, lodgepole pine were larger than whitebark pine (U = 195.5, df = 1, p < 0.001) (Table 1). Table 1 shows the mean densities of adult entrance, adult re-emergence and brood adult emergence holes by tree species for each site.

Generalized linear mixed model analysis indicated that tree DBH was significantly positively correlated with MPB entrance hole density (t = 3.83, df = 174, p < 0.001). Holding tree species constant, each one cm increase in tree DBH related to an increase of 2.9% (±0.8) more entrance holes/m^2. Holding DBH constant, there were approximately 12.5% (±6.8) more entrance holes on whitebark pine than on lodgepole pine, and this difference bordered statistical significance (t = 1.94, df = 174, p = 0.054). The interaction between DBH and tree species was not a significant predictor of entrance hole density and was not included in the final model.

There was no difference in density of holes attributed to parental adult re-emergence between tree species at any site (Vipond Park: U = 400.5, df = 1, p = 0.464, Palmer Creek: U = 398.0, df = 1, p = 0.575, Fiddler's Lake: U = 402.5, df =1, p = 0.467).

Generalized linear mixed model analysis indicated that MPB emergence rate increase by 5.8% (±1.7) for each one centimeter increase in DBH holding all other predictors constant (t=3.47, df=172, p<0.001). Across both species and all tree diameters, emergence rate declined

exponentially ($x^{-0.91\ \pm0.12}$) as entrance hole density increased (t=-7.71, df=172, p<0.001). Holding

entrance hole density and tree DBH constant, there were 8 (±5.5) times (more MPB emerging

out of whitebark pine than lodgepole pine (t=3.05, df=172, p=0.003). However, the interaction

of tree DBH and tree species was also significant (t=-2.78, df=172, p=0.006), which suggests that

the relationship between tree DBH and MPB emergence rate differs between species. Fig. 1

illustrates the significant interaction term for tree diameter and tree species where the rate of

increase between tree DBH and MPB emergence rate in lodgepole pine is significantly positive,

but there is no relationship between tree DBH and emergence rate in whitebark pine. The

density of adult re-emergence holes was not a significant predictor of emergence rate and was

not included in the final model.

Mean phloem thickness was significantly greater in whitebark pine than lodgepole pine

at both Vipond Park and Palmer Creek (Figure 2). Diameter was not a significant predictor of

phloem thickness at either site (Palmer Creek: t =1.290, df =117, p = 0.2; Vipond Park: t = 1.015,

df =118, p = 0.2571). Accounting for DBH, the mean phloem thickness of whitebark pine was

almost 1 mm larger than that of lodgepole pine at Palmer Creek (whitebark $\bar{x}$ = 2.64 mm,

lodgepole $\bar{x}$ = 1.642 mm, t = 6.486, df = 117, p < 0.001; model fit: r^2 = 0.252, F = 21.05, 2, df =

117, p < 0.001). At Vipond Park, this pattern held; a significant regression model (r^2 = 0.2571, F =

21.76, 2, df = 118, p < 0.001) showed that on average, whitebark pine's phloem was 0.86 mm

thicker than lodgepole pine's phloem accounting for DBH (whitebark $\bar{x}$ = 2.87 mm, lodgepole $\bar{x}$ =

2.01, t = 6.576, df = 118, p < 0.001). There was a significant relationship between phloem

thickness and diameter in the lodgepole pine at Palmer Creek (r^2 = 0.07257, F = 5.629, df = 58,1,

p = 0.02), but not at Vipond Park (r^2 = 0.02504, F = 2.541, df = 59,1, p = 0.1163) (Figure 2). In

whitebark pine, there was no relationship between phloem thickness and diameter at either site

(Palmer Creek: r^2 = -0.01501, F = 0.1278, df = 58,1, p = 0.7221; Vipond Park: r^2 = -0.01609, F = 0.06566, df = 58,1, p = 0.7987) (Figure 2).

MPB populations declined at all three sites, but particularly so at Vipond Park, as indicated by the strongly negative productivity values in Table 1. There were no significant differences in productivity values between whitebark and lodgepole pine at any site (Vipond Park: t =1.687, df = 58, p = 0.097, Palmer Creek: t = -1.410, df = 57, p = 0.164, Fiddler's Lake: t = 0.671, df = 58, p = 0.505). Because productivity values were not statistically different between tree species within a site, we pooled productivity values within a site to compare site productivity values. A Kruskal-Wallis one-way ANOVA on ranks indicated that significant differences existed between site productivity values (Vipond Park median = -246.5, Palmer Creek median = -63.0, Fiddler's Lake median = -190.0, H = 78.865, df = 2, p < 0.001).

Numbers of MPB emerging into cages and brood adult body size

Fifty-eight MPB were collected out of 40 emergence cages on whitebark and lodgepole pine at Vipond Park in the summer and fall of 2009. Peak emergence occurred between 18 August and 31 August, as 35 beetles (60%) were collected on 31 August. Two (3%) MPB were collected on 17 August, 13 (22%) were collected on 18 September, and eight (14%) were collected on 11 October. Emergence cages were also checked on 4 August but no MPB were present. Out of the ten lodgepole pines that were caged, only five produced MPB, whereas nine out of ten caged whitebark pines produced at least one MPB. Mann-Whitney rank sum tests indicated no difference in numbers of MPB collected from whitebark and lodgepole pine when only trees producing beetles were considered (U = 19.5, df = 1, p = 0.73). When all caged trees were considered (including ones that produced no beetles), there was also no difference in number of beetles between tree species (U = 33.0, df = 1, p = 0.20). Female to male sex ratios of beetles collected from the two tree species were similar(whitebark 1.91:1, lodgepole 1.89:1).

The distribution of male and female MPB pronotum widths within each tree species is shown in Fig. 3a. A linear mixed effects model used to test for factors influencing size of beetles emerging from whitebark and lodgepole pine showed that sex of beetle was a significant predictor of beetle size (t = -2.69, df = 43, p = 0.010). Tree species did not have a significant effect on beetle size (t = 0.70, df = 12, p = 0.500). This model estimated that, when averaged across both tree species, and all trees, male beetle pronotum widths were 0.06 (±0.02) mm smaller than female pronotum widths. Averaged across both sexes and all trees, pronotal widths of beetles emerging from whitebark pines were 0.02 (±0.03) mm larger than pronotal widths of beetles emerging out of lodgepole pine, but this difference was not significant (Fig 3b). Tree DBH and the number of entrance holes in the caging area were not significant predictors of beetle pronotum width and were not included in the final model.

Role of weather in low productivity of MPB.

Based on the low number of beetles collected at Vipond Park, it was clear that a major mortality event had occurred in the cohort of beetles that had attacked trees in summer of 2009. Bark peeled from trees used for caging revealed no signs of competition from other bark beetles such as *Ips* or *Pityogenes.* Fig. 4 shows bark peeled from a tree at this site displaying the synchronous termination of larval galleries approximately one cm from their origin. This was typical of larval galleries in all trees sampled except one that contained a few late instar larval galleries. Two whitebark and three lodgepole pines sampled contained some parent galleries in which no larval galleries were present for the length of the gallery (Table 2). A majority of both whitebark and lodgepole pine parent galleries sampled contained only larval galleries which terminated in the first or second larval instar (Table 2).

Weather patterns in relation to MPB mortality

The annual profile of daily minimum temperature (Fig. 5) near Vipond Park shows two sudden, sustained drops in temperature: one extending from 30 September to12 October 2009, and the other from 3 to 10 December 2009. Daily minimum temperatures recorded near Palmer Creek and Fiddler's Lake and other SNOTEL sites within the GYE (data not shown) during the 2009-2010 development period of the MPB emerging in 2010 display similar dips in temperature for the October and December periods indicating that these cold snaps were regional, GYE-wide events. Fig. 5 also shows the median lethal temperature needed to kill 50% of MPB (LT_{50}) predicted from BioSIM cold tolerance model (Regniere and Bentz 2007, B. Bentz personal communication) for Vipond Park in 2009-2010. The model predicts an annual probability of mortality of 54.5%, and shows that the LT_{50} was reached during the December cold snap at Vipond Park (Figure 5). The LT_{50} decreased during the October cold snap so the air temperature dropped close to the LT_{50}, but was not cold enough to cause 50% MPB mortality during that event (Figure 5).

The integrated phenological and cold tolerance model predicted only 27% survival of larvae over the 2009/2010 winter. The model predicted that a cold period in mid-September would have induced 50% mortality among larvae whose parents attacked near Julian d 215 (early August) in 2009. A subsequent inclement cold snap with temperatures dropping to -15° C in mid-October was predicted to have caused 98% mortality of brood resulting from the latter half of the attack distribution.   Because of developmental delays occasioned by cold hardening, 90% of survivors would have been first or second instar larvae during the October cold snap indicating that most mortality occurred before the third instar was reached. The models also predicted that emergence of any surviving brood would have been significantly delayed in 2010, with teneral adults not appearing until late August.

Discussion

MPB productivity

The results of this study found that the emergence rate of MPB was greater from whitebark pine than lodgepole pine. This suggests that whitebark pine is, in fact, a superior host for MPB. This finding may help explains why current MPB outbreaks in whitebark pine are so extensive, and appear to proceed more quickly than typical outbreak progression in lodgepole pine. The interaction between tree species and DBH that effects emergence rate suggests that differences in MPB emergence rates between species are governed by inconsistent relationships between beetle emergence rates and tree size. The similar, negative MPB productivity values for both species suggest that whitebark and lodgepole pine do not differ in their ability to buffer beetles against cold temperatures.

The positive relationship between DBH and MPB emergence rate in lodgepole pine observed in this study (Fig. 1) has been found in a number of other studies (Reid 1963, Cole and Amman 1969, Amman and Cole 1983). This relationship has been attributed to increasing phloem thickness, and thus increasing beetle food quantity, with increasing diameter in lodgpole pine (Amman et al. 1977, Amman 1972, Cole and Amman 1980). However, this relationship was only confirmed in one of two sites in this study, which suggests that the positive relationship between phloem thickness and lodgepole pine diameter may not be as consistent as previously thought.

Previous to this study, the relationship between tree diameter and phloem thickness had not been directly investigated in whitebark pine. Our results indicate that for the range of tree diameters observed in this study, there is no relationship between phloem thickness and tree diameter within whitebark pine. Correspondingly, we found no relationship between MPB emergence rate and tree DBH in whitebark pine at our sites. In the range of tree diameters observed in this study, whitebark pine had thicker phloem than lodgepole pine (Figure 2). This

difference in quantity of MPB food between species may be the cause of the higher emergence rates of MPB from whitebark pine than from lodgepole pine. I observed a number of small diameter whitebark pines with high MPB emergence rates (Fig 1). In contrast, there were no highly productive, small lodgepole pines (Fig 1). These findings suggest smaller whitebark pines can support substantial MPB productivity, while in lodgepole pine of similar size, productivity is constrained. This difference is most likely driven by larger amount of phloem found in small (<30 cm) whitebark pine compared with lodgepole pine of the same size (Figure 2). While this difference in phloem in small diameter trees likely influenced beetle productivity in the two tree species at our sites, it may not necessarily cause differential rates of productivity in all mixed whitebark and lodgepole stands. At two other mixed stands (D. Six and T. Dahl, unpublished data) where phloem thickness and DBH of the two species were measured, the phloem thickness of whitebark and lodgepole pine did not differ.

If whitebark pine consistently has thicker phloem than lodgepole pine, then this may help explain why MPB outbreaks are so extensive and severe in whitebark pine. Generally, as MPB outbreaks in lodgepole pine progress, successively smaller trees are killed until the outbreak ceases when the remaining trees are <20 cm in diameter (Cole and Amman 1969). In lodgepole pine of this diameter and smaller, phloem is too thin to support beetle development (Cole and Amman 1980). Lodgepole pines 20 to 23 cm in diameter produce only about one third to one half of the beetles required to kill a lodgepole tree; only trees above 30 cm in diameter produce enough beetles to successfully attack a tree (Cole and Amman 1969). Therefore, in lodgepole pine, trees smaller than 30 cm can act as sinks for beetles. In contrast, this study found that this is not the case in some small diameter whitebark pine. While MPB prefers larger diameter whitebark pines (Perkins and Roberts 2003, Six and Adams 2007, Larson 2011),

outbreaks may cause more overall mortality in whitebark than lodgepole pine if beetles continue to attack and remain productive in small-diameter trees.

I found no difference in MPB size between whitebark and lodgepole pine. If whitebark pine was nutritionally superior, it is predicted that beetles developing in whitebark pine would be larger than those that developing in an inferior host (Chapman 1998). For MPB, size is an important fitness measure with significant effects on population growth (McGhehey 1971). Because I found no difference in size of beetles emerging from whitebark and lodgepole pine, I did not find support for the hypothesis that the severity of MPB outbreaks in whitebark pine is due to body size-mediated differences in beetle fitness or survival. However, the occurrence of fall cold snaps and subsequent mortality of most beetles developing in the study trees diminished my sample size for the body size analysis likely affecting statistical power and ability to generalize these conclusions

The trend towards higher attack density in whitebark pine compared with lodgepole pine suggests that MPB attack dynamics may differ between the host species. A higher density of MPB attacks should not be confused with preference, which refers to which trees beetles select for attack, not the density of attacks once the tree is chosen (Baker et al. 1971, Waring and Six 2005, Six and Adams 2007). Higher attack rates on whitebark pine may be caused by its unique monoterpene blend which is high in myrcene, 3-carene and terpinolene. These monoterpenes were found to significantly increase trap catches of MPB (Borden et al. 2008). Traps baited with attractant pheromone plus the whitebark monoterpene blend caught 7.7 times more beetles than traps with the attractant pheromone alone (Borden et al. 2008). In contrast, the lodgepole monoterpene blend caught 4.7 times as many beetles than the traps baited with attractant pheromone alone (Borden et al. 2008). While this difference was not statistically significant, the results imply that a stronger synergism between whitebark

monoterpenes and beetle pheromones may amplify the beetle aggregation signal, thereby

drawing in more beetles to whitebark pine trees once the attack is initiated. If this is true,

whitebark pines may start off at a disadvantage due to higher attack densities. Higher attack

density causes decreased defensive resin flow as well as diminished ability of the host to

interfere with MPB communication (Raffa and Berryman 1983). Higher attack density also could

cause the finite preformed resin resource to be dispersed to the many entrance holes, therefore

reducing the quantity at any one individual attack. This may, in part, explain the paucity of well-

formed pitch tubes that has been anecdotally observed in many MPB-attacked whitebark pines.

Overall, whitebark pines also appear to have lower resin defenses (D.L. Six, unpubl. data).

MPB population decline investigation

Negative productivity values were observed at all three study sites suggesting a regional

decline in MPB populations in 2009/2010. I suspected that a cold weather event might have

been responsible for low survival in our trees, and at our sites in general. Cold temperature is a

major cause of mortality in MPB particularly in high elevations (Amman and Cole 1983).

Exposure to temperatures of -34°C or below can kill MPB larvae even after they have cold-

hardened (Safranyik and Linton 1998). However, cold hardening requires that beetles gain

exposure to gradually declining temperatures (Bentz and Mullins 1999). If abrupt dips in

temperature occur prior to cold hardening in the fall, or in spring after beetles have lost cold-

hardiness, then extensive mortality can occur even at temperatures much higher than -34°C.

The synchronous termination of first and second instar larval galleries in trees at Vipond

Park supports the hypothesis that freezing killed most larvae at this site. No other factor can

account for such synchronous and widespread mortality. Mortality due to predators or drying

would not be uniform within a site, and would not account for widespread population decline

across sites.   Likewise, while interspecific and intraspecific competition can result in high levels

of mortality, neither would result in synchronous termination of larval galleries, and therefore, both can be discounted as the cause of the population crash.

My conclusion that a cold-temperature event caused widespread mortality of larvae at our sites was corroborated by temperature profiles and the results of cold mortality and phenological models based on the temperature profiles. Two cold snaps occurred in the fall of 2009 at all three study sites (based on data from weather stations nearby sites) and other weather stations across the GYE. Given that Vipond Park and Fiddler's Lake are 470 km apart, these cold snaps occurred at a regional scale. Because fewer MPB would have been cold hardened earlier in the season, the October cold snap was likely responsible for high levels of MPB mortality observed across the region.

The 50% rate of mortality predicted for our sites using the Regniere and Bentz (2007) cold tolerance model is most likely a conservative estimate of mortality as it does not account for mortality of eggs, pupae or adults. Because the attack period at Vipond Park in 2009 appeared to be long and drawn out, and occurred during a relatively cool summer, oviposition by some beetles likely occurred quite late and it is possible that eggs were present during the October cold snap. The cold snap would have killed these eggs resulting in higher mortality rates than estimated by the model. Because the use of the cold tolerance model alone may underestimate mortality, Regniere and Bentz (2007) suggested coupling this model to the Bentz et al. (1991) phenology model. In my study, the integration of these two models produced a lower overall survival estimate (27%) and, did in fact, more accurately estimate the high degree of mortality observed in the field at our sites.

Besides more accurately predicting survival, the integrated model performed exceptionally well in predicting timing of beetle mortality and phenology in the field. The model predicted 50% mortality of larvae during a freeze in mid-September. Any eggs present at this

time also would have been killed (the model does not account for egg mortality). Several parental (egg) galleries on trees from which we peeled bark contained no larval galleries suggesting that considerable egg mortality did occur. The second corroboration of the model with field data was the prediction that most larvae would enter the winter as first and second instar larvae. I did not look under the bark of trees during the winter. However, the synchronous termination of larval galleries in the first or second instar, and model predictions of 90% mortality from cold weather before the beetles reached the third instar, match. Both findings point to the October cold snap as the cause of the population decline. Finally, the model predicted that the beetles would reach the adult stage in late August. I collected the majority of adult beetles from emergence cages in late August.

The temperature-driven mortality and phenology models accurately captured population trends at Vipond Park, but also reinforced how sensitive this insect is to temperature. The MPB has fulfilled expectations (Bentz and Mullins 1999, Logan and Powell 2001) of its importance as a bioindicator of climate change due to its sensitivity and rapid responses to local climate. The rapid range expansion of this insect northward as well as eastward into the interior of Canada (Safranyik et al. 2010) and its expansion into high elevations (Macfarlane et al. 2009) due to warming of just a few degrees shows how fast and intensely this insect can respond to increases in environmental favorability. Likewise, our results show that cold weather events occurring outside of typical cold periods can still have a strong negative impact on beetle activity.

Conclusions

The occurrence of MPB outbreaks in whitebark pine is likely predominantly a response to warmer temperatures facilitating a shift to a univoltine life cycle. However, benign temperatures alone cannot cause an outbreak because suitable hosts must be present as well.

On the landscape scale, whitebark pine size has increased and has been homogenized by fire suppression (Tomback et al. 2001).   Now that the high elevations are warm enough for MPB to thrive, whitebark pine happens to be the available, appropriately sized host (Perkins and Roberts 2003, Larson 2011). In addition, it appears that that severity and speed of MPB outbreaks in whitebark pine is due to its superior quality as a host relative to lodgepole pine.

The average global temperature is expected to warm by 1.8 to 4.0^{o}C (IPCC 2007), but the amplitude of this warming in high elevations has been shown to be greater than global average projections (Beniston et al. 1997). Therefore, high elevations will most likely remain thermally adaptive for MPB with no relief for whitebark pines.   While this situation is no doubt dire for whitebark pine and the high elevation ecosystems it supports, the MPB-whitebark pine system serves as both an early warning, and as an illustration of the sudden, catastrophic effects that warming just a few degrees can have on an ecosystem.

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Table 1. Mean (±SE) for tree diameter at breast height (DBH) and mountain pine beetle entrance holes/m^2, adult re-emergence holes/m^2, brood emergence holes/m^2 and productivity/m^2 for whitebark and lodgepole pine. Samples are from pooled north and south subsamples at three sites in the Northern Rocky Mountains, USA. Entrance holes are formed by entering pairs of parents (two beetles per hole), adult re-emergence holes are made when some parents leave the tree post-attack but before brood emergence, and brood emergence holes are produced by individual brood exiting the tree after completing development (one beetle per hole is assumed).

Site	Species	N	Mean (±SE) DBH	Mean (±SE) entrance holes/m^2	Mean (±SE) adult re-emergence holes/m^2	Mean (±SE) brood emergence holes/m^2	Mean (±SE) productivity/m^{2a}
Vipond Park	Whitebark	30	27.1 (0.54)	160.60 (10.07)	9.97 (2.29)	17.17 (2.85)	-304.03 (20.32)
	Lodgepole	30	27.4 (0.53)	132.57 (11.94)	12.07 (2.47)	13.43 (2.63)	-251.70 (23.43)
Palmer Creek	Whitebark	30	28.8 (0.81)	88.17 (6.21)	7.97 (1.52)	143.60 (15.61)	-32.73 (23.55)
	Lodgepole	29	33.3 (0.84)	96.76 (9.38)	7.17 (1.46)	116.69 (11.87)	-76.83 (20.46)
Fiddler's Lake	Whitebark	30	30.2 (0.79)	131.30 (7.14)	2.20 (0.45)	58.20 (6.84)	-204.40 (12.13)
	Lodgepole	30	32.1 (0.65)	127.83 (9.47)	3.23 (0.93)	63.33 (7.35)	-192.33 (13.26)

[a]Productivity is calculated as: # of emergence holes - (2 x # of entrance holes). A positive productivity value indicates an increase in beetles produced from the trees relative to numbers entering, while a negative value indicates the reverse.

Table 2: Percentages of mountain pine beetle oviposition galleries from which the most advanced brood stage was: eggs/or no eggs (without larval galleries), 1st or 2nd instar larvae, 3 or 4th instar larvae, or pupal chamber/new adult emergence hole.

Tree species   % of main galleries

Whitebark	Without larval galleries	Containing 1st or 2nd instars	Containing 3rd or 4th instars	Containing pupal chambers or adult emergence hole
Tree #: 1	14	86	0	0
2	4	96	0	0
3	0	100	0	0
4	0	100	0	0
5	37	60	4	0
% of all whitebark pine main galleries sampled	**13**	**86**	**1**	**0**
Lodgepole				
Tree #: 1	0	100	0	0
2	31	69	0	0
3	0	100	0	0
4	15	85	0	0
5	34	61	0	0
% of all lodgepole pine main galleries sampled	**15**	**85**	**0**	**0**

   Oviposition gallery systems were sampled from the bark in the sample area that had been caged to study adult emergence on five whitebark and five lodgepole pines at Vipond Park, in the Beaverhead-Deerlodge National Forest, MT.

Figure 1. Plot representing the tree species x tree DBH interaction term in generalized linear mixed effects model predicting emergence rate (pooled north and south emergence/m^2 divided by entrance holes /m^2) of MPB in whitebark and lodgepole pine in three sites in the Northern Rocky Mountains, USA. The relationship between lodgepole pine DBH and mountain pine beetle emergence rate is significantly positive (Pearson correlation coefficient=0.4120, n=89, p<0.001), while there is no relationship between whitebark pine DBH and mountain pine beetle emergence rate (Pearson correlation coefficient= -0.0999, n=90, p=0.349). Symbols represent emergence rate for individual trees and are coded by site (triangles=Palmer Creek, circles=Fiddlers Lake and crosses=Vipond Park) and lines are regression lines.

Figure 2. Plots of tree DBH (cm) and phloem thickness for whitebark pine and logepole pine at two of the Northern Rocky Mountain study sites, Vipond Park and Palmer Creek. Only the logepole pine at Palmer Creek displayed a significant relationship between phloem thickness and DBH (phloem= 0.024(DBH)+1.24).

Figure 3. Boxplots showing pronotal widths of (A) male and female mountain pine beetles or (B) all mountain pine beetles (males and females pooled) collected from cages on ten whitebark pine and ten lodgepole pine at Vipond Park, Beaverhead-Deerlodge National Forest, MT. Bold horizontal lines = median, top of box = 75th percentile, bottom of box = 25th percentile, dotted vertical line with bar = range, open circles = outliers, dark dots = mean, arrows = standard error.

Figure 4. Photograph of bark peeled from a whitebark pine at Vipond Park, Beaverhead-Deerlodge National Forest, MT, showing synchronous termination of first or second instar larval galleries.

Figure 5. Output of BioSim cold tolerance model for MPB (Regniere and Bentz 2007) at Vipond Park in 2009 and 2010 showing minimum air temperature (solid line) from a nearby Mulecreek

snotel site, and the estimated LT $_{50}$, (the median lethal temperature which kills 50% of larvae, dashed line). Fifty percent larval mortality is predicted to occur when the minimum temperature line touches the predicted LT$_{50}$ line, with greater than 50% mortality predicted when the minimum temperature dips below the LT$_{50}$ line.
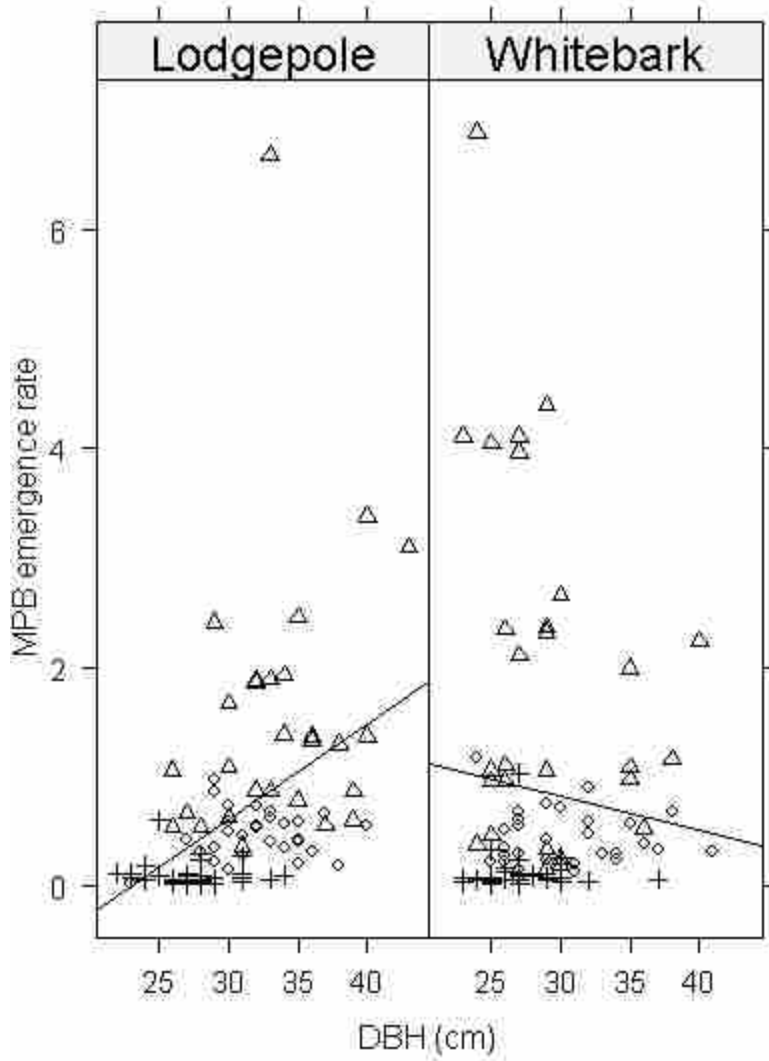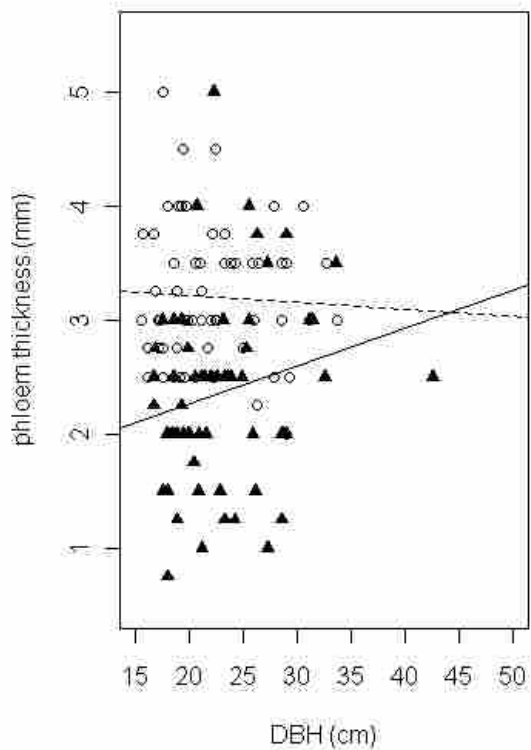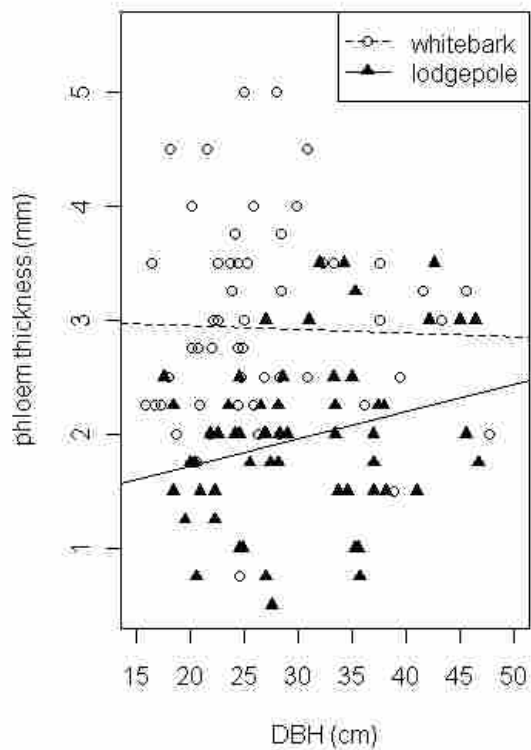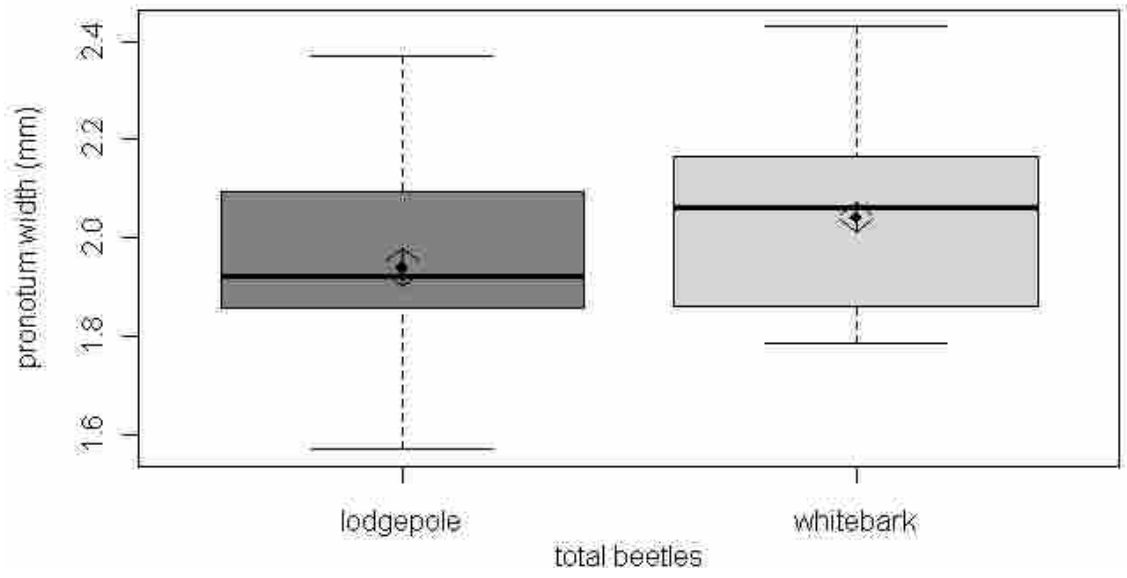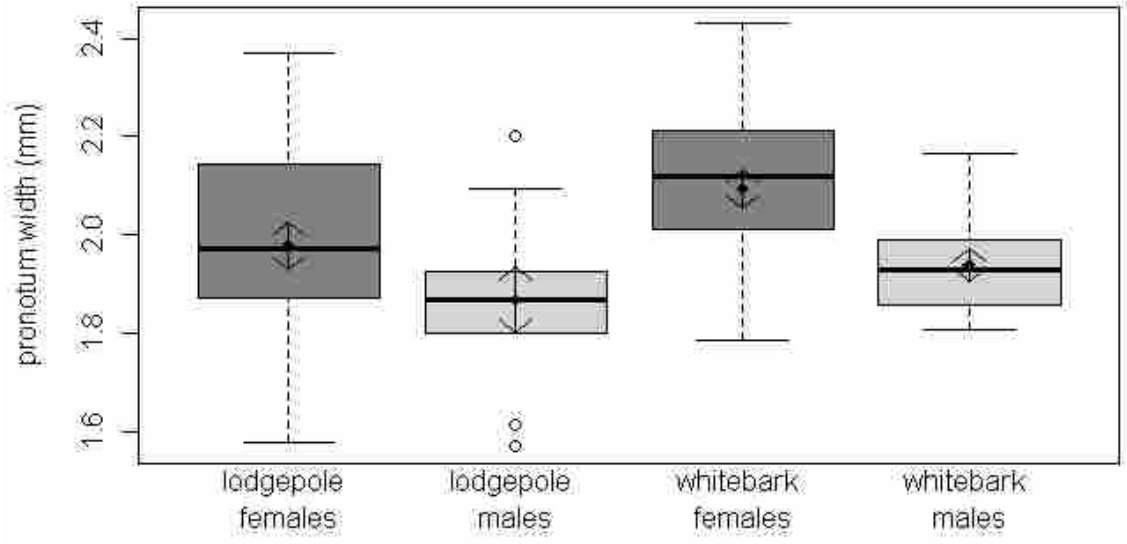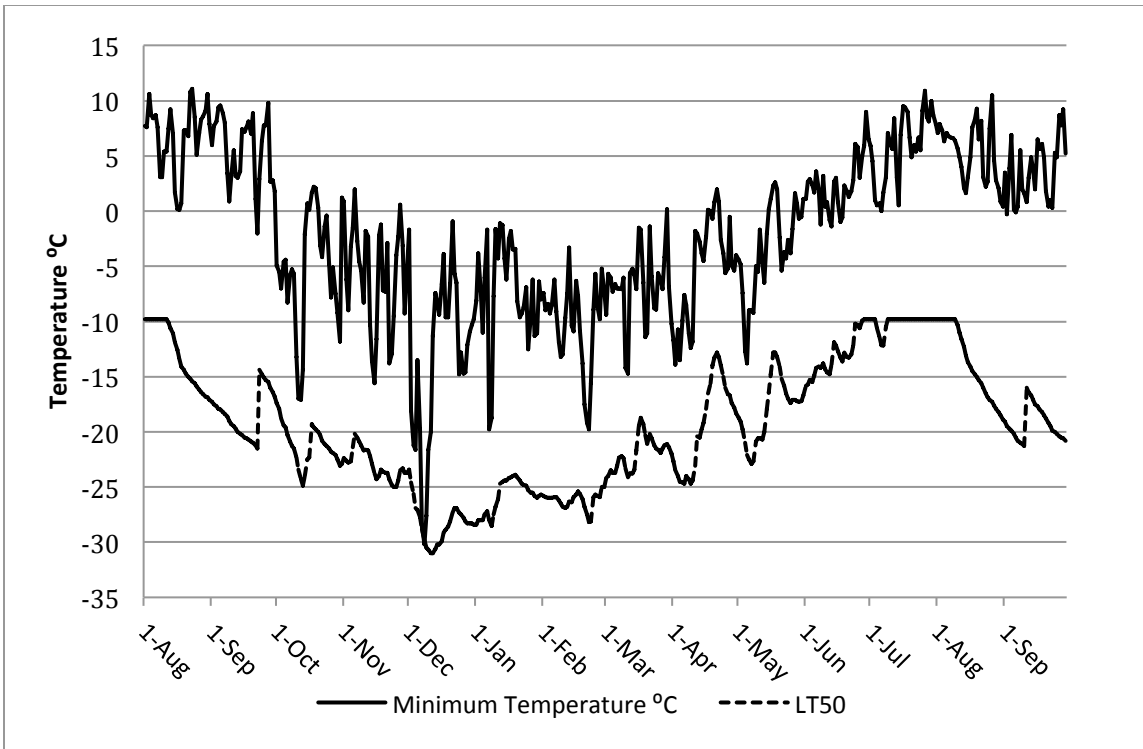
Chapter 3: Severe blister rust infection in whitebark pine alters mountain pine beetle attack rate, emergence rate and size

Abstract

Exotic fungal pathogens of trees can have devastating ecological effects on forests. These effects can be exacerbated when such infections result in the increased likelihood of attack by native insects. Whitebark pine (*Pinus albicaulis* Engelm.) is a keystone species that grows throughout high elevations forests in western North America. This tree is currently experiencing high rates of mortality from both the exotic fungus, *Cronartium ribicola* J.C. Fisch, which causes the disease white pine blister rust (WPBR), and the native tree-killing bark beetle, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB). These two primary mortality agents not only co-occur in whitebark pine, but also interact. MPB preferentially select WPBR-infected whitebark pine over healthy whitebark pine, and likelihood of attack increases with infection severity. However, it is not known if WPBR infection alters host tree suitability for MPB. I conducted a field study examining attack rates, emergence rates, body size, and sex ratio of MPB in whitebark pine exhibiting different WPBR infection severities to determine if and how WPBR infection affects MPB. MPB attack density was lowest on the most severely infected trees, but emergence rates and size of beetles from highly infected trees were greater. There were no differences in attack rate, emergence rate or sex ratio of MPB between healthy trees and any of the three lower WPBR infection categories. The low attack rates in severely infected whitebark pine may indicate that these trees have lower defensive capabilities or that beetles are less attracted to highly infected hosts. However, the latter possibility is less likely as other studies have found highly infected trees are preferred by MPB. The increased emergence rate of MPB from severely infected trees is likely due to low intraspecific competition afforded by low attack rates. Given that highly infected whitebark support high MPB productivity, these trees may serve as reservoir hosts for MPB when beetle populations are low, and could support rapid MPB population growth when environmental conditions are favorable.

Introduction

The invasion and spread of exotic forest pathogens has severely altered the composition of many North American forests. These invasions have often caused devastating results including functional extinction of affected tree species (Ellison et al. 2005). An example is chestnut blight, which decimated the once majestic American chestnut (*Castanea dentate* (Marsh.) Borkh.), and is caused by the exotic canker fungus, *Cryphonectria parasitica* (Murr.) Bar. Chestnut blight has relegated this previously dominant tree to crown sprouting shrubs and has consequently altered its ecological role in northeastern hardwood forests of the United States (Ellison et al. 2005). Other examples of rapid, extensive tree mortality caused by fungal pathogens that are known to be, or presumed to be exotic, are butternut canker (*Sirococcus clavigigneti-juglandacearum* N.B. Nair, Kostichka and Kuntz) infecting *Juglans cinerea* (L.), beech bark disease caused by the combination of *Neonectria faginata* (Lohman et al.) Castl. and Rossman and the exotic scale insect *Cryptococcus fagisuga* Lindinger infecting American beech (*Fagus grandifolia* Ehrh.), Port-Orford cedar root rot caused by *Phytophthora lateralis* Tucker & Milbrath infecting *Chamaecyparis lawsoniana* (A. Murr bis.) Parl, and white pine blister rust (WPBR) caused by the invasive rust fungus, *Cronartium ribicola* J.C. Fisch, which infects all five-needle pines (Loo 2009).

While these diseases are damaging in their own right, their ecological effects can be exacerbated when they interact with native insects that attack infected hosts. In some cases, infection by exotic pathogens results in increased likelihood of attack by native insects. This has been observed in mango plantations where infection by two putative exotic, pathogenic fungi increased attack rates of the native bark beetle, *Hypocryphalus mangiferae* Stebbing (Masood et al. 2010). This type of interaction has also been observed in California coast live oaks (*Quercus agrifolia* Née) where a number of native ambrosia and bark beetles are attracted to trees

infected with the exotic Oomycete, *Phytophthora ramorum* S. Werres, A.W.A.M de Cock (McPherson et al. 2008).

Another exotic fungus and native insect interaction is currently affecting the keystone and foundation species, whitebark pine (*Pinus albicaulis* Engelm.). This tree is experiencing high rates of mortality caused by a combination of WPBR and the native tree-killing bark beetle, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) (Tomback and Achuff 2010). These two primary mortality agents not only co-occur in whitebark pine, but also interact. MPB preferentially select WPBR-infected whitebark pine over healthy whitebark pine, and preference increases with WPBR-infection severity (Six and Adams 2007, Bockino and Tinker 2012). Within the extensive whitebark pine forests within the Greater Yellowstone Ecosystem (GYE), MPB-caused whitebark pine mortality has been more extensive than in other parts of the tree's range (Gibson 2008). By 2009, already more than 80% of the whitebark pine forests in the GYE had experienced moderate to severe MPB mortality due to the beetle (MacFarlane et al. 2009). The overall WPBR infection rate of individual whitebark pine in the GYE is approximately 20% (Jean et al. 2011). This co-occurrence of mortality agents indicates that WPBR and MPB may be interacting to exacerbate the loss of this important tree, which is a proposed endangered species (Federal Register 2011).

WPBR is a heterocyclic rust with five spore types requiring alternation of life stages between pines bearing five needles per fascile (*Pinus* section Strobus), and *Ribes, Pedicularis* or *Castellija* (Geils 2010).   WPBR infects pines through needle stomata and infections grow within the phloem of branches, and eventually spread to the bole of the tree (Spauling 1911). On the bole and branches of tree, WPBR-infected phloem forms cankers where the fungus sporulates. The cankers grow concentrically with the older centers eventually drying and cracking. Branches and entire trees die when cankers expand to the extent that they girdle the branch or the bole

(Colley 1918). Larger trees can survive infection for more than 10 years (Tomback 2001), but will exhibit increasing signs and symptoms (including reddened, swelling bark, weeping cankers and red flagged branches) the longer they have been infected. Therefore, in a WPBR-infected stand, individual trees will often display varying stages of disease progression from low (a few cankers on small, outer branches) to highly infected (a majority of the crown and often the entire upper bole affected). WPBR often kills trees from the top down, greatly reducing crown volume as infection progresses (Tomback et al. 2001).

MPB is an aggressive bark beetle that attacks many different species of pine (Wood 1982). They are usually present in low numbers in a forest but can occasionally develop outbreaks. Outbreaks are driven by a combination of appropriate stand conditions and one or more triggers (Bentz 2005). Triggers can include warm temperatures which support greater MPB productivity and survival, or drought, which increases physiological stress resulting in lowered defenses of host trees (Safranyik and Carroll 2006). Most MPB outbreaks occur in lodgepole pine (*Pinus contorta* Douglas ex Louden), which is considered to be the most coevolved host of the beetle (Cole and Amman 1980). During non-outbreak phase, MPB are limited to stressed or diseased hosts (Safranyik and Carroll 2006). After a trigger has allowed populations to expand, the beetle's pheromone-mediated mass-attack strategy enables them to overcome the defenses of even vigorous trees (Raffa and Berryman 1983, Raffa 2001). *Trans*-verbenol and *exo*-brevicomin are attractant pheromones released by attacking MPB to elicit additional attacks by both sexes (Borden 1987). The simultaneous attacks of many beetles exhaust the preformed tree defenses so that successful colonization of the phloem is possible (Raffa and Berryman 1983). When enough beetles have attacked the tree, MPB release the anti-aggregation pheromone, verbenone (Pitman and Vite 1969). This deters the accumulation of additional

attacking beetles that would no longer be beneficial for mass attack, and that would increase intraspecific competition for the limited phloem resource (Raffa and Berryman 1983).

Historically, the high elevations where whitebark pine grows were not warm enough to sustain MPB outbreaks (Amman 1973, Safranyik 1978). Outbreaks that did occur in whitebark pine were limited to periods of drought and above average temperatures such as in the 1930's and 1970's (Bartos and Gibson 1990, Perkins and Swetnam 1996, Funiss and Renkin 2003). Because of recent warming in high elevations, MPB are now able to complete their development in one year in whitebark pine (Bentz and Schen-Langenheim 2007, Bentz et al. 2011). Previously, development in this cooler habitat required more than one year and sometimes two years (Amman 1973). A longer than one year life cycle can cause asynchronous emergence, interrupt adaptive seasonality and sometimes challenge vulnerable life stages to survive two winters –all of which decrease MPB survival (Logan and Powell 2001).

Not only is whitebark pine at risk of MPB attack because warming has allowed this beetle to move into high elevations, but whitebark pine also appear to be a highly preferred host of MPB.   For example, in mixed stands of whitebark and lodgepole pine, MPB prefer to attack whitebark pine (Six and Adams 2006, Bokino 2008) and attack whitebark pine at higher densities (Bokino 2008, Dooley and Six, in prep). Additionally, my research has shown that MPB are more productive in whitebark pine than in lodgepole pine (Chapter 2). Beyond differences in preference and productivity by host tree species, WPBR-infected whitebark pines are preferred over healthy whitebark pine (Six and Adams 2006, Bokino 2012). Additionally, the likelihood of MPB attack increases with increasing WPBR-infection severity (Six and Adams 2006). No one has examined how WPBR affects MPB productivity in whitebark pine, so the question remains: are WPBR-infected whitebark better, equivalent or poorer hosts for the beetle than healthy whitebark pine?

To address this gap in knowledge, I undertook a field study examining attack and emergence rates of beetles emerging from whitebark pines of differing WPBR infection severity levels. I also measured the size and sex ratios of MPB emerging from these trees. I measured size as a fitness proxy: larger beetles produce more and larger eggs (Amman and Cole 1983, McGhehey 1971), have increased flight capability (Thompson and Bennett 1971), and show higher survival rates during cold temperatures (Atkins 1967). Sex ratio is important because the proportion of females affects the number of eggs laid, and therefore, population growth. Sex ratio can be an indicator of host tree quality because in stressful developmental conditions sex ratios become skewed towards greater numbers of females per male (Cole and Amman 1983).

There are a number of factors that may influence beetle productivity in WPBR-infected vs. uninfected tree hosts. These include effects on levels of host tree defenses and changes in host nutritional quality. If highly infected trees have lower defenses, they should be easier to overwhelm and require fewer beetles to complete a mass attack (Cates and Alexander 1982, Raffa and Berryman 1983, Lorio 1993, Paine et al. 1997). Likewise, if WPBR-infected trees have altered nutrient qualities that positively affect beetle development, then these trees may be better hosts producing more, and/or larger beetles (Amman and Cole 1983, Chapman 1998). Conversely, if defenses are higher or nutrient quality lower in WPBR-infected hosts then they may support fewer, and/or smaller MPB.

Methods

Study Site

Tom Miner basin, in the Gallatin National Forest in Montana was chosen as the field site for this study because Hatala et al. (2009) identified this area as having both recent MPB activity, and extensive WPBR infection. The site (45°08'04" N, 111°08'04" W) was located in a north-south drainage situated on the side of a larger east-west trending basin, and had an

average elevation of 2507 m. The forest was composed of whitebark pine, lodgepole pine, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Forested areas were interspersed with meadows supporting diverse grasses and forbs. Within the forest, *Vaccinium scoparium* (Leiberg ex Coville) and *Vaccinium membranaceum* (Douglas ex Torr) dominated the understory.

Field Methods

Because this study examined the influence of WPBR infection severity on MPB productivity, it was important that the whitebark pine used in the study 1) displayed a range of WPBR infection severities from trees with no WPBR infection evident, to trees with high severity WPBR infection, and 2) were in a diameter class that would typically be infested by MPB (> 15cm, Cole and Amman 1969). The WPBR rating system developed by Six and Newcomb (2005) was used to rate individual trees to identify candidates for use in this study, and to evaluate an overall stand estimate of WPBR severity and incidence. Briefly, this system divides the tree's bole and crown into thirds (top, middle and bottom). Each third of the bole and crown are rated independently with 2 as the maximum score in any crown or bole third. Therefore, total ratings for a tree using this system can potentially range from 0 (no signs of WPBR infection) to 18 (complete infection) based on the sum of scores for independent assessments of the crown and the bole (Six and Newcomb 2005).

While 18 is the highest possible score using this system, trees usually die of WPBR infection by the time they reach a rating of 12 to 14 (Six and Newcomb 2005). Therefore, trees rating 12 were the most severely WPBR-infected trees that we chose to include in this study. I performed all rust ratings to eliminate inconsistencies among observers. I chose to stratify WPBR severity estimates into distinct bins spanning two rating classes. Each bin was separated

by one rating class. This ensured that each category actually represented substantially different infection severities. The WPBR rating bins used in this study were: 0, 2-3, 5-6, 8-9, and 11-12. Hereafter, I term these rating bins as WPBR infection categories 0, 1, 2, 3, 4, respectively.

I established three 10 m x 50 m belt transects following the Greater Yellowstone Network Whitebark Pine Monitoring Group (GYNWPM) protocol (GYNWPMWP 2011) to quantify overall WPBR incidence and severity, as well as whitebark pine mortality. I substituted the rapid rating system (Six and Newcomb 2005) in place of GYNWPM's WPBR rating system, which uses counts of cankers instead of percent area affected. The three transects were placed throughout the study site to estimate overall WPBR infection incidence and severity of the stand.

I located six whitebark pine > 19 cm in diameter at breast height (DBH) (1.4 m above the ground) in each WPBR infection category for a total of 30 trees. These trees were then baited with *trans*-verbenol and exo-brevicomin MPB tree baits (Synergy Semiochemicals Corp., Burnaby, BC, Canada) on 4 August 2010. On this date, two of the pre-selected study trees were already under mass attack, so they were not baited. Trees were monitored to gauge attack progression on 6 and 7 August 2010. MPB were present on the bark of a few trees, but no mass attacks had been initiated on the baited trees during these three days. Therefore, baits were left on the trees to ensure successful attacks. On 14 October 2010, baits were removed. Phloem and bark thickness may influence beetle attack density, as well as their productivity once in a tree (Amman and Cole 1980, Amman and Cole 1983). To account for this, I measured phloem and bark thickness at the time I set the baits by making small hatchet wounds on the east and west sides of each tree at breast height and measuring the width of these layers.

From 6 to 9 July, 2011, we drew two 25 cm by 55 cm rectangles centered at 1.4 m above the ground on the north and south sides of the study trees to delineate the two subsampling

areas which were later covered by emergence cages (described below). Subsampling the north and south sides of trees captures variability in attack density (Shepard 1965) and emergence within a tree due to random influences, and variability in pheromone signals, or thermal conditions caused by differential radiation. Within these subsampling areas, I counted and marked the number of entrance holes and estimated the number of holes created by woodpeckers (for an estimate of predation). Each entrance hole can be considered to represent a male/female pair although, occasionally, males will leave to locate new females or females fail to attract a mate. Some parents also re-emerge from their initial parent galleries in the fall, or the following spring and summer to attack a new tree (Safranyik and Linton 1985, Hansen and Bentz 2003).

After counting MPB entrance holes and woodpecker holes, emergence cages were stapled over each sampling area from 6 to 9 July 2010. Cages consisted of vinyl screen with the bottom folded into a funnel that was attached to the neck and bottle cap of a plastic soda bottle. A hole was made in the cap of the bottle into which was inserted a piece of surgical tubing with a piece of screen secured over the bottom of the tube. The cap and tube assembly could be easily removed to collect all insects that fell into the tube upon emergence from the tree. A piece of No Pest Strip© (Hot Shot, Madison, WI) was placed in each tube to kill all insects that emerged into the cage. While placing caging, I checked the development of MPB in nearby, non-study trees and found the majority of MPB to be larvae in the third and fourth instars. Therefore, when exit holes (no pitch, frass or boring dust extruding) were present at this time, I counted them before installing the cages and recorded them as parent re-emergence holes.

MPB and any other insects present in the cages were collected approximately every two weeks on the following dates: 28 July, 12 August, 24 August, 3 September and 17 September,

2011. Insects collected from cages were placed in 70% ethanol in separate vials for the north

and south sides of each tree for each collection date. A Lindgren funnel trap baited with a MPB

lure (trans-verbenol, exobrevicomin and the tree monterpene synergist, myrcene) (Synergy

Semiochemicals Corp., Burnaby, BC, Canada) was installed on 7 July 2011. I collected the

contents of the trap each time MPB were collected from the cages to roughly determine when

the peak flight(s) of MPB occurred at the site. Cages and the Lindgren trap were taken down,

and the study was concluded on 17 September 2011, after beetle emergence numbers were

consistently low for two consecutive collection dates (Figure 2).

Beetle size and sex ratio:

MPB collected from the Lindgren trap and the emergence cages were counted in the

lab. Beetles with broken body parts were counted by locating pronota. All complete beetles

were sexed under 30x magnification using the gender distinct anatomy of the seventh

abdominal tergite (Lyon 1958). The dorsum of each beetle was photographed under 30x

magnification with a Leica EZ4D microscope camera (Switzerland), and the Leica Application

Suite v. 2.0.0. All photographs were calibrated by photographing a 1 mm slide ruler to set the

measurement scale in Image J software (Rasband 2011). The pronotum was measured because

the width of this body part is a standard metric of MPB body size (McGhehey 1971, Amman

1982).

Statistical Analysis

Distributions of beetle attack density, emergence rate and beetle size were checked for

normality using the Holmes Shapiro-Wilk Normality Test. Variance inflation factors were

calculated to check for covariance between factors. To test for any possible interaction

between MPB emergence pattern and WPBR infection category, I produced a running graph

(not shown) with the number of beetles emerging out of each tree at each collection date with

individual tree coded by WPBR infection category. This graph showed no differences in emergence pattern between categories, so I performed all further analyses based on total number of beetles collected throughout the season, instead of analyzing by collection dates separately.

To test for differences in numbers of MPB entrance holes and numbers of emerging beetles between the north and south subsampling areas, I used a t-test for entrance holes, and a Mann-Whitney rank sum test for the number of emerging beetles (emergence data did not meet the assumptions of a parametric test). Because I found no differences in the number of entrance holes (south $\bar{x}$= 20.143, north $\bar{x}$= 20.286, t= -0.0563, df= 64, p= 0.955) or beetles collected (south median= 16, north median= 19, U= 326.000, t= 864.000, p= 0.283) between the subsampling areas, I added the north and south side values for each tree, and converted both counts into a per m^2 basis for further analysis.

A generalized linear model with a Poisson distribution and logarithmic link function was fit with maximum likelihood estimation to test for differences in attack density (entrance holes/m^2) between WPBR infection categories. The tree covariates DBH, bark thickness and phloem thickness were included during model fitting to test for their significant effects on MPB attack rate. The residuals of the Poisson model were overdispersed, so to correct the reported standard errors, I recalculated the variance as the mean times the dispersion parameter (Zuur et al. 2009). Attack model estimates were exponentiated to convert them to the normal scale, and estimate standard errors were calculated using the delta method. To elucidate if MPB attack density was influenced more by crown or bole infection, or crown and bole infections in different thirds of the tree, I calculated Pearson correlation coefficients between entrance rate and the WPBR infection scores of the following divisions: total crown, total bole, top crown, middle crown, bottom crown, top bole, middle bole and bottom bole.

To analyze the total number of beetles emerging from each WPBR category of tree, I modeled this value as emergence rate (# beetles emerging/m^2 /# entrance holes/m^2), because the number of brood emerging is dependent on the number of parent pairs forming galleries. The distribution of emergence rate best approximated a negative binomial distribution, so I used a generalized linear model with a negative binomial distribution and a log link. I modeled emergence rate by WPBR infection severity category by predicting number of beetles emerging/m^2 with number of entrance holes/m^2 entered as an offset variable. Additional tree covariates entered into the model during model fitting to check for their significant effects on emergence rate were: entrance holes/m^2 (Berryman 1976), average bark thickness, average phloem thickness, tree DBH, average number of woodpecker holes/m^2 and number of parent re-emergence holes/m^2. Emergence model estimates were exponentiated to convert them to the normal scale, and estimate standard errors were calculated using the delta method. I tested for differences in estimates between each WPBR infection category that were predicted by both the attack density and emergence rate models using Tukey's test for multiple comparisons.

To test for difference in beetle size (measured as pronotum width) between WPBR infection categories, I used a linear mixed effects model with individual tree from which the beetle emerged as a random factor. Additional covariates entered into the model to check for their respective effects on beetle size were: average phloem thickness, average bark thickness and DBH of the tree out of which the beetle emerged, the sex of the beetle, the subsampling side (north or south) from which the beetle emerged, the Julian date on which the beetle was collected, and the number of entrance holes in the immediate subsampling area (to serve as a measure of intraspecific competition). For all three models (attack density, emergence rate and body size), all biologically plausible variables and interactions between variables were entered, but only variables or interactions which showed significance, or marginal significance for

variables which are known to be important to MPB biology (i.e. DBH and phloem thickness, Cole and Amman 1969, Amman 1972, Cole and Amman 1980), were included in the final model.

For each tree, I calculated sex ratio (#females/#males) of all beetles that were measured for size, and tested for difference in sex ratio between WPBR infection categories using a one-way analysis of variance (ANOVA).

Results

WPBR Transects

Data from the three WPBR incidence and severity belt transects were pooled. Overall, 77% (119) of the 154 surveyed whitebark trees taller than 1.4 m were dead. Of the live whitebark trees (n= 35), 71% were infected with WPBR (n = 25), 29% were healthy (n = 10), and the overall WPBR infection severity was 5.6 (±0.7). The mean DBH of all live whitebark surveyed was 10.90 (±1.62) cm, whereas the mean DBH of WPBR-infected trees was 11.58 (±1.77) cm. The mean WPBR severity of WPBR-infected whitebark was 7.5 (±0.7) cm. Considering only live whitebark pine large enough for MPB attack (> 15 cm DBH), the mean DBH was 25.52 (±2.00) cm and mean WPBR severity was 6.7 (±1.5).

Attack Density

Numbers of entrance holes in north and south subsampling areas averaged for each WPBR category are shown in Table 1. Two category 4 trees were not successfully attacked even though they were baited. I modeled attack density (entrance holes/m^2) of all trees (n = 30), including the two non-attacked trees. I included these trees because their values are informative in that they may reflect a non-preference by MPB for category 4 trees. Results of the generalized linear model predicting attack density for all study trees showed that when compared with healthy, category 0 trees, only category 4 trees significantly differed in attack density (t = -2.783, df = 24, p = 0.0103) (Figure 1). Attacks on category 4 trees were approx. 58

(±13) % lower in number than on category 0 trees. This model also found that phloem thickness was a significant predictor of attack density (t = 2.802, df = 24, p = 0.0099); holding WPBR category constant, attack density increased by approx. 43 (±18)% with each 1 mm increase in phloem thickness. Multiple comparison tests revealed that category 4 trees had significantly lower attack rates than each of the other three categories, while attack rates on categories 0 through 3 trees did not differ from one another (Figure 1). Bark thickness and DBH were not significant predictors of attack density and were not included in the final model.

I also modeled attack densities using only attacked trees (n = 28) to determine if the lower attack density of the category 4 trees estimated by the previous model was simply an artifact of the zero values of the non-attacked trees, or if estimated attack density of attacked trees in category 4 was still lower than all other categories. In this model, category 4 attack densities were no longer significantly lower than the category 0 healthy trees at p < 0.05, but the difference approached significance (-1.817, df = 22, p = 0.0828). This model estimated that attack densities in category 4 trees were approx. 38 (±16) % lower than those in category 0 trees. Multiple comparison tests using Tukey's test showed that estimated MPB attack densities on category 4 trees were significantly lower than attack densities of trees in categories 1 and 2. No other comparisons between attack densities of trees in other WPBR categories showed any significant differences for the attacked trees-only model. This model also found phloem thickness to be a significant predictor of attack density (t = 3.363, df = 22, p = 0.0028); holding WPBR category constant, each 1 mm increase in phloem thickness elicited approx. 43 (±15) % more attacks/m^2. Similar to the attack model with all trees included, bark thickness and DBH were not significant predictors of attack density and were not included in the final model.

Attack density was more closely related to total WPBR bole score (Pearson correlation coefficient = -0.29, N = 30) than to total WPBR crown score (Pearson correlation coefficient = -

0.19, N = 30). Pearson correlation coefficients show that within each crown third, attack

densities were weakly negatively related to WPBR score (crown top = -0.13, crown middle = -

0.16, crown bottom = -0.20, N = 30). Within bole thirds, there was almost no correlation

between MPB attack density and WPBR score in the bottom bole third (Pearson correlation

coefficient = -0.01, N = 30) and weak correlation in the middle bole third (Pearson correlation

coefficient = -0.09, N = 30). The top bole third showed the strongest negative correlation

between attack density and WPBR score (Pearson correlation coefficient= -0.36, N=30) meaning

that as WPBR infection severity score of the top of the bole increased, MPB attack density

decreased.

Emergence of MPB

A total of 1234 beetles were collected from 28 attacked trees. The temporal pattern of

emergence of adult MPB throughout the season did not appear to differ between WPBR

categories (Figure 2). All WPBR categories show two peaks of emergence: one between 9 July

and 28 July (28 July collection) and one between 12 August and 24 August (24 August collection)

(Figure 2). These MPB emergence peaks matched peaks of beetles captured in the Lindgren

funnel trap (Figure 2), which captured a total of 3499 beetles over the study period.

The number of beetles collected from each subsampling area per tree, averaged for all

trees within each WPBR infection category is shown in Table 1. Boxplots showing the pooled

north and south subsample emergence rates for all trees within a WPBR category indicate that

category 4 (highly infected) trees had higher MPB emergence rates than trees in all other

categories, but also, that the variance of emergence rates among trees in this category was

much larger. These findings were confirmed by the generalized linear model which used WPBR

category and log(attack density) to predict beetle emergence rate. Emergence rate was related

to attack density in a negative exponential ($x^{-0.68 \pm 0.30}$) manner (t = -2.30, df = 22, p = 0.02). WPBR

category 4 was the only level of this variable that approached significance in this model (t = 1.945, df = 22, p = 0.052). The estimated emergence rate of MPB from category 4 trees was 233 (±101) % higher than from category 0 (healthy trees). Multiple comparison tests indicated that emergence rates did not differ between any category (Figure 3). The covariates parent re-emergence holes/m^2, woodpecker holes/m^2, tree DBH and bark thickness were not significant predictors of emergence rate and thus were not included in the final model.

Beetle Size

Out of the 1234 beetles collected from emergence cages, 1054 beetles were intact and could be sexed and measured for pronotum width. The average widths of pronota of male and female beetles emerging from north and south sides of trees by WPBR category are shown in Table 2. In addition to WPBR category, other variables that were significant predictors of beetle size in the linear mixed effects models were: Julian date on which the beetle was collected (t = -8.43, df = 1024, p < 0.001), sex of the beetle (t = -15.39, df = 1024, p < 0.001) and phloem thickness (bordered on significance, t = 1.82, df = 22, p = 0.083). The only WPBR category that was a significant predictor of beetle size was category 4 (t = 2.45, df = 22, p = 0.023). Holding sex, collection date and phloem thickness constant, beetles in category 4 trees were on average 0.06 (±0.03) mm larger than beetles emerging from category 0 trees. Holding all other variables constant, male MPB were estimated to be on average 0.15 (±0.01) mm smaller than female beetles. Each additional day into the emergence season, beetles were on average 0.01 (±0.00) mm smaller holding WPBR category, phloem thickness and sex constant. Each additional 1 mm increase in phloem thickness related to a 0.03 (±0.01) mm increase in pronotum width holding all other predictors constant.

Sex Ratio

MPB female to male sex ratios calculated for each tree grouped by WPBR infection category are shown in Figure 5. The average sex ratio of beetles emerging from category 4 trees was higher than for beetles in all other categories indicating there were more females per male. The variance in sex ratio for beetles from category 4 trees was also much higher. An ANOVA failed to detect significant differences in sex ratios of beetles emerging from the five WPBR categories of trees (F = 2.021, df = 4, p = 0.125).

Discussion

I found that WPBR infection severity influenced MPB attack density and marginally affected emergence numbers. MPB attack density was lower in highly WPBR-infected whitebark pines (category 4) than in all other WPBR infection categories. This pattern existed when the two un-attacked trees in category 4 were included in the model. This trend was also present (although not significant) when attack density was modeled without their inclusion. While not statistically significant, (likely because of the high within category variance in attack density for category 4 trees) (Figure 1), there was a trend of decreasing attack density with increasing WPBR severity (Figure 1, Table 1). Interestingly, while attack density was lowest in category 4 trees, the number of adult beetles emerging from these trees was the highest, and MPB emerging from these trees were the largest.

The lower attack density on severely WPBR-infected trees supports the hypothesis that diseased trees with weak vigor have lower defenses, thus requiring a smaller threshold number of beetles to successfully complete a mass attack (Paine et al. 1997). Correspondingly, the high emergence rates of MPB from trees in the highest WPBR infection category may have resulted from low intraspecific competition due to lower numbers of parents attacking these trees. In lodgepole pine, attack densities above $75/m^2$ (Raffa and Berryman 1983) or $97/m^2$ (Cole 1962) resulted in intraspecific competition among brood, which reduced the number of emerging

brood per attack. In this study, the significant negative effect of entrance hole density on emergence rate confirmed that intraspecific competition did affect brood success. Trees in categories 0-3 all had average attack densities greater than $100/m^2$. This density is at the highest end of observed MPB attack densities in lodgepole pine (Reid 1963, Raffa and Berryman 1983) and falls within the range where MPB mortality from intraspecific competition is expected (Raffa and Berryman 1983). In contrast, the MPB attack rates on category 4 trees were slightly lower than the optimal attack density which would produce the greatest emergence rate of brood beetles (based on data on MPB in lodgepole pine) (Raffa and Berryman 1983).

MPB emerging from highly WPBR-infected whitebark pine were significantly larger than those emerging from trees in other WPBR infection categories. Based on the relationship between MPB size and fecundity in lodgepole pine (McGhehey 1971), the increase in mean female size of beetles emerging from category 4 trees compared to category 1 trees would result in the production of approximately 15 more eggs/female. Larger beetle size from category 4 trees may be due to decreased intraspecific competition. Amman and Pace (1976) found that at lower attack densities, MPB adult size was greater due to decreased intraspecific competition. While these data suggest that reduced competition may have affected beetle size, when I entered attack density into the model to test for the effects of competition on body size, I found no significant effect of this variable on beetle size. However, the attack density data cannot inform of larval crowding during development. To truly get a measure of localized competition among larvae, I would need to have peeled the bark from trees to determine egg and larval densities (Cole 1973, Amman and Cole 1983). Therefore, it is unclear if beetles emerging out of WPBR category 4 trees were larger because of decreased competition, or increased nutritional content of phloem.

Beetle size and emergence rates may have been greater in category 4 trees because of increased nutrition due to the presence of *C. ribicola* mycelium in the phloem. WPBR cankers are surrounded by swollen, reddened bark. These areas remain living but contain mycelium of the fungus which has been found to extend approximately three cm beyond the margin of the swollen area (Ehrlich and Opie 1940). WPBR-infected tissues of *Pinus monticola* Douglas ex D. Don have increased concentrations of starches, which if ingested by MPB, would likely confer a nutritional benefit. However, benefits of eating *C. ribicola*-colonized phloem would only occur for beetles infesting severely infected whitebark pine with large bole cankers, and not all trees infected with WPBR (particularly those with only branch cankers). Additionally, any increase in phloem nutrients contributed by the presence of *C. ribicola* mycelium would be patchy in occurrence and would lead to high variability in MPB productivity within a tree, and among trees. This patchiness could explain the high variance I observed in attack rate, emergence rate and sex ratios in highly infected trees. Conversely, the nutritional content of the phloem of WPBR-infected trees may be lower if the rust affects this tree in a similar manner to how a related rust fungus, *Cronartium comandrae* Pk (Comandra blister rust), affects lodgepole pine. Lodgepole pine that was lightly to moderately infected with *C. comandrae* was significantly lower in nitrogen, sugars and starches (Nebecker et al. 1995) indicating that infection by this rust actually lowers the nutritional quality of infected trees. If this were the case for whitebark pine with WPBR, then lightly to moderately infected trees would be inferior to healthy trees for developing brood. Unfortunately, I cannot determine how nutrient quality of host trees is affected by WPBR from my study.

While I found no significant differences in MPB sex ratios between WPBR infection categories, category 4 trees tended to have high female to male sex ratios ($\bar{x}$ =3.5, Figure 5). Sex ratios of MPB from trees in this category had high variance and a low sample size (n=4 trees),

which may have affected our ability to detect significant differences. The female-skewed sex ratios in some category 4 trees may have been due to differential survival between males and females (Amman and Cole 1983). Male MPB have been show to have higher mortality rates than females when developing in thin, dry phloem (Cole et al. 1976). Category 4 trees had thinner phloem than trees in other categories. It has also been found that WPBR-infected whitebark have lower sapwood moisture content (Six and Adams 2006).

It was striking that despite the application of aggregation tree baits, two trees –both in the highest WPBR infection severity category- were not successfully attacked by MPB. Size of tree likely did not play a role as other trees of similar diameter were successfully attacked. It is possible that MPB simply did not recognize these trees as hosts because severely diseased trees may emit different monoterpene profiles than healthy trees. This phenomenon has been observed in lodgepole pine infected with Comandra rust (Nebecker 1995).   The attractant baits used in this study emit a MPB attractant pheromone blend, but do not include the synergistic monoterpenes which typically are emitted by the tree (Borden et al. 2008) (and commonly included in trap lures). If monoterpenes emitted by highly infected trees differ greatly from those emitted by healthy hosts, beetles may exhibit reduced attraction.

I found attack rate to be most related to high bole severity scores for the top third of the tree. The general progression of the disease in WPBR-infected trees is death of small, outer branches, followed by larger branches, and eventually top kill caused by girdling from bole cankers. Category 1 and 2 trees generally have more crown symptoms than bole symptoms. The incidence of bole cankers increases in trees in categories 3 and 4. Once infections have grown into the bole, it is conceivable that tree defenses against MPB are lower than in healthier trees because a majority of the photosynthetic engine for making defensive compounds (the crown) has been killed (Christiansen et al. 1987).

At this site, there were two main peaks in the MPB flight during the extended (>70 day) MPB emergence period in summer 2011. Based on beetles captured in the Lindgren trap, it appears that the first peak of beetles was larger than the second peak. This early, larger peak probably included the re-emerged parents that had overwintered in trees in 2009/2010. Similarly, it is likely that some of the beetles collected out of our cages during the first peak were re-emerged parents, but I have no way of determining their incidence in my dataset. The prolonged flight of MPB in this stand supports the finding that MPB do not emerge synchronously in high elevation whitebark pine stands (Bentz and Schen-Langenheim 2007, Schen-Langenheim 2010).

Overall, it appears that WPBR infection severity does not influence MPB emergence rate or size until infection is very advanced. It is unclear, however, if the increases in emergence rate and size from the severely WPBR-infected trees I observed is ecologically relevant because, as evidenced by the two baited category 4 trees that were not attacked, MPB might be reluctant to attack severely diseased trees. Two studies have reported increased likelihood of attack by MPB with increasing WPBR infection severity (Six and Adams 2007, Bokino and Tinker 2012). Six and Adams (2007) report mean WPBR infection severity of MPB-selected and not selected trees, so it is unclear if the range of WPBR-infected whitebark available for MPB selection included trees scoring 11 and higher on the WPBR infection scale. Bokino (2008) reports host selection probabilities for five categories of WPBR severity, but these categories are not directly comparable to the rapid rating system used in this study. Therefore, it is possible that MPB tree selection may be nonlinear, increasing with infection only to a point, after which it decreases.

If the reluctance of MPB to attack the two highly infected trees were an anomaly –and as has been suggested in other studies, MPB are actually more likely to attack highly infected trees- lower defensive capabilities and corresponding increases in beetle body size and

productivity could translate to rapidly expanding beetle populations in stands where infection levels are high. High MPB productivity out of severely WPBR-infected whitebark pine could exacerbate the decline of this species, and supports Larson's (2011) scenario of accelerated loss of whitebark pine due to multi-scale interactions between MPB and WPBR. While my results are not definitive, they indicate likelihood that highly WPBR-infected trees have lower defenses and higher MPB productivity. This indicates a potential synergism between an exotic fungus and a native insect whereby the effects of the two mortality agents combined may be greater than the effects of each individually.

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Table 1. Summary statistics (means (± standard errors)) for whitebark pine characteristics, white pine blister rust (WPBR) severity rating scores, mountain pine beetle (MPB) entrance holes, MPB parent re-emergence holes, woodpecker holes, and adult MPB collected from emergence cages by WPBR infection category. Infection categories range from 0 (not infected) to 4 (highly infected) (see text for description of how trees were binned by infection severity). N = 6 trees for all categories except category 4 where N = 4 because two trees were not successfully attacked.

WPBR infection category

	0	1	2	3	4
DBH (cm)	25.92(0.69)	28.83(1.40)	28.33(1.61)	27.17(2.65)	27.00(0.71)
Phloem (mm)	2.50(0.25)	2.42(0.15)	2.29(0.28)	2.21(0.33)	2.06(0.16)
Bark (mm)	3.67(0.33)	3.54(0.44)	4.04(0.56)	4.75(0.46)	5.19(0.19)
WPBR crown rating	0(0)	1.67(0.33)	2.83(0.17)	4.83(0.48)	6.75(0.85)
WPBR bole rating	0(0)	0.83(0.17)	2.67(0.21)	3.50(0.50)	4.75(0.63)
WPBR total rating	0(0)	2.50(0.22)	5.5(0.22)	8.33(0.21)	11.5(0.29)
Entrance holes:					
North	22.83(1.22)	21.00(1.10)	24.83(5.33)	19.17(4.08)	10.25(1.31)
south	17.33(3.97)	28.33(4.06)	22.83(3.63)	18.33(2.95)	10.75(5.36)
Parent re-emergence holes					
north	0.33(0.33)	0.33(0.21)	0.66(0.49)	1.17(0.65)	0.75(0.75)
south	0.66(0.49)	0.50(0.50)	0.17(0.17)	0.33(0.33)	1.50(0.65)
No. beetles collected					
north	19.00(3.04)	19(4.42)	21.83(7.46)	23.00(5.26)	34.75(16.86)
south	13.00(3.09)	30.67(12.99)	25.00(8.74)	14.50(4.58)	23.25(12.07)
Woodpecker holes					
north	18.67(4.13)	19.50(4.89)	30.83(5.39)	30.50(14.42)	27.00(17.84)
south	33.00(6.88)	22.67(7.22)	16.67(2.11)	24.50(15.11)	10.75(4.25)

Table 2. Means (±standard errors) of mountain pine beetle (MBP) pronotum widths for males and females emerging from north and south subsampling areas on 28 whitebark pine by white pine blister rust (WPBR) infection severity category. Infection categories range from 0 (not infected) to 4 (highly infected) (see text for description of how trees were binned by infection severity). N = 6 trees for all categories except category 4 where N = 4 because two trees were not successfully attacked.

WPBR Infection Category

	0	1	2	3	4
Females:					
north	2.00(0.02)	2.01(0.02)	2.02(0.02)	2.03(0.02)	2.06(0.01)
(N)	57	58	66	75	103
south	1.97(0.02)	2.00(0.01)	2.01(0.01)	1.99(0.03)	2.00(0.02)
(N)	48	103	103	46	53
Males:					
north	1.89(0.02)	1.90(0.03)	1.83(0.02)	1.83(0.03)	1.94(0.02)
(N)	38	27	42	38	37
south	1.75(0.03)	1.86(0.02)	1.86(0.02)	1.85(0.03)	1.90(0.03)
(N)	20	52	31	33	24

Figure 1. Attack density by white pine blister rust category. Boxplots of attack density (entrance holes/m^2) for 30 whitebark pine in five white pine blister rust categories representing trees ranging from no infection (category 0) to high infection severity (category 4). Diamonds indicate means, arrows indicate standard errors and circles represent outliers. Different letters denote significantly different means as estimated by the Poisson GLM attack density model. N for each category = 6.

Figure 2. Numbers of beetles collected through time. Top panel: Numbers of beetles collected from emergence cages on whitebark pine averaged by white pine blister rust category at five collections dates from 28 July to 17 September, 2011. Bottom panel: Number of beetles collected in a baited Lindgren funnel trap set near the center of the study site for the same period.

Figure 3. MPB emergence rate by white pine blister rust category. Boxplots of emergence rate (# entrance hole/m^2/#beetles collected/m^2) for 28 whitebark pine in five white pine blister rust categories representing trees ranging from no infection (category 0) to high infection severity (category 4). Diamonds indicate means, arrows indicate standard errors and circles represent outliers. Different letters denote significantly different means as estimated by the negative binomial GLM emergence model. Categories 0-3, N=6, category 4, N=4 (two baited category 4 trees were not attacked).

Figure 4. MPB size by white pine blister rust category. Boxplots of MPB pronotum widths of beetles emerging from 28 whitebark pine in five white pine blister rust categories representing trees ranging from no infection (category 0) to high infection severity (category 4). Diamonds indicate means, arrows indicate standard errors and circles represent outliers. Number of MPB for each category: 0=163, 1=240, 2=242, 3=192, 4=217.

Figure 5. MPB sex ratio by white pine blister rust category. Boxplots of sex ratio (#female/#male, calculated for each tree) of MPB emerging from 28 whitebark pine in five white pine blister rust categories representing trees ranging from no infection (category 0) to high infection severity (category 4). Diamonds indicate means, arrows indicate standard errors and circles represent outliers. Different letters denote significantly different means as calculated by a one way ANOVA. Categories 0-3, N=6, category 4, N=4 (two category 4 baited trees were not attacked).

white pine blister rust infection category

female to male sex ratio

white pine blister rust infection category