Geographic Variation in the Effect of Lodgepole Pine Characteristics on Mountain Pine Beetle Attacks and Productivity in British Columbia

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Abstract

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is the most destructive bark beetle in mature lodgepole pine (*Pinus contorta* Dougl. Ex Loud.var. *latifolia* Engelm.) forests in western Canada (Safranyik 1974). The current outbreak in British Columbia is the largest in recorded history (Westfall and Ebata 2008).

Host factors and historic climate affecting attack dynamics and pupal chamber productivity of MPB on lodgepole pine were examined in southern and north central BC. Trees were felled and intensively sampled in fourteen pine-leading stands. A between-subjects two-by-two factorial ANOVA was conducted to analyze the effects of historic climate and biogeoclimatic subzone on MPB attack and productivity parameters. The effect of dbh on mean gallery start densities was not different between regions, while mean pupal chamber density was significantly higher in areas of historically low climatic suitability than in areas with historically high climatic suitability.

Results indicate that north central trees are more suitable for pupal chamber production than southern. Lack of selection pressure in areas of low climatic suitability for mountain pine beetle may be the explanation for this relationship.

Keywords: Lodgepole pine, host effects, attack, brood production, pupal chamber production, mountain pine beetle, climatic suitability class, suitability, susceptibility, selection pressure

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1. Introduction

1.1 Background

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is the most destructive bark beetle in mature lodgepole pine (*Pinus contorta* Dougl. Ex Loud.var. *latifolia* Engelm.) forests in western Canada (Safranyik 1974, McMullen 1986) and the western United States (Wood 1963, Amman et al. 1977), and is generally considered the most destructive of all western forest insects (Furniss and Carolin 1977). On average, the mountain pine beetle annually affects 50,000 ha of forested lands in British Columbia (Wood and Unger 1996), although large epidemics occur periodically (Taylor et al. 2006). An estimated 41 million trees were killed in the 1983 outbreak, which affected areas totaling approximately 482,000 hectares (Wood et al. 1985). The current outbreak in BC is the largest in recorded history, and, as of 2007, about 10.3 million hectares had been infested to some extent (Westfall 2008).

At endemic populations the mountain pine beetle persists at low population levels in suppressed and dying trees (Rudinsky 1962, Safranyik 1988a). It is a poor competitor, which presumably restricts population growth under endemic circumstances (Rankin and Borden 1996, Safranyik et al. 1998). When environmental and forest conditions are right, however, mountain pine beetle populations may increase to epidemic levels (Amman 1978, Raffa 1988a), when beetles attack and kill mature, healthy lodgepole pine.

There has been a great deal of research on the population dynamics of the mountain pine beetle (Safranyik et al. 1974, Coulson 1979, Amman and Cole 1983, Berryman et al. 1985, Stock and Amman 1985, Raffa and Berryman 1986, Safranyik et al. 1999a). Most research was done in southern BC and the United States, but little is known about population dynamics outside the beetle's historic range. This is particularly true at more northerly latitudes and higher elevations where current range expansion is occurring in western North America.

Little research has been done on the geographic variation of mountain pine beetle populations, possibly because of the difficulty to coordinate research efforts over large geographic areas. For example, many studies have provided information on how stand and tree parameters affect mountain pine beetle attack densities (Amman and Pasek 1986, Raffa 1988b, Safranyik 1988b), reproductive success (Reid 1963, Amman and Bartos 1991), emergence levels (Amman 1972, Safranyik and Linton 1985) and beetle size (Rasmussen 1980, Bentz et al. 2001), but there is a deficiency in the literature on geographic variation regarding the relationship between tree size and attack and emergence parameters. Stock et al. (1984) found little genetic variation among beetles from different geographical locations, but other studies have suggested that genetic differences may indeed be significant (Anderson et al. 1979, Stock and Guenther 1979, Miller et al. 1997, Bentz et al. 1999). Bentz et al. (2001) investigated latitudinal variation of mountain pine beetle development in the United States, but no study has focused on regions as far north as north central BC Similarly, no previous study compares southern populations with those of north central BC Consequently, many aspects of the current infestation in central and north central BC are not well understood.

Geographical variation also exists in characteristics of the mountain pine beetle's primary host tree, lodgepole pine. The range of the lodgepole pine variety *latifolia*, the variety focused upon in this study and most commonly attacked by mountain pine beetle, extends along the Rocky Mountains from 40-60° north latitude. Due to the magnitude of the area that lodgepole pine inhabits, one would expect that there is some variation in the composition of trees across this range. Kim et al. (1988) has shown that ash, lignin, and holocellulose levels are negatively correlated with latitude, while alpha-cellulose had a positive correlation. Polysaccharide variation in lodgepole pine may also be influenced by climate and site conditions (Campbell et al. 1990). Monoterpene pattern-types of oleoresin from lodgepole pine also have been shown to differ significantly across its geographic range (Forrest 1980). Ying et al. (1984) provided further evidence for geographic variation in lodgepole pine, showing that site and provenance variables markedly affect the growth of the species. Such host differences could lead to differences in the insect-host interactions, and ultimately in beetle population dynamics.

There is a need for more information about how beetle populations are related to variation in host characteristics at high latitudes and altitudes. Population levels during the current epidemic are such that trees of a diameter much smaller than usual are being attacked and killed; therefore, the role of small diameter trees in these epidemics is of particular interest. Due to this current condition, it will be possible to quantify and compare gallery start densities, pupal chamber production and emergence of beetles from trees of a large range of diameters.

The current outbreak spans nearly the entire latitudinal range in British Columbia (from the U.S. border to just north of Fort St. John), allowing a comparison of southern and north central populations with respect to insect-tree interactions. No such comparison has been made previously. Increased knowledge of geographic variation of mountain pine beetle populations may aid in future management of the lodgepole pine resource in British Columbia, and potentially help to mitigate future outbreaks of the magnitude seen today.

1.2 Purpose and General Objectives

The purpose of this thesis is to increase our understanding of mountain pine beetle – lodgepole pine interactions, with particular reference to geographic variation during the epidemic population phase. The general objective of this research is to determine if there are significant differences in the insect – host interactions among differing ecological and latitudinal extents of the current outbreak, and if so, whether this is related to latitude and/or the fact that mountain pine beetle has not been in these systems historically.

I address three specific objectives in this thesis. In Chapter 2, I compare and contrast beetle attack dynamics in north central sites (Prince George) with that in southern sites (Kimberley) as a function of host characteristics (susceptibility). In Chapter 3, host suitability in relation to pupal chamber production for the two regions are compared and analyzed. In Chapter 4, I examine whether trees in areas of low historic climatic suitability (Carroll et al. 2004) for mountain pine beetle have significantly higher beetle production than those of high historic suitability. In Chapter 5, I synthesize the information from this research.

1.3 The Mountain Pine Beetle

The mountain pine beetle is usually univoltine, i.e., its life cycle is completed in one year. Two years may be required at north central latitudes and high elevations (Amman 1973, Safranyik 1978), and there may be two generations per year in warmer, more southerly latitudes at lower elevations (Reid 1962a). Like other bark beetles, the mountain pine beetle spends the vast majority of its life under the bark of its host tree, with only a few days outside while searching for a host. Beetles typically emerge and disperse to new hosts during the months of July and August, and it is the female beetles that select a host and attract males using aggregation pheromones to mate with (Safranyik 1988b).

After mating at the gallery entrance, the female begins constructing a vertical ovipositional gallery, which may be as long as 1.5 m in length (Reid 1962b). Although the average number of eggs laid is 60 per female, as many as 200 eggs have been observed in a single gallery (Reid 1962b). Egg density ranges from 2.4 to 4.2 eggs/cm, and eggs are usually more spaced at the start and end of a gallery (Reid 1962b, McGhehey 1971). Once the eggs hatch, the larvae mine at right angles from the egg gallery. The majority of the mountain pine beetle's life is spent in the larval stage, which has four instars. The larval stage is where the greatest mortality occurs (Amman and Cole 1983). At the end of the fourth instar, the mature larva creates a pupal chamber where pupation occurs. After 10-14 days pupae metamorphose to adults. These young adults are called teneral or callow adults. Before emergence, beetles engage in maturation feeding under the bark, and their exoskeleton hardens and becomes darker. On average, the female to male ratio is 1.6:1 (Reid 1962a). Females are usually larger than males.

1.3.1 Mountain Pine Beetle Geographic Distribution

The mountain pine beetle is native to North American pine forests, from northern Mexico to north central British Columbia, and from the Pacific Ocean east to the Black Hills of South Dakota (Wood 1982). Dispersal is generally relatively localized, and Safranyik et al. (1992) estimated that only 2.4% of beetles fly above the forest canopy, which is a prerequisite for long-range dispersal. Consequently, beetle populations are effectively separated by geographic and ecological barriers such as mountain ranges and discontinuous distribution of susceptible hosts.

1.3.2 Host-Insect Interactions

Economically, the most important hosts of the mountain pine beetle are ponderosa (*P. ponderosa* Dougl. ex P. & C. Laws), western white (*P. monticola* Dougl.), sugar (*P. lambertiana* Dougl.), and lodgepole pines (Amman and Cole 1983). Other hosts include Coulter (*P. coulteri* D. Don), whitebark (*P. albicaulis* Engelmann), limber (*P. flexilis* James), pinyon (*P. edulis* Engelmann), bristlecone (*P. aristata* Engelmann), and foxtail (*P. balfouriana* Greville and Balfour) pines (Wood 1963). Jack pine, *P. banksiana* Lamb., occurs outside of the range of the beetle, but it has been shown to be a suitable host (Cerezke 1995). Occasionally non-hosts such as Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), grand fir (*Abies grandis* (Dougl.) Lindl.), incense-cedar (*Libocedrus decurrens* Torr.) (Evenden et al. 1943) and white spruce may be attacked (Huber et al. 2009), but usually brood is not produced in these tree species.

The food source for mountain pine beetles is the nutrient-rich phloem between the outer bark and the cambium of the host tree, in addition to nutrients from the associated fungi (Six 2003). Consequently, phloem quality is an important factor affecting beetle productivity (Reid 1963, Safranyik and Jahren 1970, Amman and Pace 1976, Berryman 1976). Female beetles require bark (outer bark and phloem combined) at least 2.4 mm thick to develop (Safranyik 1971), and thicker bark usually results in larger, more productive beetles (Amman 1972, Rasmussen 1980). Diameter is also positively related to beetle survival and production (Reid 1963). Due to a positive relationship between diameter and phloem thickness, beetles prefer larger trees (Amman 1969, Shrimpton and Thompson 1985). There is also some evidence that monoterpene concentration in lodgepole pine increase with phloem thickness and diameter, e.g., Amman and Cole (1983) showed that β-phellandrene, β-pinene and αpinene concentration all increased with increasing phloem thickness (up to 5mm), and reached peak concentrations at diameters between 20-30 cm. Host selection is at least in part affected by chemical cues from the host and attacking beetles (Raffa and Berryman 1983, Borden 1989, Moeck and Simmons 1991, Miller and Borden 2000, Wallin and Raffa 2000, Raffa 2001). As a result of these factors, the largest diameter trees within a stand tend to be attacked first (Hopping and Beall 1948),

1.3.3 Population Dynamics

At any given point in time and space, mountain pine beetle populations[1] exist in four phases: the endemic, incipient, epidemic, and post-epidemic. During the endemic phase, beetles exist mainly in dead and dying trees, and the population is relatively static (Safranyik and Carroll 2006). However, more recent studies have found that populations may exist in such small numbers that not a single live large diameter tree may be successfully attacked (Safranyik and Carroll 2006).

Once large, healthy trees can be successfully mass attacked, the population is defined as "incipient" (Safranyik and Carroll 2006). In the incipient phase, the beetle population starts to increase due to increased host susceptibility (caused by drought, aging, high stem density, etc.) or due to an influx of beetles from neighboring areas. Safranyik et al. (1974) suggested that sustained increases in populations are associated with a combination of consecutive years of mild winters and warm, dry weather during the dispersal periods. Shrimpton and Thompson (1983) looked at several infested areas and found that in all cases, outbreaks were in areas of reduced tree growth.

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[1] In this paper, the term "population" refers to the local population, or number of beetles within approximately 100 m of any given point.

The onset of the epidemic phase is marked by a sustained, yearly, nonlinear increase in beetle populations. Small incipient patches coalesce and new patches appear in the surrounding stands (Safranyik and Carroll 2006). As compared to incipient populations, which are at a localized level, epidemics are characterized as being at a landscape level and are very resilient to abiotic factors which would regularly keep sub-epidemic populations in check.

The post-epidemic phase marks the collapse of the epidemic, and is caused by the exhaustion of resources, or an abiotic event such as an extreme cold period or a large-scale fire. The same type of trees attacked during an epidemic are attacked during the post-epidemic, but because of the low numbers of beetles many attacks are only partial (i.e., strip attacks and/or pitch outs), or the rate of accumulation of mass attacks is reduced (Safranyik and Carroll 2006).

1.3.4 Geographic Variation

Geographically isolated populations may be influenced by different biotic and abiotic factors, leading to differences in natural selection and co-evolution between the beetle and its primary host (Mitton and Sturgeon 1982). Lodgepole pine has a vast geographic range, and varies significantly among different populations. Both genetic and chemical variation has been documented (Forrest 1980, Kim et al. 1988, and Campbell et al. 1990). Given the importance of the host in the beetle's ecology, beetle and host populations could therefore be expected to co-vary significantly across the range of the mountain pine beetle.

Climatic differences in seasonal temperatures may be pronounced at different latitudes and altitudes, and play an important role in the synchrony and phenology of the beetle (Logan and Bentz 1999). As with all ectothermic organisms, mountain pine beetle growth, development and survival are influenced by ambient temperatures (Furniss and Carolin 1977, Safranyik 1978, Zaslavski 1988).

Bentz et al. (2001) found significant differences in beetle size and development rates between mountain pine beetle populations in southern Utah and central Idaho, and suggested that this was due to genetically based differences in the two populations. At a constant 21°C, beetles from northern parents (collected near Stanley, Idaho: 44°07'N, 114°51'W) emerged about 20 days earlier on average than beetles from southern latitudes (Panguich Lake, Utah: 37°30'30"N, 112°37'30"W). The median emergence time for the northern generation was 64 d, while the median for the southern generation was 82 d. The southern beetles had a median pronotal width of 2.3mm for males and 2.6mm for females, while the northern beetles were significantly smaller with median pronotal widths of 1.9mm and 2.1mm for males and females, respectively. Bentz et al. (2001) suggested that beetles in the north may be better adapted to cooler summer temperatures, decreasing the importance of temperature as the limiting factor for beetle survival and reproduction.

1.3.5 Beetle Development in Relation to Weather and Climate

A number of studies have demonstrated differences in beetle development related to weather and climate (Reid 1962a, Safranyik 1988b, Bentz and Mullins 1999, Logan and Bentz 1999, Logan and Powell 2001). Data from studies conducted at southern latitudes showed that the beetle's development and survival varies inversely with increases in elevation (Amman 1973, Amman et al. 1977, Safranyik et al. 1975). Amman et al. (1977) suggested that more research is needed to determine if an increase in latitude has the same effect on beetle development as an increase in elevation.

Temperature “extremes” are very important for larval development rates, population synchrony, and adaptive seasonality (Logan and Bentz 1999, Logan and Powell 2001). Adaptive seasonality refers to an ovipositional period that meets the temperature requirements allowing for an emergence time (adult stage) that is late enough in the summer to avoid lethal freezing temperatures, but still early enough for the next generation (larval stage) to develop cold hardiness before winter. At more southern latitudes the combination of drought and extremely hot summer days limits the abundance of the beetles (Logan 2001). Below average summer temperatures may be a limiting factor in both northern and southern regions (Safranyik 1978, Carroll et al. 2004, Logan and Powell 2004). In north central BC, the main limiting factor for beetle survival is cold winter temperatures (Amman and Cole 1983, Safranyik 1988).

Reid (1962a) reported that near Invermere BC, 12,000 degree-hours (500 degree-days above 10°C, which is equivalent to 896 degree-days above 5.6°C to compare with Safranyik (1978) discussed below) were required from the time of egg deposition to reach the teneral adult stage, but no comparable data were collected for mature adults. No diapause was detected. He also measured subcortical temperatures in relation to brood survival and reported that winter mortality was not a significant factor on his study sites (Reid 1963).

Safranyik (1978) summarized the effects of climate on the mountain pine beetle’s distribution and abundance, and concluded that of all the climatic variables, temperature is the most important limiting factor. Safranyik and Whitney (1985) studied beetles from southern BC, and reported that the optimal constant temperature for beetle development is between 24° and 27°C. At constant temperatures of 27°C and 24°C, 673 and 674 degree-days above 5.6°C respectively, were required for beetle development from egg to adult. At constant temperatures of 32 and 35°C, only 22 and 18% of eggs hatched, and none survived more than 10 d. At constant temperatures of 10 and 15°C, development stopped when larvae were fully developed. It is interesting to note that Amman and Cole (1983) were successful in rearing beetles from Southeastern Idaho to the adult stage at 15°C, and suggested that this may have been due to differences in the subpopulations between the two different geographic regions (Safranyik and Whitney 1985).

1.3.5.1 Effect Latitude and Elevation

Temperature decreases with an increase in latitude and/or elevation. Although factors such as topography and proximity to coastal areas may also have a profound effect on mean temperatures, latitude is the biggest factor (Geiger at al. 1965). According to Lambert's Cosine Law (Geiger et al. 1965) the direct energy of the sun varies with the cosine of the latitude due to the curved surface of the earth. The equatorial regions get direct solar radiation on up to 23.5° N/S latitude. The angle of the sun then gets increasingly oblique with latitude. A model involved with climate normals in British Columbia (Murphy 1996) suggests that for a one degree increase in latitude, there is a 1°C decrease in annual mean daily temperature. However, this is the average throughout the year, and may differ when only the growing season temperature means are considered.

Elevation also has a similar effect on temperature. Every 1°N latitude increase is roughly equivalent to 120 m increase in elevation while staying at the same latitude according to Hopkins Bioclimatic Law (Hopkins 1919). Safranyik (1978) found that this adjustment is remarkably similar to the equivalent range of mountain pine beetle in terms of altitudinal and latitudinal boundaries. For instance, near the northern limit of the beetle's range, the altitudinal limit for beetle survival is roughly 750 m above sea level, while at the southern most range the altitudinal limit is approximately 3650 m (Struble and Johnson 1955).

Carroll et al. (2004) has created a spatially explicit climatic suitability class (CSC) overlay for historic mountain pine beetle populations within British Columbia adapted from work done by Safranyik et al. (1975). This classification takes into account the historic weather periods, along with factors such as elevation, slope and aspect. In overlaying these historic data with current mountain pine beetle infestations, Carroll et al. (2004) reported an expansion in the range of benign habitats, as well as an increase (at an increasing rate) in the number of infestations since 1970 in previously climatically unsuitable habitats. They suggest that with the predicted warming trends associated with climate change, the range of mountain pine beetle will expand further north and to higher elevations than currently reported.

Chapters 2-4 have been written in the format of independent manuscripts intended for publication. Some duplication of information is therefore unavoidable.

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2. Lodgepole Pine Tree Characteristics Affecting Mountain Pine Beetle Attack: A Comparison Between North Central and Southern British Columbia

Abstract

Host factors affecting attack dynamics of the mountain pine beetle on lodgepole pine were examined in southern and north central British Columbia (BC) at the end of the outbreak cycle. Trees were felled and intensively sampled in three southern and five north central pine-leading stands. Results from the southern BC sites corresponded well with reports from the literature. Results from north central BC differed in that diameter did not significantly affect attack (gallery start) densities, and attacks extended much higher up the bole, particularly on small trees, than in southern BC. Overall attack densities were similar in the south and north, but on small diameter (<15 cm dbh) trees they were significantly higher in north central BC than in southern BC. Gallery start density declined with relative height in the south, but not in north central BC. A suggested explanation is that at exceptionally high population levels the beetles are not affected as much by diameter but instead are attacking whatever is available, whereas during the initial stages of the outbreak only the largest diameter trees were attacked.

Keywords: Lodgepole pine, host effects, mountain pine beetle, attack

2.1.Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is the most destructive bark beetle in mature lodgepole pine (*Pinus contorta* Dougl. Ex Loud.var. *latifolia* Engelm.) forests in western Canada (Safranyik 1974, McMullen 1986) and the western United States (Wood 1963, Amman et al. 1977). The current outbreak in British Columbia is the largest in recorded history, and as of 2007 about 10.3 million hectares had been infested to some extent (Westfall and Ebata 2008). The current outbreak spans most of the beetle's latitudinal range in British Columbia, allowing a comparison of southern and north central populations with respect to insect-tree interactions. No such comparison has been made previously.

When mountain pine beetles attack a host tree, they (in addition to ophiostomoid fungi) must kill all or part of the subcortical tissue beneath the bark of the tree to survive. This requires hundreds of beetles to "mass attack" the tree within a short time. Raffa and Berryman (1983) suggested that a minimum of 40 attacks per square meter of bark surface was needed to kill an average tree. In order to accomplish this, female pioneer beetles produce an aggregation pheromone when they bore into a suitable host. This pheromone attracts male and female beetles (Pitman et al. 1968, Billings et al. 1976), leading to a mass attack. Ryker and Yandell (1983) and Borden et al. (1986, 1987) describe this process in more detail.

The mechanism for host selection is debated in the literature. Some studies have shown that beetles land at random while flying through a forest (Hynum and Berryman 1980), while others suggest that chemical cues function as primary attraction (Moeck and Simmons 1991). Other studies have shown that visual stimuli are most important, where beetles have been attracted to large, dark silhouettes (Shepherd 1966) and vertically oriented cylinders (Billings et al. 1976). A more recent study suggests that random landing and primary attraction may both be important at different scales (Saint-Germain et al. 2007).

The relationship between mountain pine beetle attack parameters and host size has been studied intensively (Cole and Amman 1969, Safranyik and Jahren 1970, Amman and Cole 1983). There is considerable evidence to suggest that during epidemics the largest trees in a stand are selected first (Hopping and Beall 1948, Cole and Amman 1969, Klein et al. 1973; Raffa 1988a, Safranyik 1988a). Another factor that has been found to be important in host selection by the mountain pine beetle is the growth rate of the host. Several studies have shown that slow-growing trees are more susceptible to beetle infestation than fast-growing trees (Mitchell et al. 1983, Shrimpton and Thomson 1983, Hard 1985). In related species, measurements of the mean basal area index (Doak 2004) and the mean cumulative growth (Bleiker et al. 2003) have been used to show that hosts are more susceptible to spruce beetle, *Dendroctonus rufipennis* Kirby, and western balsam bark beetle, *Dryocoetes confusus* Swaine respectively, when growth has slowed. Studies focusing on the relationship between growth rates and phloem thickness (Shrimpton and Thomson 1985) have found that the best predictor of phloem thickness was the basal area increment.

Attack density is partially influenced by bark roughness. Shepherd (1965) showed that attacking beetles require physical aspects of rough bark such as bark scales, crevices, and fissures as points to aid in initial boring into the bark. Safranyik (1971) showed that the number of potential boring points was higher in the rough bark of older, larger trees. Evidence from these studies suggests that older, larger trees with rougher bark usually have higher gallery start densities.

In the area of the bole below the crown, attack densities are usually higher on the north than the south aspect (Reid 1963, Shepherd 1965, Safranyik 1971). This is due to increased light intensity and higher temperature on the south aspect during the beetle's peak flight, which occurs mainly in the afternoon on sunny days during the months of July and August (Reid 1962). Shepherd (1966) suggested that increased light intensity and high bark temperature stimulate beetles to continue flying.

Attack density has also been shown to have an inverse relationship with attack height. Reid (1963) found that attack density was greatest at the base of the tree and decreased with height. This trend was also reported by Shepherd (1965), Safranyik (1968) and Klein et al. (1978). Shepherd (1965) suggested that the greatest source of population variance was due to changes in attack density with tree height. Safranyik investigated several methods for measuring attack density and emergence levels accurately (1968, 1988a). He recommended that sampling should be done at multiple levels throughout the attacked height along the bole rather than just at dbh due to a vertical gradient in both tree and beetle parameters.

The influences of these tree characteristics may vary considerably with geographic location. The mountain pine beetle is native to North American pine forests from northern Mexico to north central British Columbia, and from the Pacific Ocean east to the Black Hills of South Dakota (Wood 1982). Due to the magnitude of the area that lodgepole pine inhabits, it is likely that there is some variation in the chemical composition of trees across this range. Campbell et al. (1990) reported that variation in polysaccharide levels of lodgepole pine may be influenced by site and climate conditions. Kim et al. (1988) showed that ash, lignin, and holocellulose levels were negatively correlated with latitude, while alpha-cellulose was positively correlated. Monoterpene pattern-types of oleoresin from lodgepole pine also differed significantly across its geographic range (Forrest 1980). Such host differences could lead to differences in the insect-host interactions, and ultimately in beetle population dynamics.

2.2. General Objective

The objective of this research was to investigate potential differences in attack dynamics in lodgepole pine stands with similar infestation characteristics in north central and southern British Columbia. Specifically, I measured how tree parameters (e.g., diameter at breast height (dbh = 1.3 m), bark roughness) affected attack parameters (e.g., gallery start density, relative attack height, absolute attack height, and maximum attack height) on lodgepole pine. Data from southern stands allowed me to compare parameters both to literature information and to data from north central stands.

2.3. Methods

2.3.1. Study Sites

Sampling for this study was done in two regions during the summer of 2005. north central sites were selected in the Prince George Forest District in north-central British Columbia (approx. 53.9° N, 123.5°W), in the dry, warm subzone of the Sub-Boreal Spruce biogeoclimatic zone (Meidinger et al. 1991). Southern sites were selected in the Rocky Mountain Forest District in southeastern B.C. (approx. 49.5°N, 116.2°W) in the dry, mild subzone of the Engelmann Spruce-Subalpine Fir biogeoclimatic zone (Coupé et al. 1991). The southern sites were at a higher elevation than those in the north to keep climatic influences similar in spite of the latitudinal difference, in accordance with Hopkins Bioclimatic Law (Hopkins 1919). This law states that every 1° increase in latitude is roughly equivalent to 120 m increase in elevation.

2.3.2. Stand Selection

Five stands in the north and three in the south were sampled. In both north central and southern regions, the stands selected for sampling were lodgepole pine-leading 80 years old or older. I attempted to select stands with similar density and species composition to minimize differences among sites. The species composition for each region is shown in Table 1.

Table 1. Tree species composition % in study plots in two forest districts in British Columbia (Pl=lodgepole pine, Sx=white spruce, Fd=Douglas-fir, Bp=paper birch, Lw=western larch, Pw=whitebark pine).

Forest District	Pl	Sx	Fd	Bp	Lw	Pw
Prince George	84.0	14.7	1.1	0.2	-	-
Rocky Mountain	94.2	-	3.2	-	1.1	1.4

All stands were at least 10 hectares in area and a minimum of 1 km apart. Stands were selected in areas in which the mountain pine beetle epidemic was assumed to be in the final stages, and therefore no significant additional tree mortality was expected to occur in the stand. The five north central stands were at elevations ranging from 870 m – 950 m, while the southern stands ranged in elevation from 1525 m – 1835 m (Table 2). Mean age of the trees in the north central stands ranged from 89-148 years, and for southern stands this range was 103-112 years. Stand densities and species compositions varied, but were considered comparable among regions (Table 2).

A minimum of eight randomly selected, variable-radius plots per stand were surveyed using a prism with a basal area factor (BAF) of 4. A baseline was established at a randomly selected angle from a point of commencement. Transects off the baseline were then put in at randomly selected distances by selecting numbers between 80 and 150 m from a random number table. In each plot, tree species, diameter at breast height (dbh), and attack status [unattacked, current attacks, and old attacks (beetles had already emerged)] were recorded for each tree over 7.5 cm dbh.

Table 2. Summary data for the five north central and three southern stands sampled in 2005. (Björklund, unpublished data).

*Stands with no current attacks recorded

**Percent mortality is the % killed of available lodgepole pine in the stand.

Forest District	UTM Zone	Easting	Northing	Elevation (m)	Stand Density (trees/ha)	# Plots	# Trees	Mean Age (yrs)	Mean Dbh (cm)	Mean Height (m)	% Pine	%** Mortality
Prince George	10	470781	5954686	950	2571	11	147	113	21.5	21.0	75	45
Prince George*	10	473990	5958146	870	1942	11	76	132	23.0	21.2	79	61
Prince George*	10	469617	5963807	876	1976	10	114	89	18.6	20.0	97	43
Prince George	10	454912	5921661	898	1760	10	95	148	19.5	18.6	82	86
Prince George	10	453836	5920708	938	1400	10	98	146	20.5	20.8	88	67
Rocky Mountain	11	554894	5496659	1551	1006	8	67	112	22.3	16.8	91	80
Rocky Mountain	11	557322	5499133	1835	2162	10	110	103	17.5	16.5	92	41
Rocky Mountain	11	556843	5499053	1525	1584	10	100	109	19.8	21.9	99	43

2.3.3. Felled Tree Selection

At each plot, a minimum of two trees (old attacks) were selected and felled for intensive sampling. To maintain an equal representation of diameters, at least six trees from each of the following five diameter classes were selected from each stand if available: <15 cm, 15-19 cm, 20-24 cm, 25-29 cm, and >30 cm. If the desired tree size was not available from within the plot, the closest tree to the plot center in the desired diameter class was felled. Trees selected for intensive sampling were at least 50 m from edges of stands, lakes, or any open area to minimize edge effects. At least one dominant or co-dominant tree was selected from within the plot so that an age count could be recorded from the stump.

2.3.4. Intensive Sampling

A minimum of thirty successfully attacked trees were felled for intensive sampling of attack parameters in each stand. Attack height was measured on each felled tree, and was defined as the distance from the base of the tree to the highest pitch tube and/or gallery start. The attacked portion was cut into 3 equal length segments, and the diameter at the midpoint of each segment was measured. Sampling was conducted in two 15x30 cm rectangles (Safranyik 1968) on the north and south aspect, respectively, at the midpoint of each segment. This made it possible to also calculate the height above ground of each sampling point from the overall attack height. Bark roughness was subjectively classified in one of five categories: extremely smooth, smooth, medium, rough, extremely rough. Gallery start density was obtained by peeling off the outer bark to reveal each gallery and its starting point, and this number was multiplied by 22.22 to obtain density per square meter. (All gallery starts were counted regardless of whether successful or unsuccessful).

Mean gallery start density was calculated for each tree from the segment means. The gallery start total for each tree was calculated by multiplying the mean gallery start density by the total surface area of the attacked portion of the bole.

2.3.5. Data Analysis

A linear regression was conducted to analyze the relationship between mean gallery start density and dbh for both north and south regions. Homogeneity of variance was tested using a two-sample Kolmogorov-Smirnov test ($P = .106$). A one-way ANOVA was used to test for between-region differences.

One-way and two-way ANOVAs were used to analyze the effect of bark roughness on gallery start density as well as the between-region differences. To test for a difference in mean gallery starts between segments, a between subjects one-way ANOVA was used. The between-region differences in attack height were tested using a two-way ANOVA, with dbh class and maximum attack height as fixed factors. A two-way ANOVA was used in determining the significance in the difference between the effect of dbh on gallery start density between regions.

A linear regression was used to analyze the relationship between mean gallery start density and absolute height above ground for both north and south regions. Homogeneity of variance was tested using a Mann-Whitney U test, in which the assumption was not met ($P = .005$). However, after a logarithmic transformation the assumption was met ($P = .270$).

Linear regressions were used to analyze the relationship between dbh and maximum attack height, and a two-way ANOVA was used to analyze the between-region comparisons.

Significant ANOVA's were followed up by Tukey's multiple comparisons tests. Variables were assessed for normality using histograms and scatter plots. The level of significance was set at 0.05 for all statistical tests. All data were analyzed using SPSS 13.0 (SPSS Inc., Chicago, IL, USA). All graphs were created using SigmaPlot 9.0 (Systat Software Inc., Port Richmond, CA, USA).

2.4 Results

2.4.1 Stand-level Mortality

Percent mortality from the stand data was compiled and found to be similar at the stand level and by diameter class between the north central and southern sites (Björklund, unpublished data). The percentage of beetle-killed pine in the north central sites was 60%, compared to 54% in the south (Table 2).

2.4.2 Effect of Tree Characteristics on Gallery Start Density

2.4.2.1 Effect of Dbh on Gallery Start Density

The relationship between dbh and mean gallery start density within the tree was not significant for the north central sites ($R^2 = 0.014$, $P = 0.800$). Square root or logarithmic transformations did not affect this lack of significance. There was a positive relationship between dbh and mean gallery start density in the southern sites ($R^2 = 0.296$, $P < 0.001$) (Figure 1).

Absolute diameter, i.e., the diameter at the height of sampling, had a very similar relationship as diameter at breast height with mean gallery start density. There was no relationship between absolute diameter and mean gallery start density within the tree segment in north central sites ($R^2 = 0.000$, $P = 0.765$) but a positive relationship existed in southern sites ($R^2 = 0.21$, $P < 0.001$).

Mean ± SE gallery start density for all tree sizes, with all sampling heights and aspects combined was 70 ± 2.58 /m^2 in the north and 66 ± 3.64 /m^2 in the south and did not differ significantly between regions (*F* = 0.711, df=1, 261, *P* = 0.400). The effect of dbh on mean gallery start densities was also not different between regions (*F* = 0.013, df=1, 253, *P* = 0.910), although there were significant regional differences in two of the five diameter classes (Figure 2). A Tukey's post hoc test showed that the <15cm dbh class was significantly different from all other dbh classes (*P* < 0.001, SE = 6.17).

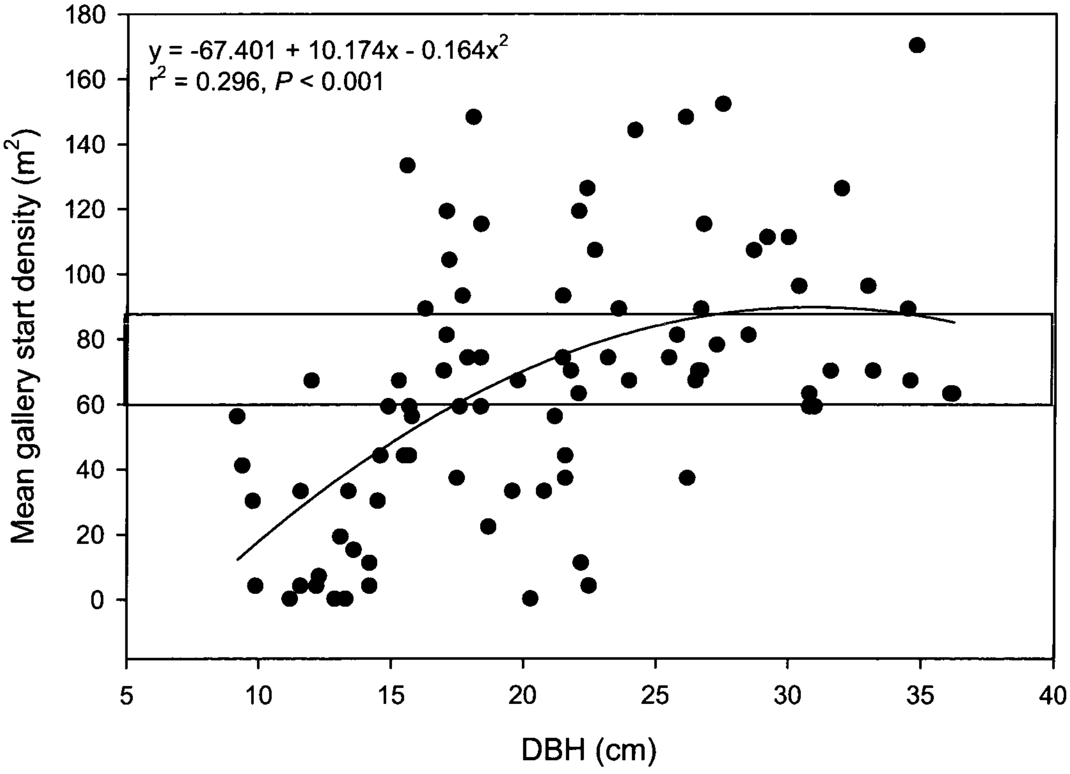

Figure 1. Relationship between diameter at breast height and mean gallery start density for southern sites. Area between horizontal lines represents optimum attack density, from 60/m^2 (Raffa and Berryman 1983) to 75-85/m^2 (Reid 1963).

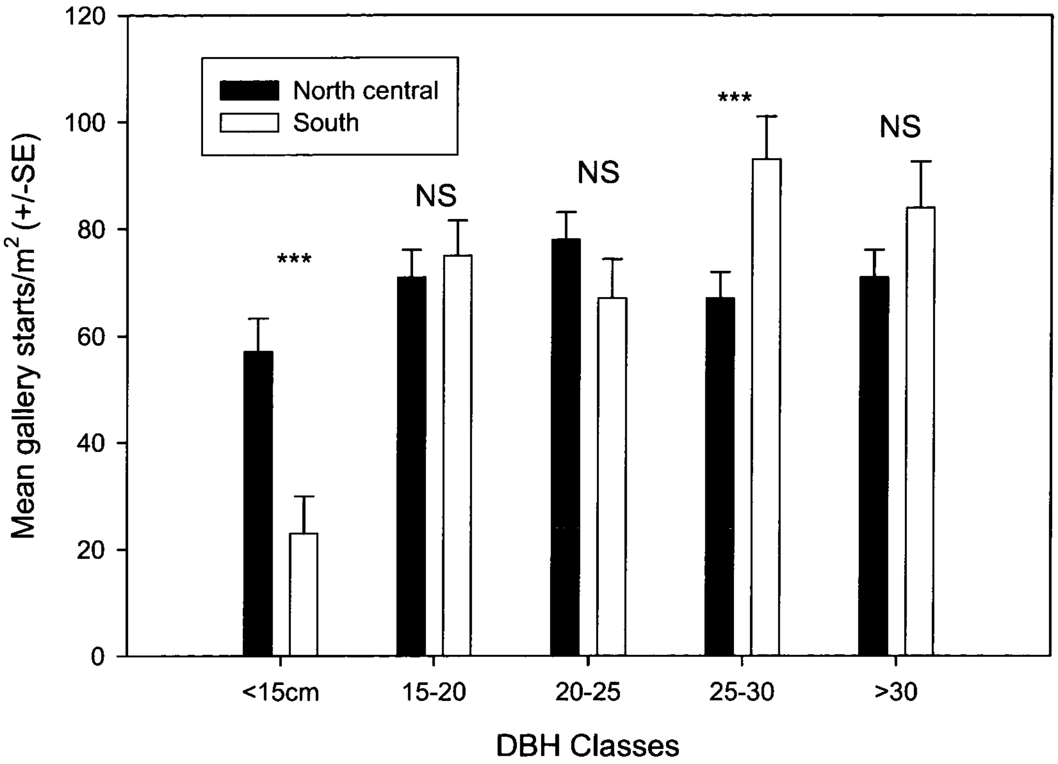

Figure 2. Mean mountain pine beetle gallery densities by diameter class on lodgepole pine trees in southern and north central British Columbia. NS = not significantly different, *** = significantly different at $P < 0.001$. Vertical lines represent standard error.

2.4.2.2 Effect of Bark Roughness on Gallery Start Density

The majority of lower tree segments were classified as having “moderate” roughness. The “extremely smooth” or “extremely rough” categories had very high variation due to small sample sizes (Figure 3), and were therefore included with the smooth and rough categories, respectively, for analysis. As expected, bark generally was rougher at the lower portion of the bole, becoming smoother with height. This pattern was similar between north and south aspects, so aspects were pooled for the analysis.

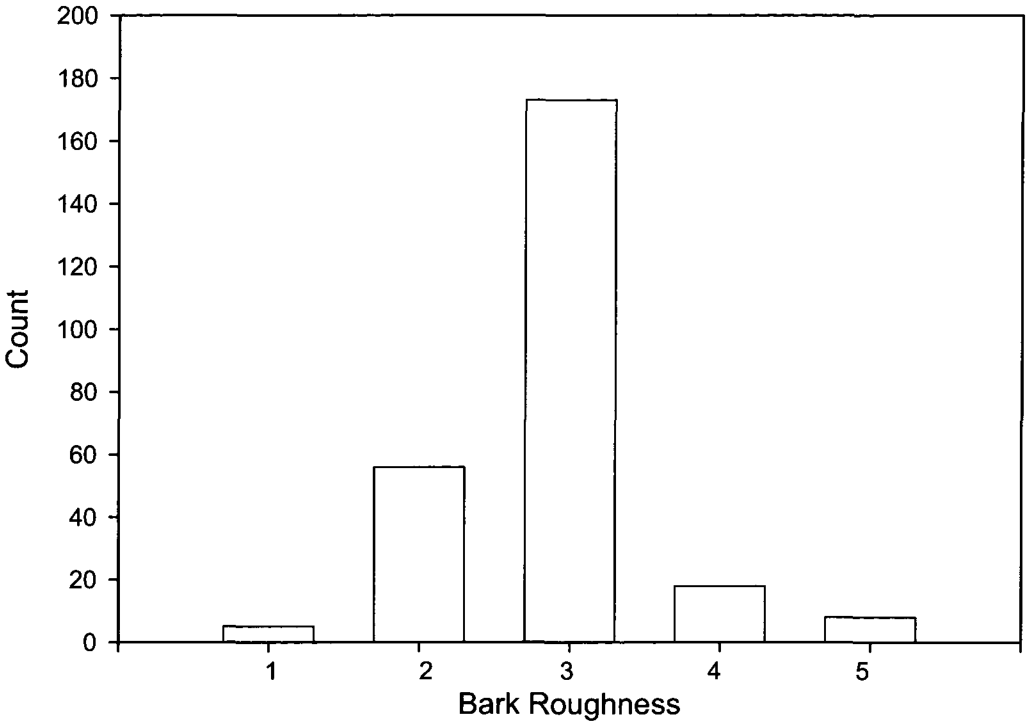

Figure 3. Distribution of bark roughness categories for the lower segment of all trees from both regions (1 = extremely smooth, 5 = extremely rough).

Mean gallery start density within a tree increased significantly with increased bark roughness for southern trees (*F*= 4.11, df=2, 70, *P* < 0.05), but not for north central trees (*F* = 2.34, df=2, 171, *P*= 0.099) (Figure 4). Pairwise comparisons among means revealed that for southern trees the difference was not significant between smooth and moderate bark (Tukey's HSD (Honestly Significantly Different) test, *P* = 0.776, SE = 9.07), but was significant between smooth and rough (*P* = 0.015, SE = 15.9) and between moderate and rough (*P* = 0.033, SE = 14.6).

When analyzed between regions, the effect of bark roughness on mean attack density on a tree was significant (*F* = 5.35, df=2, 254, $P<0.05$), as was the effect of region (*F* = 18.59, df=1, 254, $P<0.001$) (Figure 4), but there was no significant bark roughness by region interaction (*F* = 1.70, df=2, 254, $P = 0.185$). A Tukey's post hoc multiple comparisons test showed that all three bark roughness classes differed significantly from one another when dbh classes were pooled.

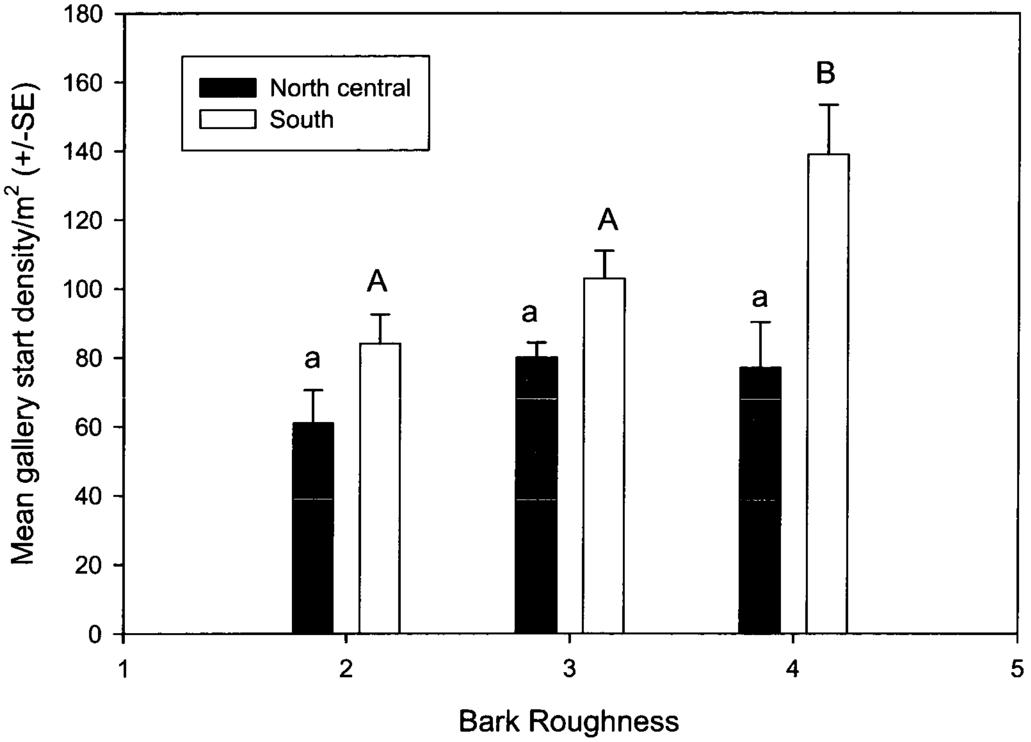

Figure 4. Difference in the effect of bark roughness on gallery start density between north central and southern BC (2=smooth, 3=moderate, 4= rough). Bars within each region followed by the same letter are not significantly different ($P < 0.001$). Vertical lines represent standard error.

2.4.2.3 Relationship Between Relative Height and Gallery Start Density

Mean gallery start densities were significantly higher on the lowest segment of intensively sampled trees, decreasing at the middle segment and more so at the upper segments (Figure 5).

The one-way ANOVA showed that in the north, mean gallery start densities differed significantly among segments ($F = 6.34$, df=2,522, $P<0.01$). This was also the case for the south ($F = 34.98$, df=2,261, $P<0.001$).

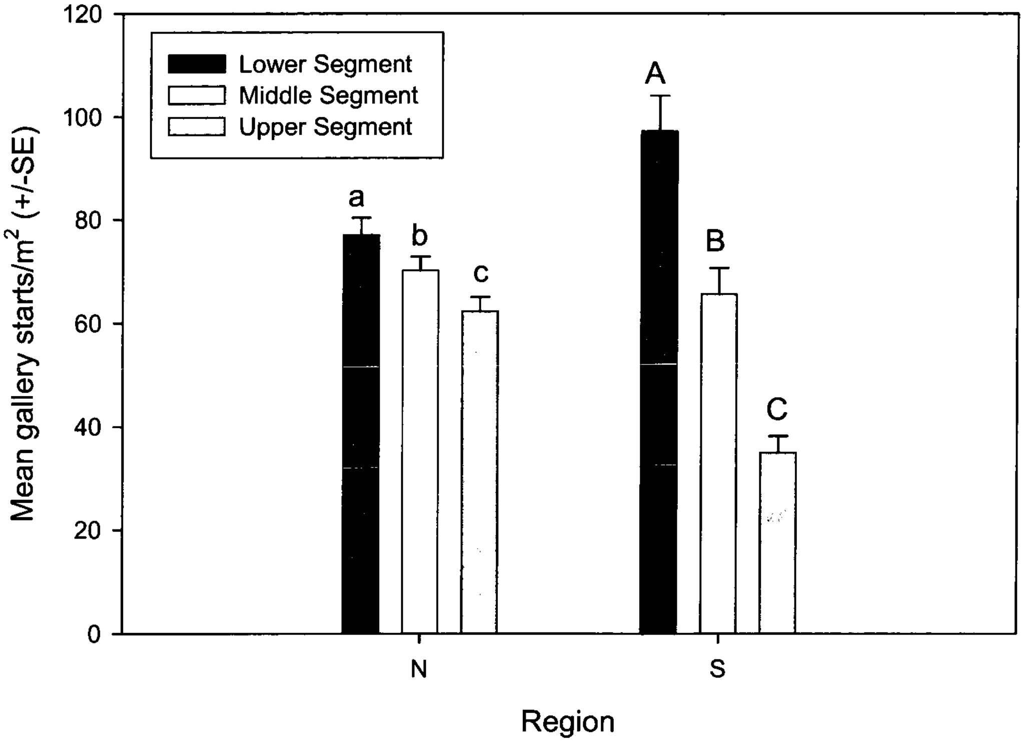

Figure 5. Mean gallery start densities for the lower, middle, and upper segments of attacked trees in the southern and north central regions. Bars within each region followed by a different letter are significantly different ($P < 0.001$). Vertical lines represent standard error.

A two-way ANOVA with region and relative height as fixed factors showed no difference between regions ($F = 1.48$, df=1,783, P=0.224), but a significant difference for relative height ($F = 47.69$, df=2,783, P<0.001). There was also a significant region by relative height interaction ($F = 18.09$, df=2,783, P<0.001).

2.4.2.4 Relationship Between Absolute Height and Gallery Start Density

A logarithmic transformation was used on the relationship between absolute height and gallery start density to satisfy the assumption of homogeneity of variance. The relationship was not significant for either region (F= 0.346, df=1, 502, $P = 0.557$, R^2=.001 and F= 1.164, df=1, 231, $P = 0.282$, R^2=.005 for north central and southern sites, respectively). Separating trees out by diameter class did not improve this relationship.

2.4.2.5 Relationship Between Maximum Attack Height and Dbh

Maximum attack height significantly increased with increasing dbh for both north central ($R^2 = 0.68$, $P < 0.001$) and southern sites ($R^2 = 0.69$, $P < 0.001$) (Figure 6). A 2-way ANOVA showed that the effect of region was significant ($F = 166.11$, df=1, 253, $P < 0.001$), and the average attack height difference was about 5m (Figure 7). The effect of dbh class ($F = 114.09$, df=4, 253, $P < 0.001$). The interaction effect of region and dbh class was not significant ($F = 0.27$, df=4, 253, $P = 0.898$). A Tukey's post hoc test showed that the mean attack height for all diameter classes was significantly higher in the north central region.

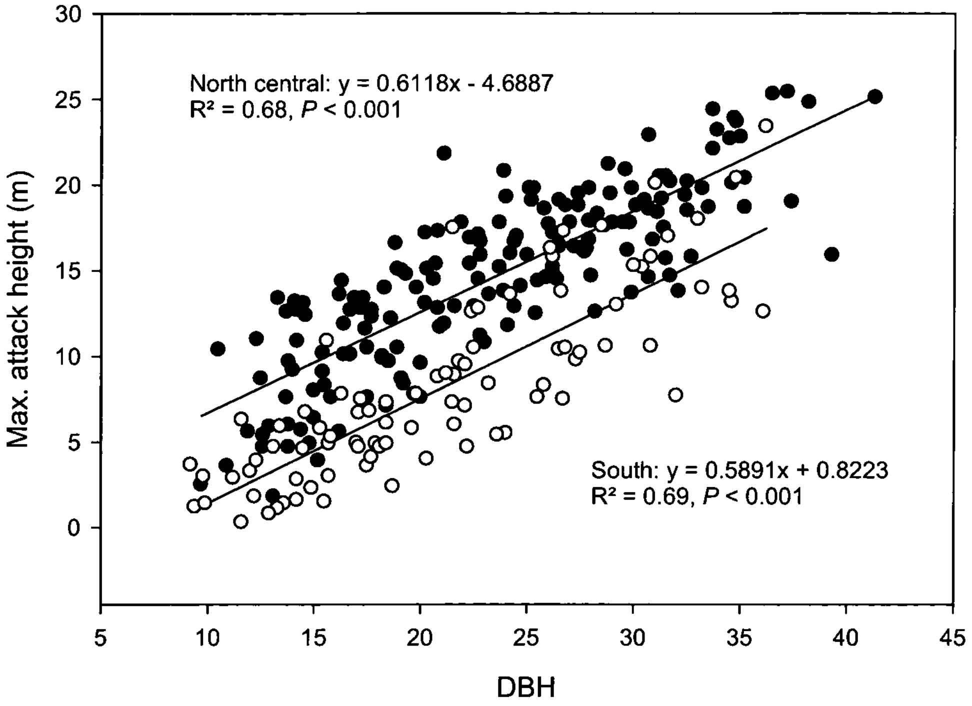

Figure 6. Relationship between maximum attack height and diameter at breast height on mountain pine beetle-attacked lodgepole pine trees in southern and north central British Columbia. Circles filled in black represent north central trees while open circles represent southern trees.

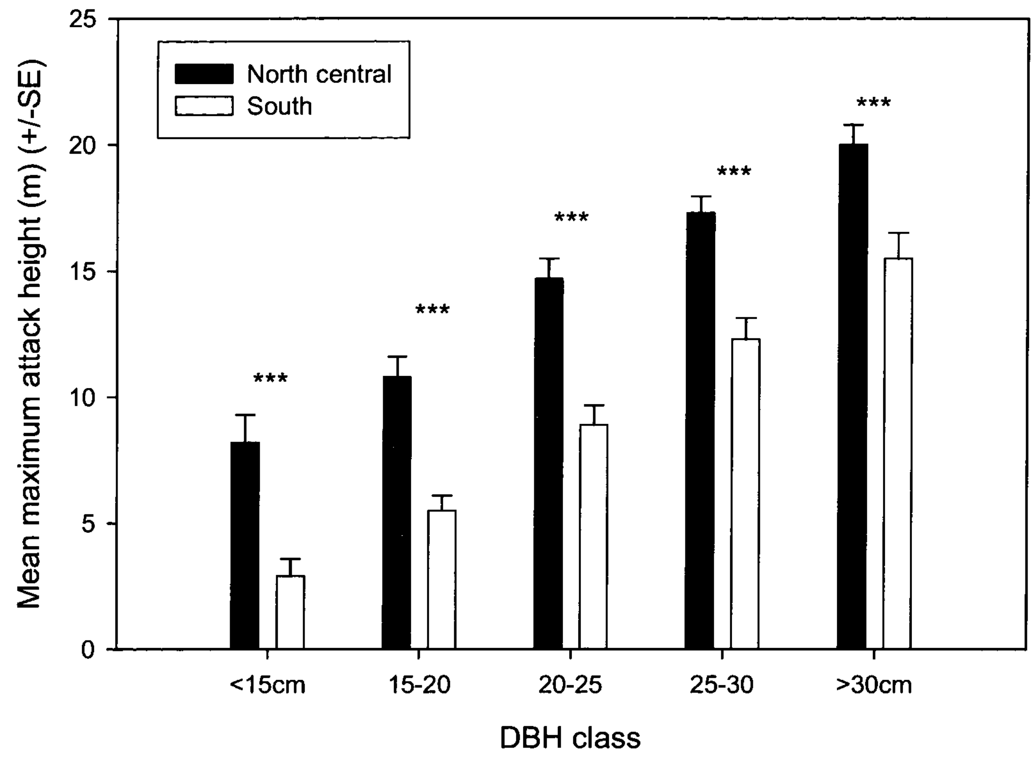

Figure 7. Mean attack height differences on mountain pine beetle-attacked lodgepole pine trees in southern and north central British Columbia (grouped by diameter class). ***= north significantly different from south within diameter class at $P < 0.001$. Vertical lines represent standard error.

2.5 Discussion

2.5.1 Stand Information

The landscape area affected by mountain pine beetle is much larger around the north central sites, but the local population levels impacting a given stand are probably very similar. This is supported by the fact that percent mortality at the stand level differed by only 4% between the two regions. In a study on another eruptive bark beetle, *D. rufipennis*, Wallin and Raffa (2004) found heritable traits relating to host-selection behavior within populations during outbreaks. Beetles from epidemic populations were more aggressive than those from endemic populations, but only in the presence of additional beetles. The size of the epidemics in their study was not exactly the same (populations were taken from different outbreaks in Alaska, Yukon, and Utah), but beetles from outbreak populations had more similar host selection behavior to other outbreak beetles than to beetles from endemic levels.

A similar relationship is likely for the mountain pine beetle, suggesting that differences in host selection behavior between the north central and southern sites in my study are unlikely to be due to overall regional population sizes. This is supported by Björklund and Lindgren (unpublished data), which showed that there was no difference in the percent mortality as related to median dbh between the north central and southern sites in this study.

2.5.2 Effect of Dbh on Gallery Start Density

Gallery start densities for trees in the southern region were similar to that of previous studies from southern BC (Safranyik 1968, 1988b) and other southern latitudes (Cole and Amman 1980, Rasmussen 1980), indicating that the stands I sampled were representative of typical epidemic conditions as described in the literature. An infestation rate of approximately 130 females/m^2 of bark surface is a density commonly observed in the field during epidemics (Cole and Amman 1980). Other results from studies done at more southern latitudes have reported mean gallery start densities of 104-113/m^2 (Rasmussen 1980) and 103/m^2 (Safranyik 1988a) during epidemics. On average, the optimum gallery start density for pupal chamber production is from 60/m^2 in Northeast Oregon (Raffa and Berryman 1983) to between 75-85/m^2 in Southeast BC (Reid 1963). Above 96 attacks/m^2 competition may become a significant factor (Safranyik et al. 1974).

My finding that gallery start density increased with dbh in the south was compatible with similar findings from Cole and Amman (1969) and Reid (1962). This relationship was not found for the north central sites in this study, however. Similarly, Klein et al. (1978) found no difference in gallery start density between diameter classes during an epidemic in Yellowstone National Park, Wyoming. This may suggest that during extremely large epidemics, although the beetle pressure may be similar on a localized scale between regions, there is a greater source of beetles on a landscape level scale (i.e., North central BC) which may cause a more randomized and variable pattern in host selection with regard to tree diameter (especially as larger trees are removed from the system), similar to what has been shown by Bentz et al. (1996) and Powell et al. (1998). The lower gallery start densities on the largest diameter trees are most likely due to the population being lower during the initial years of the outbreak, when only the largest trees were attacked.

On north central trees, gallery start densities (untransformed data) had a much higher variation for trees <20 cm dbh than on larger trees in the. This may have been due to a spillover effect where smaller trees that were near larger ones were attacked with larger-than-needed numbers of beetles. Populations with lower fitness levels may have required more beetles to overcome the smaller diameter trees, thus explaining the high densities for some of the small diameter trees. Because there may be large differences in gallery start densities among years throughout an epidemic (Klein et al. 1978), this may have contributed to the high variation in both the north and south regions. Klein et al. (1978) showed that the density of attacking beetles increased throughout the course of the epidemic regardless of tree diameter. Therefore, the fact that I found no relationship between gallery start density and tree diameter for the north central trees may be due to several years of successive attacks within a given stand.

There was not a significant difference in overall gallery start densities between regions (Figure 2), further supporting the assumption that the population levels were relatively similar.

2.5.3 Effect of Bark Roughness on Gallery Start Density

The small sample size of the extremely smooth and extremely rough bark is due partially to the sampling technique and partially to what occurs in nature. Bark roughness is normally distributed, with most trees being classified as having moderately rough bark. This measurement was very subjective, so some of the extreme cases were probably misclassified based on observer bias and human error. Regardless of the cause for the small sampling size, the extremely smooth and extremely rough cases were lumped in with the moderately smooth and moderately rough cases, respectively.

The trend of gallery start densities increasing with increasing bark roughness in the southern sites is consistent with previous studies (Shepherd 1965, Safranyik 1971). However, in the north central sites there was no significant trend, which may have been due to some difference in the beetle's ability to initiate a gallery in smoother bark. Safranyik (1971) suggests an upper limit in bark roughness, or a threshold where gallery initiations have reached their maximum potential, meaning gallery starts may plateau even with increasing bark roughness.

This threshold is only partially responsible for the lack of a trend in the north central sites, because what ultimately limits the gallery start density is male beetles producing *exo*-brevicomin (Ryker and Rudinsky 1982) and females ceasing the production of *trans*-verbenol (Hunt and Borden 1989) to reduce competition. While bark roughness influences the potential sites for female beetles to initiate a gallery, the final density of successful attacks is controlled by tree defenses, chemicals from both insect and host, and insect behavior. Therefore, the lack of a significant relationship between bark roughness and gallery start density in the north is probably related more to the year the tree was attacked (the population size growing throughout successive years of attack) than to the roughness of the bark.

2.5.4 Relationship Between Relative Attack Height and Gallery Start Density

The inverse relationship of gallery start density and height on the tree has been shown numerous times in the literature, and has been attributed to thinner phloem and less access due to branches (Reid 1963, Safranyik 1968, Klein et al. 1978). The studies by Reid (1963) and Safranyik (1968) were both done in close proximity to my southern study sites. Bark roughness also decreases with increasing height, which may reduce gallery start density. Therefore it was not surprising that this same relationship was found for both the southern and north central sites (Figure 5). Other studies that showed a decrease in gallery start density with increasing tree height did not measure the maximum attack height (Reid 1963, Shepherd 1965). Reid (1963) only measured up to 1.52 m, and Shepherd (1965) measured up to 5.36 m but the maximum attack heights were not reported.

2.5.5. Maximum attack height

My report of the significant increase in maximum attack height with increasing dbh is comparable to the 5-15 m attack heights of Safranyik (1968) for my southern sites. However, maximum attack heights averaged 5 m higher for each diameter class in north central trees (see Figure 7). This was more similar to the findings of Klein et al. (1978) who reported maximum attack heights of 22.5 m in trees over 40 cm.

As mentioned in section 2.5.2. (the relationship between dbh and gallery start density), the gallery start density varies throughout the course of an epidemic. I have shown in this study that the attack dynamics in the southern sites are very comparable to the literature. However, the north central sites were either significantly different as in the maximum attack height or not significant at all as in the relationship with dbh. This suggests that something other than host characteristics is driving these differences in the north central sites. The main differences between the north central and southern sites are the biogeoclimatic subzones (moisture and nutrients) and historic climatic suitability for mountain pine beetles to survive and successfully reproduce (Carroll et al. 2004). Further research on this area is needed.

According to the biogeoclimatic system for British Columbia, the southern sites which were in the Engelmann Spruce-Subalpine Fir zone (Coupé et al. 1991) were drier than those in the north central Sub-Boreal Spruce zone (Meidinger et al. 1991). Therefore an alternative to host characteristics as an explanation to the difference in attack height may be that the water uptake is lower in the southern, drier sites than in the wetter north central sites (Safranyik, unpublished data). This is supported by the study by Klein et al. (1978), which was conducted in the extreme southwest corner of Yellowstone National Park, WY, which is moister than the region where Safranyik (1968) and my southern sites were established.

Trees in the north central BC sites were generally taller (mean 20.3 m) than those in the southern BC sites (18.4 m). It is therefore possible that some of the difference may be due to sufficiently thick bark for successful attack extending higher up the bole in the north central BC trees than in the southern trees.

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3. Influence of Tree Characteristics on Mountain Pine Beetle Productivity: A Comparison Between Southern and North Central British Columbia

Abstract

Host factors affecting potential brood productivity of the mountain pine beetle on lodgepole pine were examined in southern and north central British Columbia at the end of the outbreak cycle. Trees were felled and intensively sampled in three southern and five north central pine-leading stands. Diameter accounted for 52.3 % and 42.8 % of the variation in brood production (pupal chamber density) in north central and southern BC, respectively. When expressed as total number of pupal chambers per tree, tree diameter accounted for 71.9 and 64.5% of the variation for north central and southern BC sites, respectively. Gallery start density added less than 1%, indicating that gallery start densities were not generally high enough to generate significant intraspecific competition. Regression analyses indicated that in the south, a 1:1 or greater pupal chamber to gallery start ratio occurred in trees larger than 16.2 cm dbh, whereas in the north, this ratio was achieved at 13.7 cm dbh. Pupal chamber densities in north central trees were as high or higher than in the most productive part of the southern trees (the lower third) regardless of relative height, indicating significantly higher host tree suitability in north central trees. Brood productivity at my southern sites compared with reported productivity from the literature, whereas productivity was higher in the north. My results indicate that north central trees are more suitable for brood production than southern trees. I hypothesize that this is in part due to a lack of selection pressure on north central pine populations, since these stands have been in climatically unsuitable areas until recently.

Keywords: Lodgepole pine, host effects, pupal chambers, brood production, mountain pine beetle

3.1 Introduction

Insect productivity is related to population growth and rate at which the population increases. The reproductive potential of insects depends on fertility, length of life cycle, mortality factors, and sex ratio (Coulson and Witter 1984). A high reproductive potential only indicates the potential rate of increase when environmental conditions (eg. temperature, moisture, and available food resources) are optimal for the insect species.

In British Columbia, the population dynamics of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is highly dependent on the availability and quality of its primary host, lodgepole pine (*Pinus contorta* Dougl. Ex Loud.var. *latifolia* Engelm.).

The food source for mountain pine beetles is the nutrient-rich phloem between the outer bark and the cambium, including fungal symbionts growing there. The phloem is one of the most important factors affecting beetle brood productivity (Reid 1963, Safranyik and Jahren 1970, Amman 1972, Amman and Pace 1976, Berryman 1976, Rasmussen 1980). In many studies, mountain pine beetle "productivity" refers to reproductive characteristics such as gallery length and density, number of eggs oviposited per female, density of emerged brood, and beetle size. However, in this paper the term "productivity" refers only to pupal chamber density and overall pupal chambers per tree as a measure of host suitability.

Amman (1972) and Berryman (1976) suggested that phloem thickness is the single most important factor regulating mountain pine beetle reproduction. Amman (1972) found a linear increase in the number of emerged brood adults with an increase in phloem thickness when food supply (phloem tissue) limited production. Emergence densities ranged from 344/m^2 to 2,024/m^2 for phloem 2.3mm and 5.8mm thick, respectively. When food supply was not limiting, there was an exponential increase in emergence with increasing egg gallery length. Rasmussen (1980) found an increase in emergence levels for both males and females as phloem thickness increased, and reported emergence densities of 152.8 females/m^2 and 88.2 males/m^2 from trees with a phloem thickness of 1.1 -1.6 mm, and 216.3 females/m^2 and 143.1 males/m^2 from trees with a phloem thickness of 2.2 – 3.2 mm.

Shrimpton and Thompson (1985) proposed that the basal area increment in the last 6-10 years before sampling was the best predictor of phloem thickness. Trees in dense stands have thinner phloem than those in open stands (Amman et al. 1977), which results in lower beetle production in dense stands. Some studies have suggested that mountain pine beetle epidemics are dependent upon hosts with thick phloem (Reid 1963, Cole and Amman 1969). A minimum phloem thickness of approximately 3mm has been suggested for successful brood production (Cole 1973), and in the US very little emergence has been observed from trees with a phloem thickness of less than 1.5mm (Amman 1975, Amman and Pace 1976).

Phloem thickness is positively correlated to diameter at breast height (dbh) in lodgepole pine (Cole 1973). Reid (1963) reported that the single most important factor in overall brood survival was tree size (although he also measured phloem thickness), and that the trees of larger diameter had the highest productivity in both total brood produced per tree and brood density. In agreement with this finding, Amman (1969) reported that the greatest proportion of thick-phloemed trees were in the greatest diameter classes. In studies that have not investigated phloem thickness, diameter is the most significant factor in productivity (Cole and Amman 1969). Berryman (1976) analyzed data collected from 11 separate locations in the United States and Canada by several different researchers, and concluded that diameter correlated poorly with beetle productivity when all 215 trees from these studies were pooled together. When individual stands were analyzed separately, however, diameter was a significant factor in some stands, suggesting that diameter is useful in predicting which trees within a stand will be the most productive, but not in predicting overall productivity among stands. Nevertheless, the majority of studies have found that diameter, phloem thickness, and beetle brood productivity are highly correlated; therefore, it may be possible for phloem thickness and tree diameter to be used as surrogates for predicting beetle productivity.

Although the major reason for the positive relationship between dbh and brood production is thicker phloem occurring primarily in larger trees, it has also been shown that smaller trees with thin bark dry more rapidly after being killed by beetles (Amman 1976), and this decreases the available moisture in the phloem for developing larvae (Reid 1961). Cole (1974) suggested that an important mortality factor of mountain pine beetle is cold winter temperatures followed by excessive drying of the tree.

On average, trees less than 25 cm dbh have more attacking beetles than emerging, i.e., they are population sinks. In trees greater than 25 cm, the ratio of emerging to attacking beetles increases with increasing diameter (Safranyik 1974). Brood production also decreases with increasing height up the tree due to decreasing phloem thickness and higher attack densities (Safranyik 1968, Safranyik 1974, Klein et al. 1978).

3.2 General Objective

The objective of this research was to compare host suitability in relation to brood production between north central British Columbia (Prince George Forest District) and southeastern BC (Rocky Mountain Forest District). Relationships between tree characteristics and pupal chamber density were analyzed separately for each region. I measured how diameter at breast height (dbh = 1.3m) and diameter at sequentially higher points up the tree bole affected phloem thickness, pupal chamber density, and pupal chamber per gallery start ratios. The results for the southern sites allowed for a comparison against previous studies, while the results from the north were investigated for differences from the south.

3.3 Methods

3.3.1 Study Sites

Sampling was done in lodgepole pine stands in southern and north central British Columbia during the summer of 2005. The north central sites were in the Prince George Forest District in north central British Columbia (approx. 53.9° N, 123.5°W), in the dry, warm subzone of the Sub-Boreal Spruce biogeoclimatic zone (Meidinger et al. 1991). The southern sites were in the Rocky Mountain Forest District in southeastern B.C. (approx. 49.5°N, 116.2°W), in the dry, mild subzone of the Engelmann Spruce Subalpine Fir biogeoclimatic zone (Coupé et al. 1991). The southern sites were at a higher elevation (approx. 1525 m – 1835 m) than those in the north (900m) so that climatic influences were kept similar in spite of the latitudinal difference, in accordance with Hopkins Bioclimatic Law (Hopkins 1919), which states that every 1° increase in latitude is roughly equivalent to 120 m increase in elevation.

3.3.2 Stand Selection

Five stands in the north and three in the south were sampled. In both north central and southern regions, the stands in which the sampling was done were lodgepole pine-leading stands 80 years old or older, and of similar density. The species composition for each region is shown in Table 1 of Chapter 2.

All stands were at least 10 hectares in area and a minimum of 1 km apart. Stands were selected in areas in which the mountain pine beetle epidemic was in the final stages and therefore the majority of the population had left the stand. Particular emphasis was placed on selecting stands with similar local beetle populations.

A minimum of 8 randomly selected plots per stand were established, and the trees to be measured were selected using a prism with a basal area factor of 4. In each plot, tree species, diameter at breast height (dbh), and attack status [unattacked, current attack or old attack (beetles had already emerged)] was recorded for each tree over 7.5 cm dbh. For plot randomization, a baseline was established at a randomly selected angle, and transects off the baseline were also put in at randomly selected distances greater than 80 m and less than 150m. This was accomplished by skipping over any number selected from the random number table that was less than 80 and higher than 150.

Phloem thickness was measured from all green trees (both unattacked and green attacks) in all plots. A 10 mm diam. circular piece of bark was collected from the tree at breast height (1.3 m) on the south and north aspect of each tree using a leather punch (Arch Punch®, C.S. Osborne and Co., Harrison, NJ, USA). Each circular piece was removed from the bark punch, and then gently sliced in half so as not to compress the phloem material. The thickness of the phloem and outer bark was then measured at the midpoint of the cut to the nearest hundredth of a millimeter using a 0-150mm / 6" Electronic digital caliper (Youfound Precision Co. Ltd., Changxing, Zhejiang province, China).

3.3.3 Felled Tree Selection

At each prism plot, a minimum of two trees (old attacks) were selected and felled for intensive sampling. To obtain equal sample size across the range of diameters in the stand, at least six trees from each of the following five diameter classes were selected if available: <15 cm, 15-20 cm, 20-25 cm, 25-30 cm, and >30 cm. If a tree in the desired diameter class was not available in the plot, the closest tree to the plot center in the desired diameter class was felled. Trees selected for intensive sampling were at least 50 m from edges of stands, lakes, or any open area to minimize edge effects. At least one dominant or co-dominant tree was selected from each plot in order to record the age from the stump. The trees and sections of bark sampled herein were the same ones sampled in Chapter 2.

3.3.4 Intensive Sampling

A minimum of thirty successfully attacked trees (ie. at least six per diameter class) up to 40 cm in dbh were felled in each stand. The attack height, defined as the distance from the base of the tree to the highest pitch tube and/or gallery start, was measured on each felled tree. The attacked portion was cut into 3 equal segments, and the diameter at the midpoint of each segment was measured. The sampling unit was a 15x30 cm rectangle (Safranyik 1968) cut in the bark at the midpoint of each of the three segments. This allowed the absolute height above ground of each sampling point to be calculated from the overall attack height. Pupal chamber density was obtained by peeling off the outer bark to reveal each individual pupal chamber, and this number was multiplied by 22.22 to obtain the density per square meter.

Mean pupal chamber density was obtained for each tree based on the average of each segment height. The pupal chamber total for each tree was calculated by multiplying the mean pupal chamber density by the surface area of the attacked portion of the bole. Pupal chamber per gallery start density was calculated by dividing the number of pupal chambers by the number of gallery starts (both successful and unsuccessful galleries).

Woodpecker activity was sampled by estimating a percentage of bark affected in each sampling unit. No significant relationship was found between percentage of bark affected and pupal chamber density. Although woodpecker damage will affect the outer bark parameters such as number of pitch tubes and exit holes that are visible, inner bark parameters such as gallery starts and pupal chambers were the variables used in the analysis. I was only interested in the potential productivity of the trees, not the realized reproductive fitness. Therefore the amount of woodpecker activity did not affect my results.

3.3.5 Data Analysis

Linear regressions were conducted on log-transformed data to analyze the relationship between dbh and phloem thickness as well as the effect of dbh on pupal chamber per gallery start ratios. A stepwise multiple regression was used to test the effects of dbh and gallery start density on pupal chamber density. Homogeneity of variance was tested using Levene's tests. The assumption of homogeneity of variance was not met for either region, but was met after data were transformed as $x' = \log_{10}(x+1)$. Thus, these analyses were conducted on transformed data.

Pupal chamber density comparisons among segment heights in trees were conducted using a between subjects one-way ANOVA. Two-way ANOVAs were used to test for significant differences: in the effect of region and dbh in phloem thickness among diameter classes between regions; between the effect of dbh on pupal chamber density between regions; in the mean pupal chamber per gallery start ratios between regions and between diameter classes; and between regions in the effect of absolute height above ground on mean pupal chamber densities. A nested three-way ANOVA was used to test for differences between regions in mean pupal chamber densities with regard to relative height.

A linear regression was conducted to analyze the relationship between absolute height above ground and pupal chamber density for both north and south regions. Because square root and logarithmic transformations failed to meet assumptions of homogeneity of variance, a two-sample Kolmogorov-Smirnov test ($P = 0.126$) was used.

A two-way ANOVA was conducted to test for differences between regions in the effect of absolute height above ground on mean pupal chamber densities. A three-way ANOVA was run to analyze the regional differences, among diameter classes, in mean pupal chamber density and the effect of absolute height for each individual dbh class.

Significant ANOVA's were followed up by Tukey's post hoc tests. Variables were assessed for normality using histograms and scatter plots. Homogeneity of variance was tested using Levene's tests. The level of significance was set at 0.05 for all statistical tests. All data were analyzed using SPSS 13.0 (SPSS Inc., Chicago, IL, USA). All graphs were created using SigmaPlot 9.0 (Systat Software Inc., Port Richmond, CA)

3.4 Results

3.4.1.1 Phloem Thickness and Dbh

A linear regression showed that there was a significant increase in phloem thickness with an increase in dbh for both north central (R^2=0.25, P<0.001) and southern sites (R^2=0.36, P<0.001).

Phloem thickness did not differ significantly between regions (ANOVA, F =0.802, df=1, 248, $P = 0.371$), but differed significantly between diameter classes for both regions, F= 31.058, df=3, 248, P<0.001 (Figure 1).

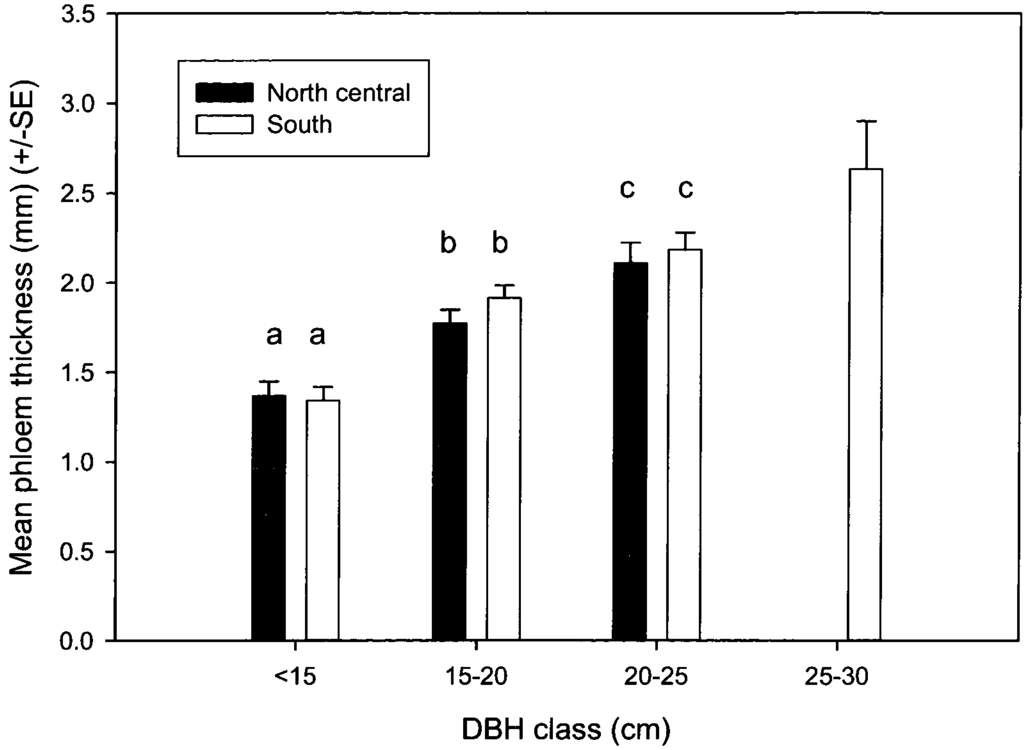

Figure 1. Comparison of mean phloem thickness among regions and diameter classes (there were no unattacked or current attacks in the 25-30cm diameter class in the north central region, and therefore no phloem samples for this diameter class). NS = not significantly different at $P < 0.001$. Vertical lines represent standard error.

3.4.1.2 Effect of Dbh

A stepwise multiple regression to test for the effects of dbh and gallery start density on pupal chamber density revealed that dbh accounted for 52.3% and 35.7% ($P < 0.001$) of the variation in pupal chamber density, for north central and southern trees, respectively (Figures 2 and 3). Gallery start density added just an additional 0.5% and 0.6% of variation, respectively.

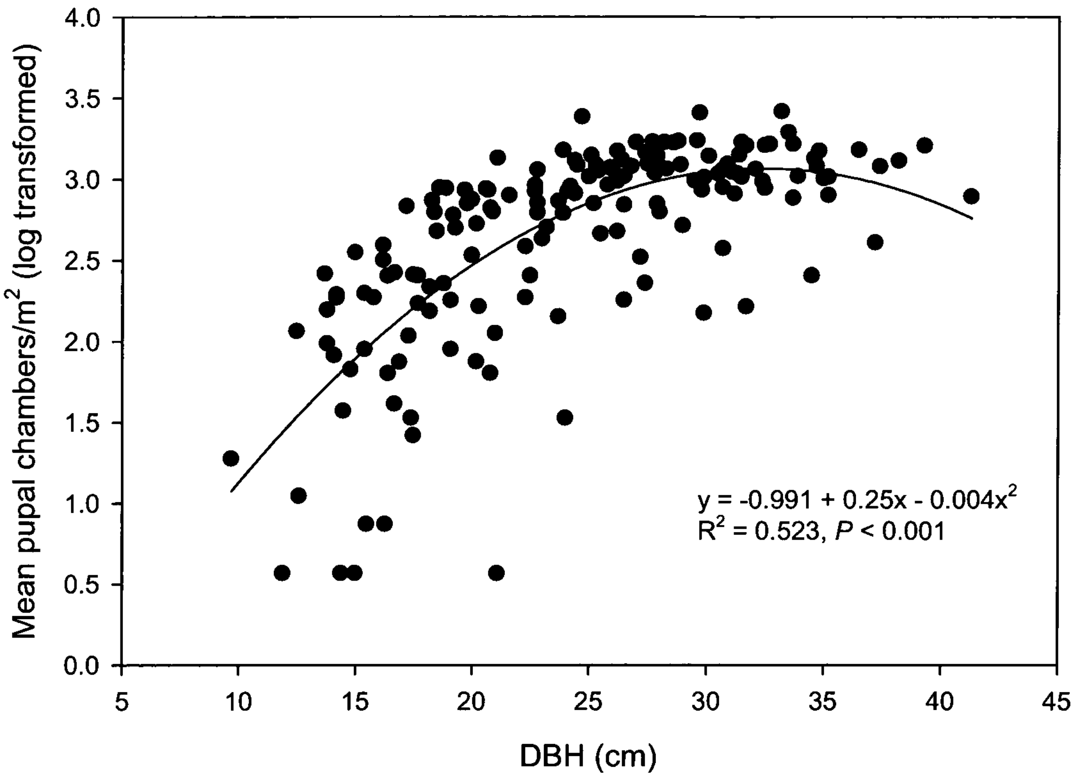

Figure 2. Logarithmic relationship between diameter at breast height and mean pupal chamber density for trees attacked by the mountain pine beetle in north central British Columbia.

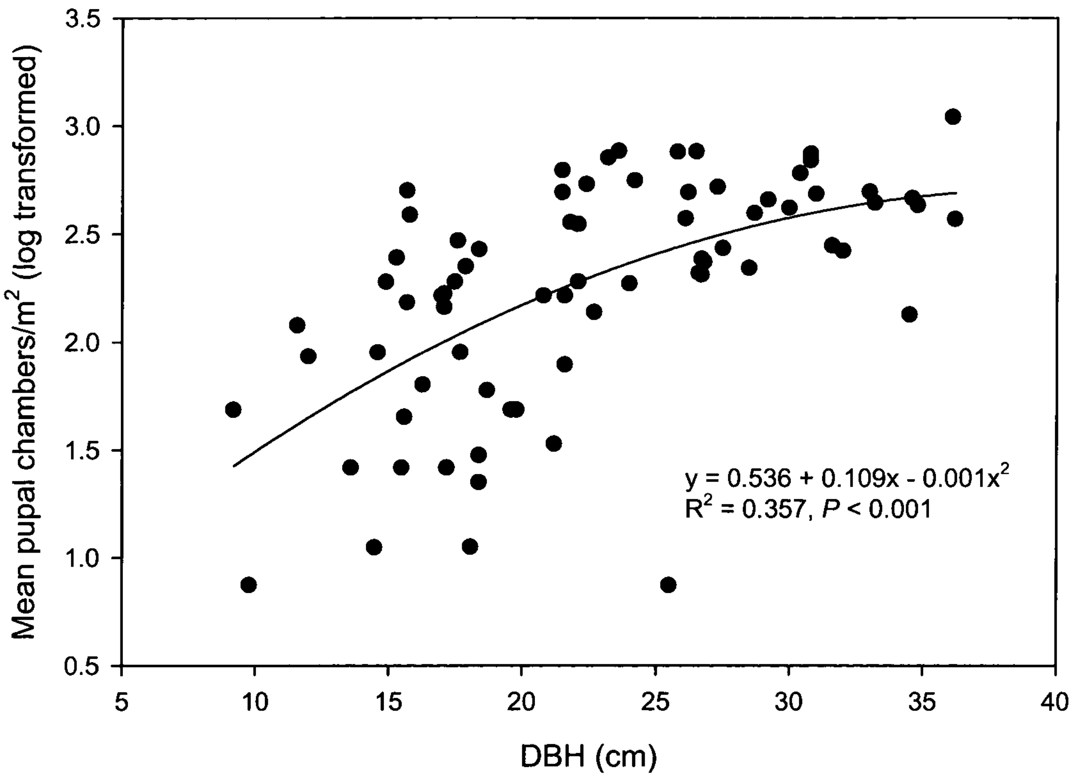

Figure 3. Logarithmic relationship between diameter at breast height and mean pupal chamber density for trees attacked by the mountain pine beetle in southern British Columbia.

The effect of dbh had a stronger relationship on total number of pupal chambers per tree. A log-transformed regression showed a highly significant increase in pupal chambers with increasing dbh for both north central (R^2=0.719, P<0.001) and southern (R^2=0.645, P<0.001) trees (Figures 4 and 5).

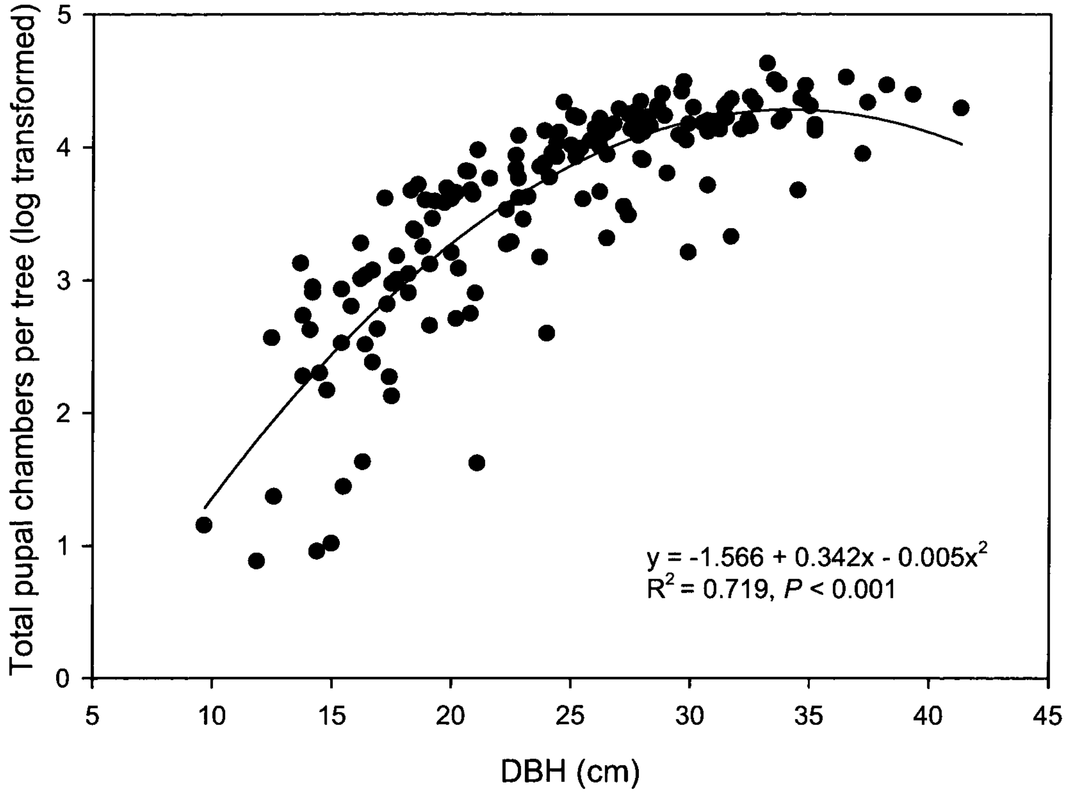

Figure 4. Logarithmic relationship between diameter at breast height and total pupal chambers per tree for trees attacked by the mountain pine beetle in north central British Columbia.

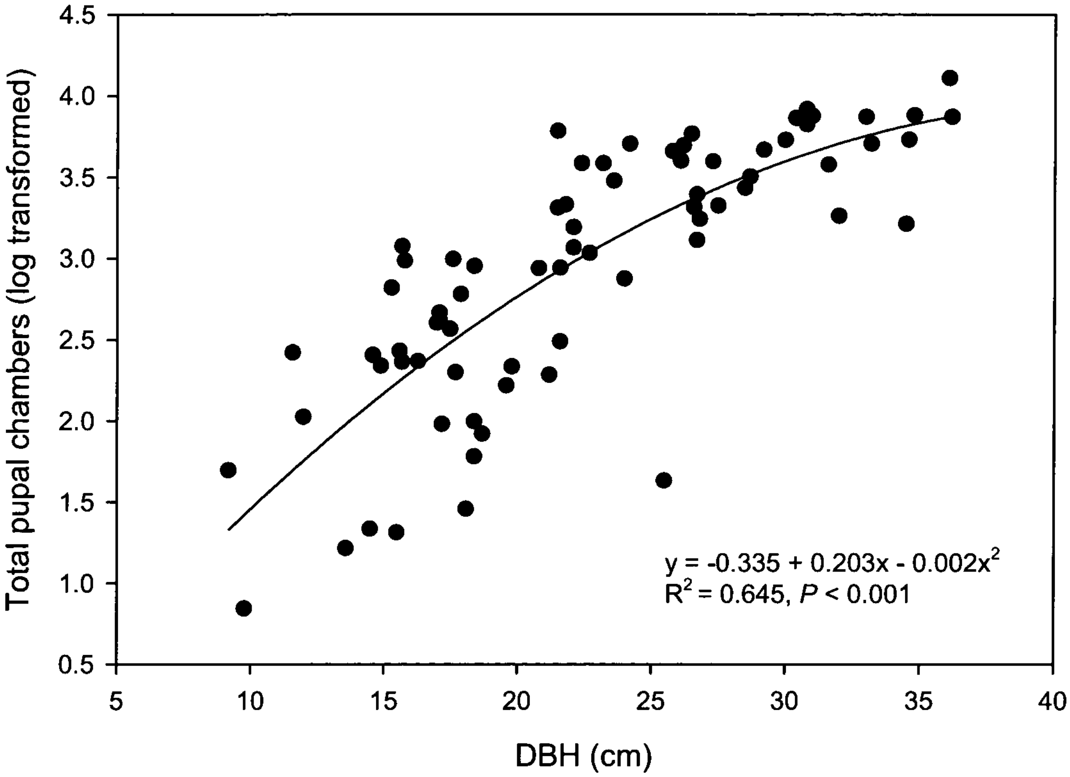

Figure 5. Logarithmic relationship between diameter at breast height and total pupal chambers per tree for trees attacked by the mountain pine beetle in southern British Columbia.

The influence of dbh on pupal chamber density differed significantly between regions. Mean pupal chamber density was significantly higher for north central than southern trees (ANOVA, $F = 64.16$, df=1,253, $P<0.001$) (Figure 6). The effect of dbh was also significant (ANOVA, $F = 37.0$, df=4,253, $P<0.001$) The region by diameter class interaction was also highly significant ($F = 7.95$, df=4,253, $P<0.001$). A Tukey's HSD multiple comparisons test revealed that for all diameter classes except <15 cm the difference between regions was significant at $P<0.001$. The multiple comparison test also showed that the pupal chamber densities did not differ significantly between the 25-30 cm and >30 cm classes within either of the two regions (Figure 6).

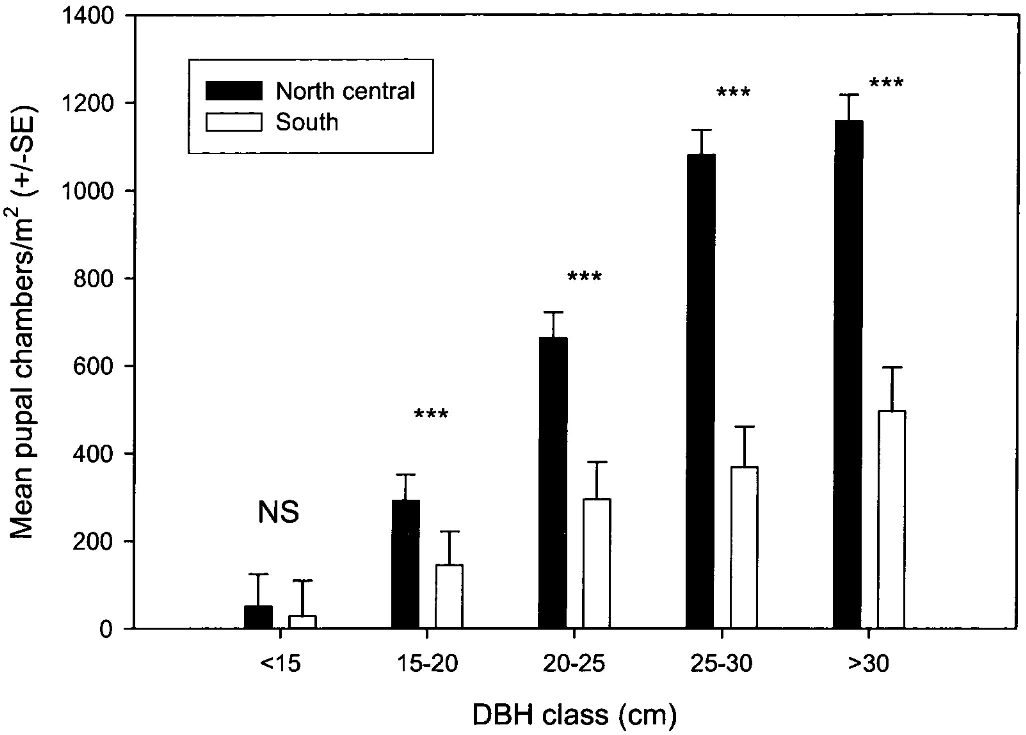

Figure 6. Mean pupal chamber densities by diameter at breast height class and region. NS = not significantly different, *** = significantly different at $P < 0.001$. Vertical lines represent standard error.

The influence of dbh on total pupal chambers also differed significantly between regions. A two-way ANOVA indicated that north central sites had significantly higher total pupal chambers per tree than southern, $F = 84.11$, df=1,251, $P<0.001$ (Figure 7). The effect of dbh was highly significant ($F = 56.85$, df=4,251, $P<0.001$) as was the interaction effect of region and diameter class ($F = 15.61$, df=4,251, $P<0.001$). A Tukey's HSD multiple comparisons test revealed that for all diameter classes except <15 cm ($P=0.818$) the difference between regions was significant at $P<0.001$ (Figure 7).

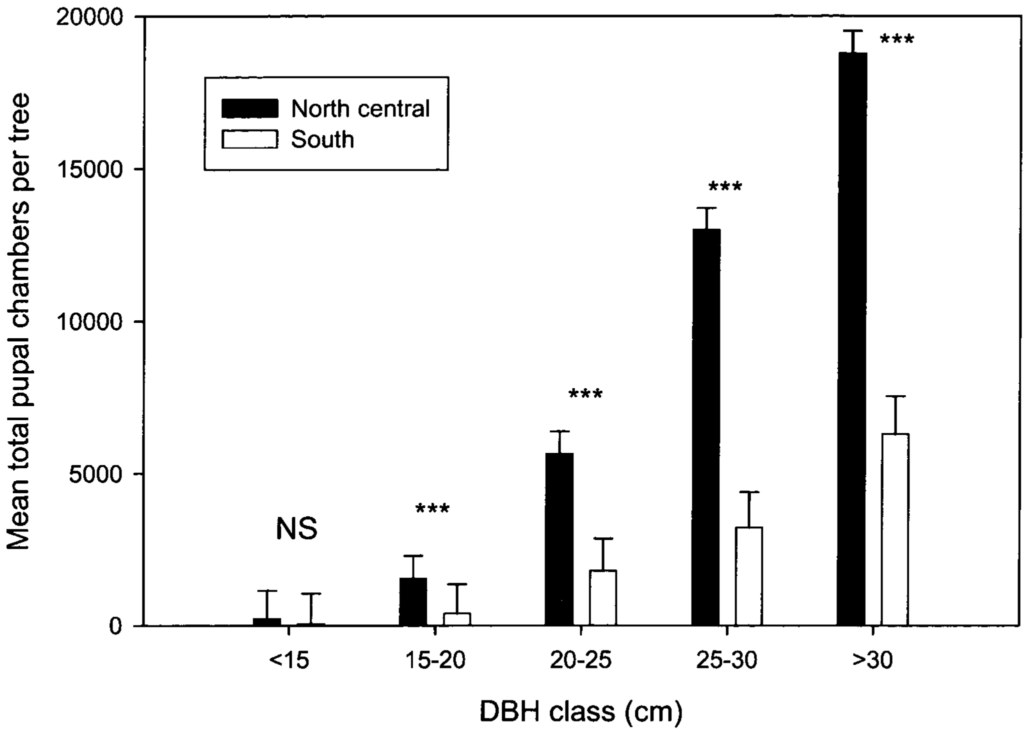

Figure 7. Mean total pupal chambers per tree by diameter at breast height class and region. NS = not significantly different, *** = significantly different at $P < 0.001$. Vertical lines represent standard error.

3.4.1.3 Ratio Between Pupal Chambers and Gallery Starts

A logarithmic regression showed that there was a significant increase in the number of pupal chambers per gallery start with increasing dbh for both north central (Figure 8) and southern trees (Figure 9). For north central sites, dbh accounted for 44.5% of the variation in pupal chambers per gallery starts ($P<0.001$) and for southern sites dbh accounted for 20.5% ($P<0.001$).

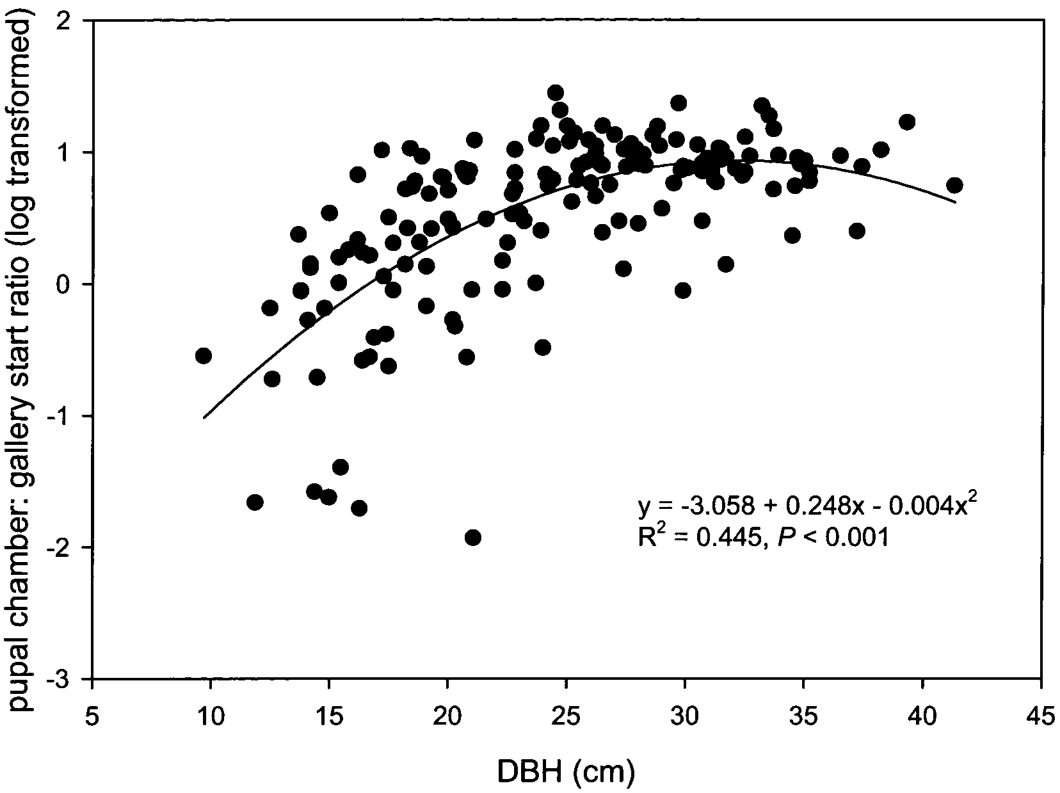

Figure 8. Log transformed relationship between diameter at breast height and pupal chamber: gallery start ratio for trees attacked by the mountain pine beetle in north central British Columbia.

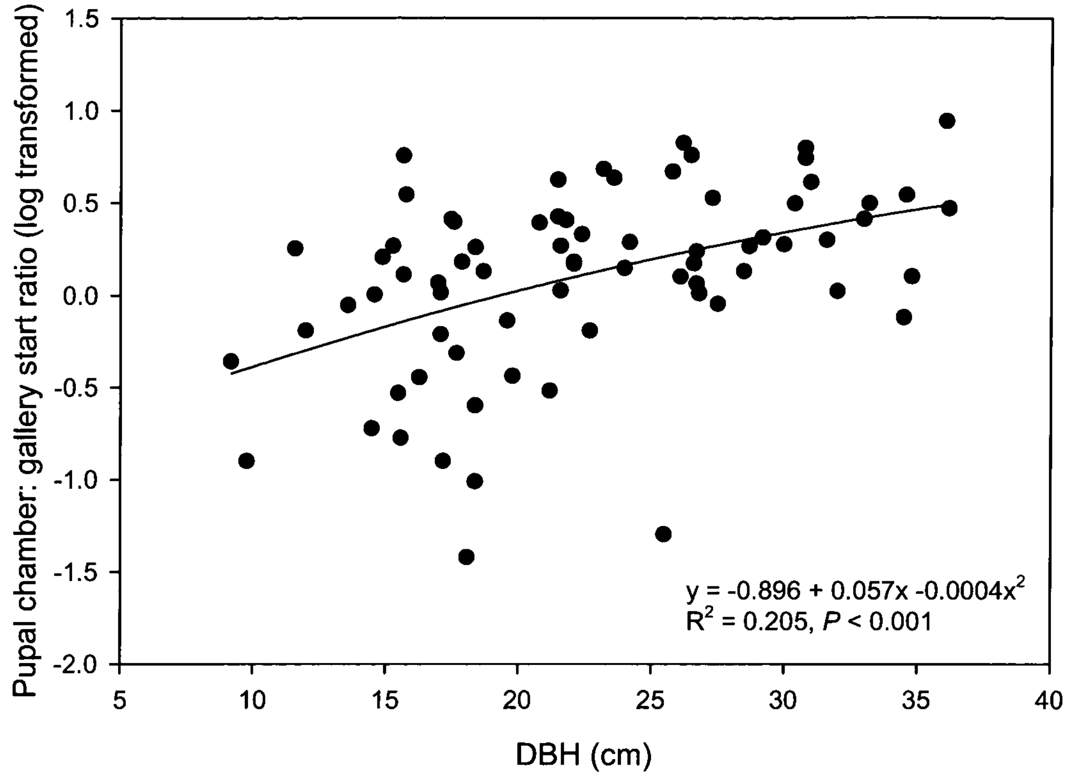

Figure 9. Log transformed relationship between diameter at breast height and pupal chamber: gallery start ratios for southern trees.

Pupal chambers per gallery start ratios were significantly different between regions (*F*=47.48, df=1,247, *P*<0.001) for all except the <15cm diameter class (*P*=0.121). The effect of dbh was significant (*F*=17.12, df=4,247, *P*<0.001) as was the interaction effect of region and diameter class (*F*=5.30, df=4,247, *P*<0.001) (Figure 10).

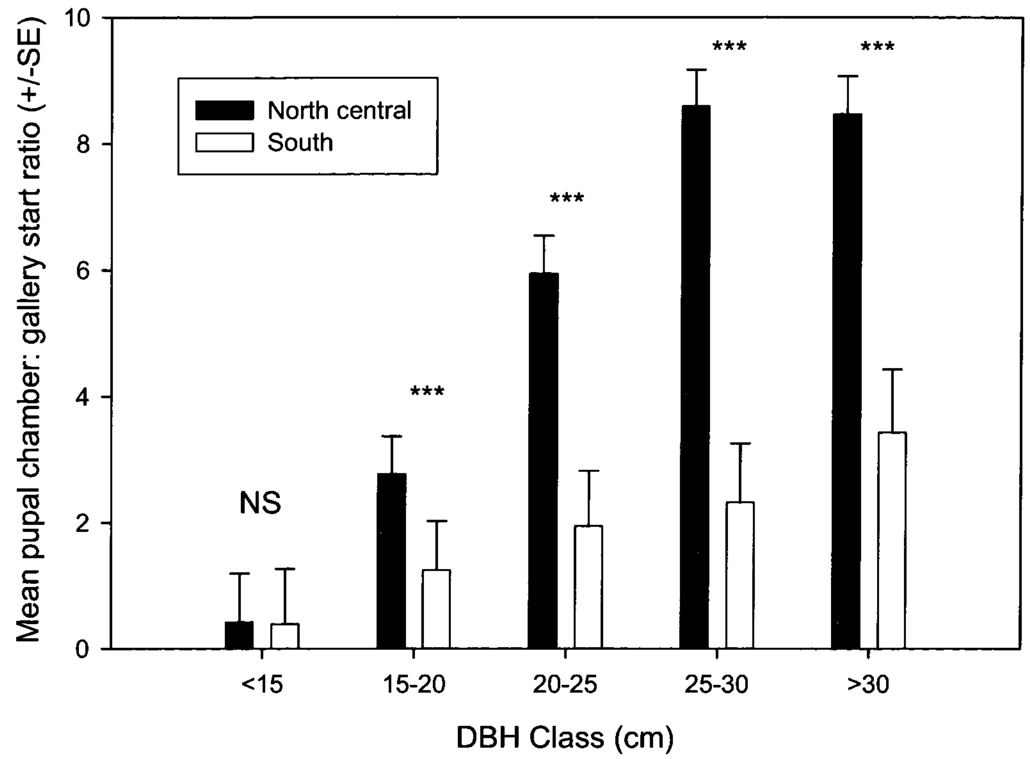

Figure 10. Comparison of pupal chamber: gallery start ratios between the north central trees and southern trees for all diameter at breast height classes. NS = not significantly different, *** = significantly different at $P < 0.001$. Vertical bars represent standard error.

3.4.1.4 Relative Height

In the north central trees there was a significant decrease in mean pupal chamber density from the lower segment to the upper, $F = 22.11$, df=2,522, $P<0.001$ (Figure 11), with mean pupal chamber densities of 922/m^2, 728/m^2, and 453/m^2 for all lower, middle and upper segments, respectively. A Tukey's HSD multiple comparisons test revealed that this decrease was significant between the lower and middle segments ($P<0.05$) as well as between the middle and upper segments ($P<0.001$).

A somewhat different pattern was observed for southern sites (Figure 11). Mean pupal chamber densities for the lower, middle, and upper segments were 414/m^2, 151/m^2, and

153/m^2, respectively. Although there was a significant difference in pupal chamber density between the three segments ($F = 20.38$, df=2,261, $P<0.001$), the Tukey's post hoc test disclosed that this difference was only significant between the lower segment and the other segments ($P<0.001$), while there was no difference between the middle and upper segments ($P=0.999$) (see Figure 11).

A similar trend in both regions was observed when trees were separated by diameter class, but the difference was most visible in the 25-30cm and >30cm diameter classes (Figure 12).

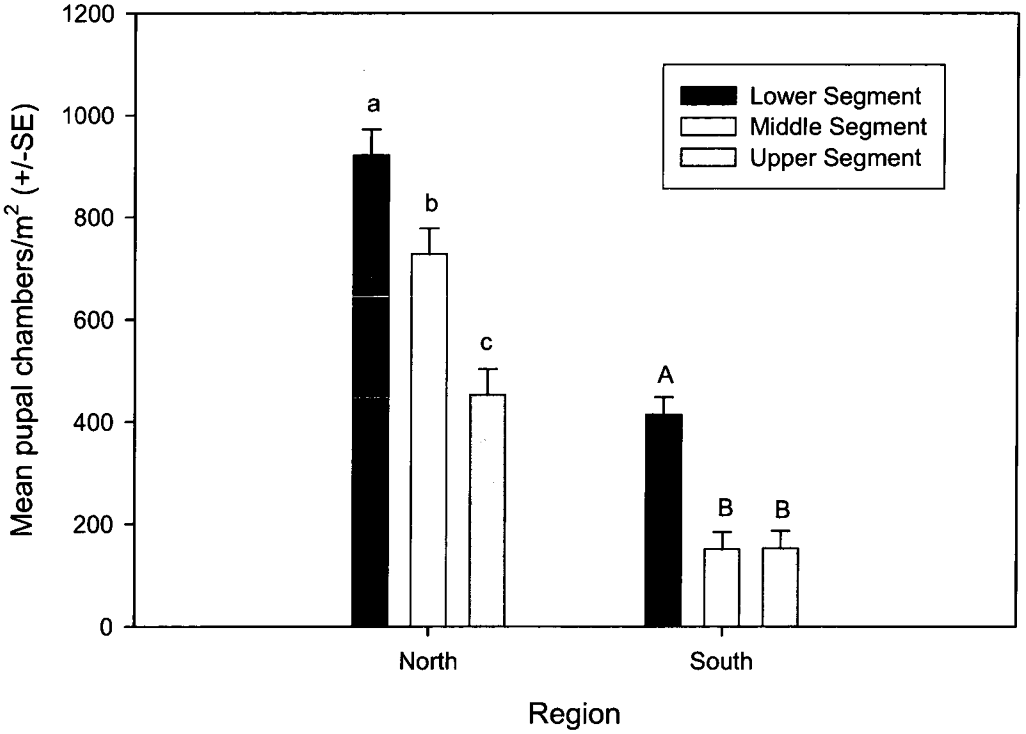

Figure 11. Mean pupal chamber densities for lower, middle and upper segments of trees from the north central and southern sites in British Columbia. Bars within each region followed by a different letter are significantly different ($P<0.05$), those followed by the same letter are not significantly different ($P>0.05$). Vertical bars represent standard error.

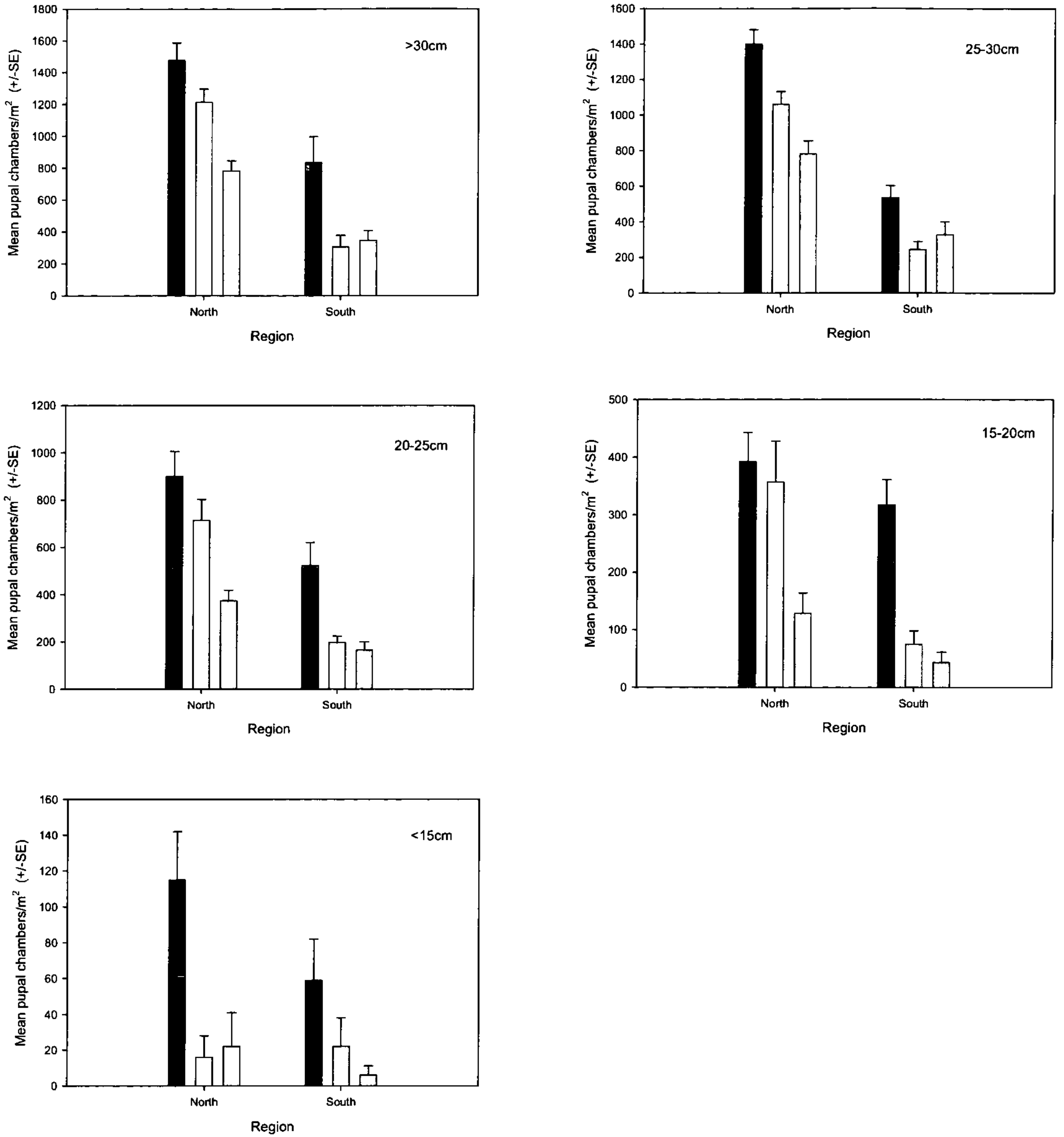

Figure 12. Mean pupal chamber densities for lower, middle and upper segments of trees from the southern and north central sites. Graphs are separated out by diameter class, with lower, middle and upper segments being represented by black, light gray, and dark gray bars, respectively. (Notice differing values on y-axis between graphs).

A nested, three-way ANOVA showed that mean pupal chamber densities on the lower (*F* = 63.37, df=1, 6.14, *P*<0.001), middle (*F* = 57.41, df=1, 6.17, *P*<0.001), and upper segments (*F* = 38.56, df=1, 6.16, *P*<0.001) of trees from the north central sites were significantly higher than those from the southern sites. This pattern was consistent among stands within regions.

3.4.1.5 Relationship Between Absolute Height and Pupal Chamber Density

A linear regression indicated that there was no significant relationship between pupal chamber density and absolute height above ground for either north central (R^2=0.000, P=0.788) or southern trees (R^2=.003, P=0.407) (Figures 13 and 14, respectively). When analyzed by absolute diameter, the highest regression coefficient was obtained for the 25-30 cm class in the south (R^2=0.221), but when analyzed by dbh class, the highest regression coefficient was obtained for the 15-20 cm class in the south (R^2=0.203). Most other r^2 values were less than 0.1.

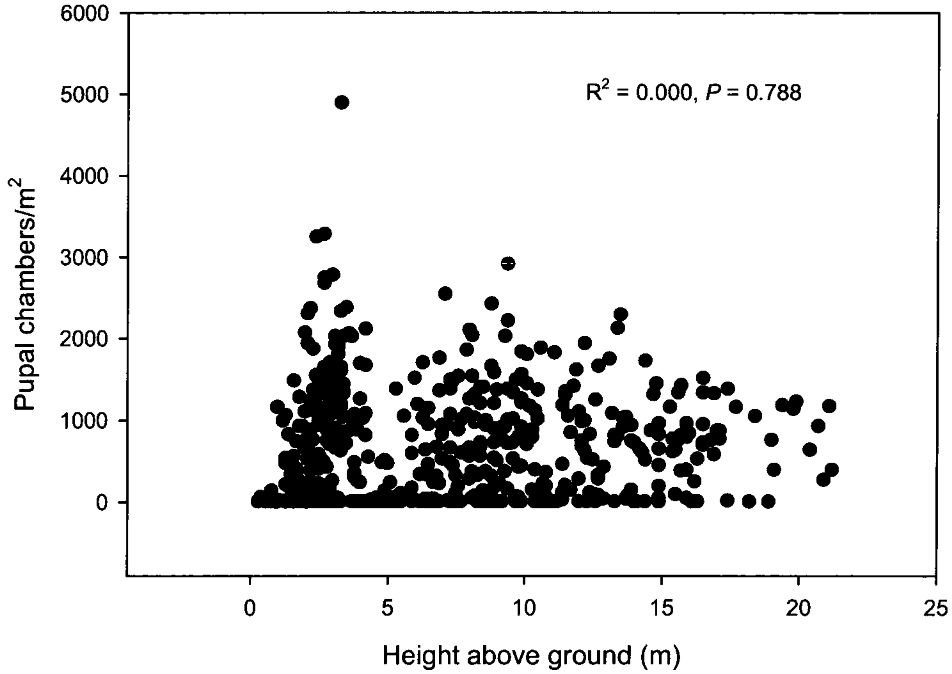

Figure 13. Untransformed data for relationship between pupal chamber density and absolute height above ground in north central trees in British Columbia.

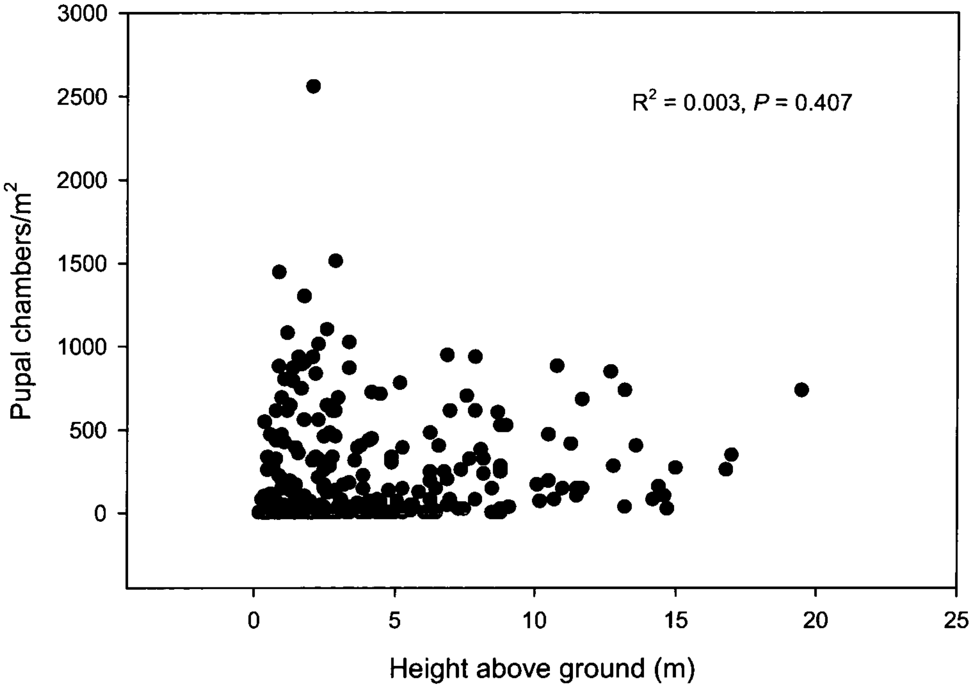

Figure 14. Untransformed data for relationship between pupal chamber density and absolute height above ground in southern trees in British Columbia.

There was no significant relationship between mean pupal chamber densities and absolute height above ground for either region (F = 0.677, df=3, 781, P = 0.566) (Figure 15). However, mean densities were significantly higher in north central than southern trees at all heights (F = 16.12, df=1, 781, P<0.001).

In all diameter classes, the north central sites had significantly higher pupal chamber density than the southern (F = 34.18, df=1,757, P<0.001) (Figure 16). The effect of absolute height was also significant (F = 9.28, df=3,757, P<0.001), but only between the 0-5 m and >15 m range (P<0.05). Mean pupal chamber densities were significantly higher with each successive dbh class (F = 37.44, df=4,757, P<0.001) with the exception of the two largest ones, which did not differ significantly ($P = 0.302$). The interaction effect of region and dbh class was also significant ($F = 9.05$, df=4,757, $P<0.001$).

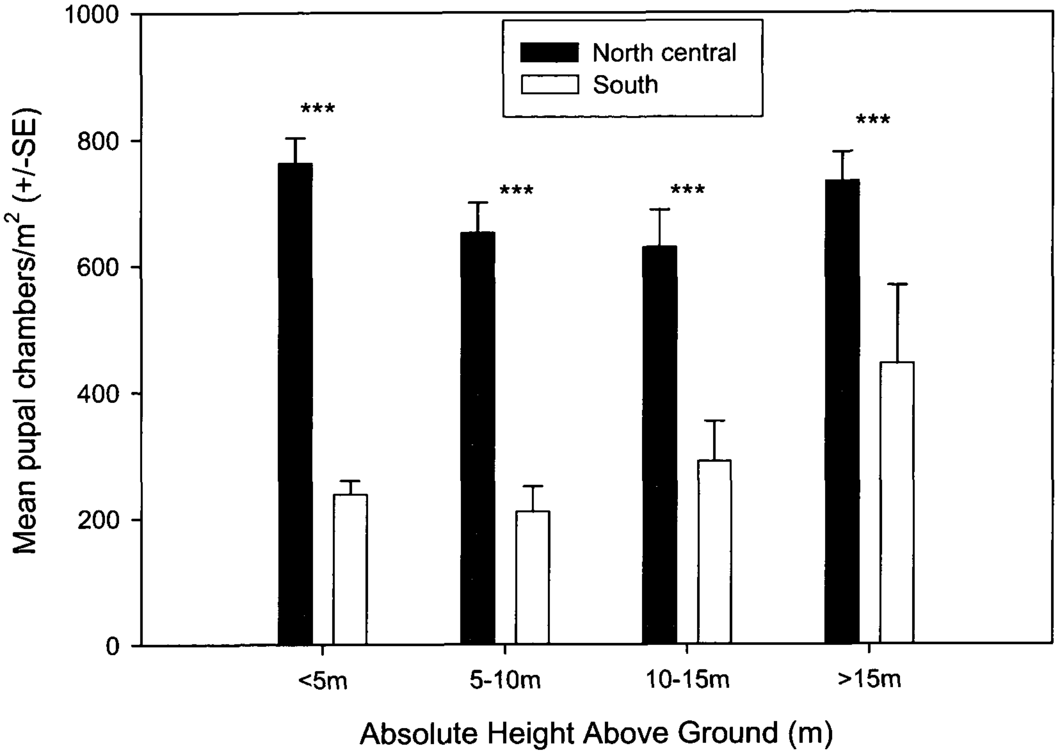

Figure 15. Comparison between regions of effect of height above ground on pupal chamber density. *** = significantly different within absolute height class at $P < 0.001$. Vertical bars represent standard error.

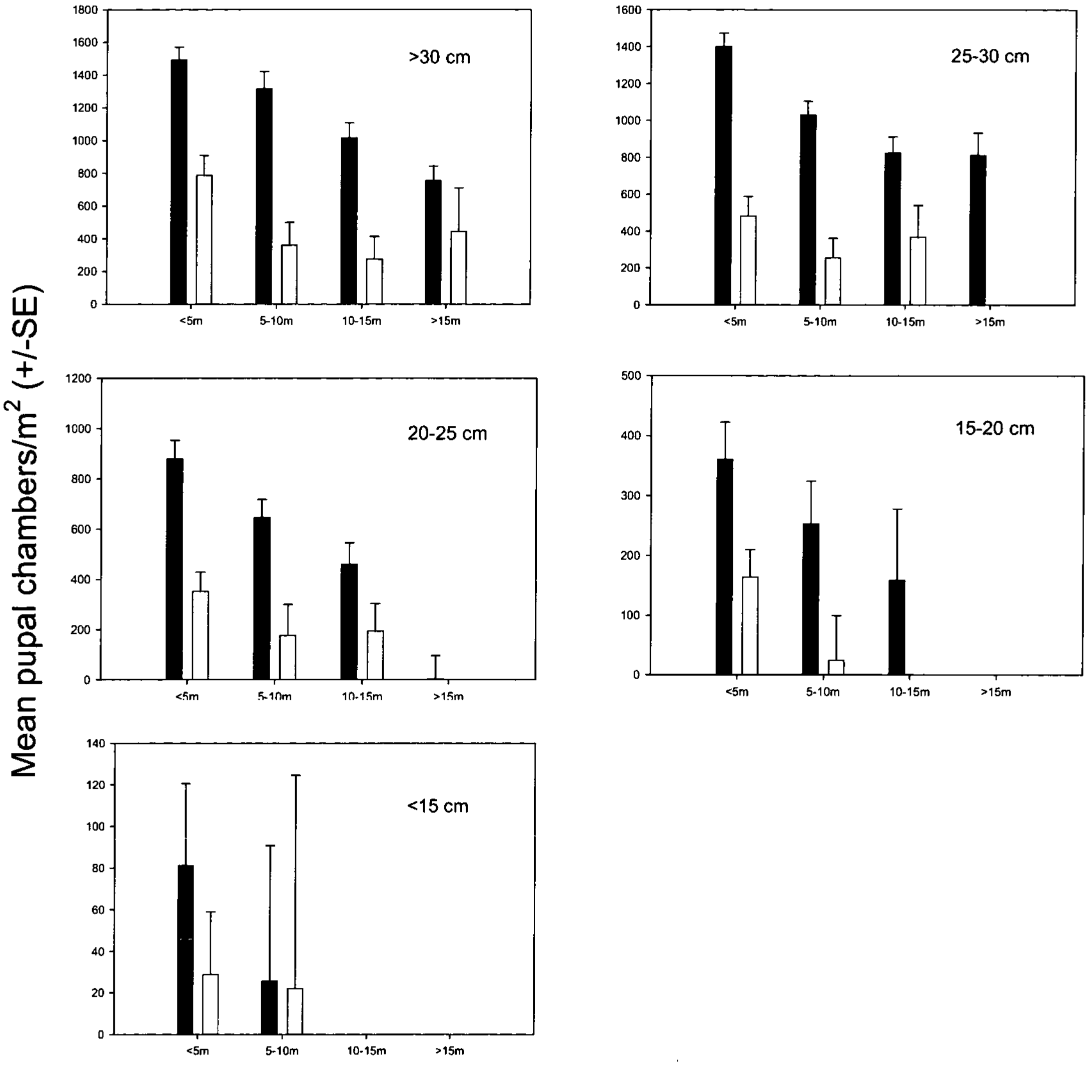

Figure 16. Comparison between regions of effect of height above ground on pupal chamber density (five diameter classes separated out, with black bars representing the north central trees and gray bars representing the southern trees).

3.5 Discussion

Studies concerning mountain pine beetle productivity can be difficult to compare because of different methods of sampling, or studies may have been done in locations at different latitudes or elevations with different climate. For example, Amman (1972), Amman (1975), and Cole and Amman (1969) conducted their studies at high elevations in Utah, southeast Idaho, and western Wyoming, while Berryman (1976) studied mountain pine beetle in northern Idaho and Montana, and Reid (1963) and Safranyik (1968) conducted their studies in southeastern British Columbia. Although all of these studies focused on some aspect of the effect of tree parameters on brood production, the significance of some factors may be different due to different limiting factors in these areas.

3.5.1 Phloem Thickness

Reid (1963) reported a mean outer bark thickness of 11.8 ± 1.39 mm (n = 7) for trees 20-25 cm dbh, 9.9 ± 0.60 mm (n = 4) for trees 25-30 cm, and 10.9 ± 0.00 mm (n = 2) for trees > 30 cm. I also measured total bark thickness, and the maximum for all tree sizes in both regions was 5.9 mm. Although Reid's (1963) values are much higher than those I obtained, he also shows a general, albeit weak, trend (other than Reid's 20-25 cm class) of increasing phloem and bark thickness with increasing diameter. Amman (1975) measured actual phloem thickness, and reported thicknesses similar to my sites (Figure 17). However, the variability was very high in Amman (1975) and sample numbers low in Reid (1963). Also, in my study the phloem was only measured on the remaining unattacked trees, since phloem on attacked trees would have dried out. Trees that were attacked may have had thicker phloem. It is also interesting to note that in my study, there were no green trees in the

25-30 cm class[2] available for phloem thickness measurements in the north central stands, but there were four in the southern stands (see Figure 1). This may have been due to chance because the four green trees were found in three separate stands[3] with randomly selected plots.

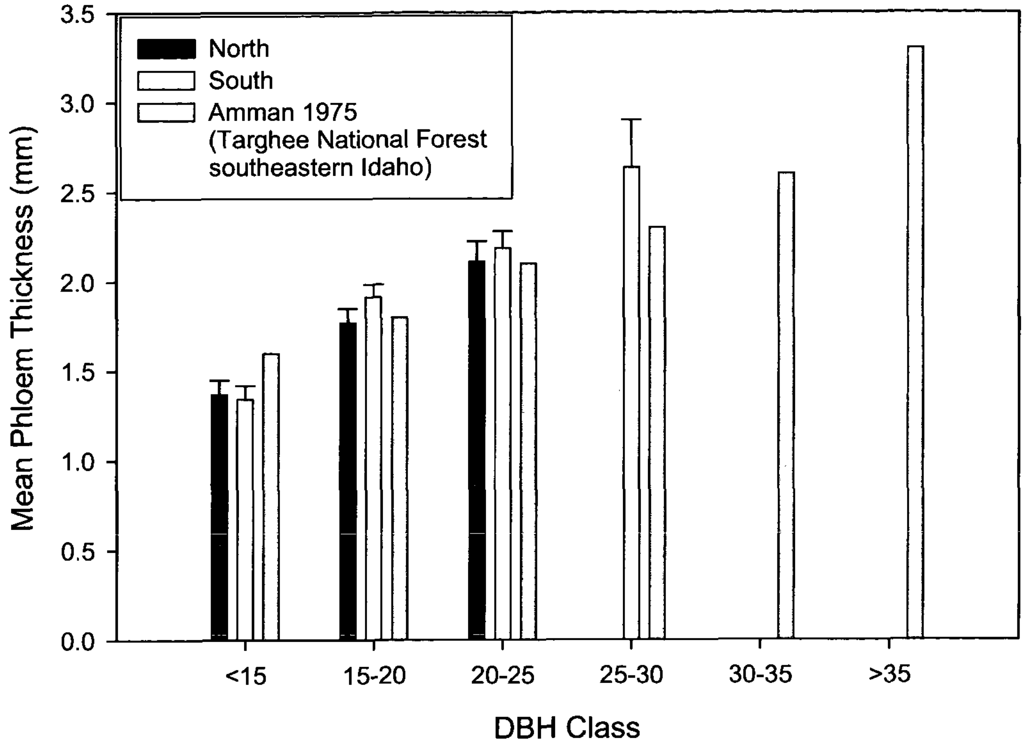

Figure 17. Mean phloem thickness comparisons between the north central and southern sites, and data from Amman (1975). Vertical bars represent standard error, and are not available from Amman (1975) due to insufficient access to original data.

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[2] There were no trees in the >30 cm class in either the northern or southern stands available for phloem thickness measurements.

[3] Two were in Alki-2, one in Alki-3, and one in Alki-5.

The important outcome from my results is that the influence of dbh on phloem thickness was about the same for both regions (Figure 1), and in both regions there was a significant increase in phloem thickness with increasing dbh. In addition, phloem thicknesses did not differ significantly between regions (Figure 1), but the means within two of three diameter classes were slightly higher for southern trees. This was somewhat unexpected given the higher densities of brood produced in the north central trees, and that Amman (1972) showed that phloem thickness was the most important factor in brood production. It has been reported that the nutritional quality of phloem may vary between trees (Miller and Keen 1960, Reid 1963), and in this case the phloem in the north central trees may have had higher nutritional quality than in trees in the southern sites. Other potential explanations may be that beetles in the north may be smaller or have smaller fat reserves (Bentz et al. 2001), and/or that trees in the north may have a lower defense. Also, there may be possible differences in ophiostomoid fungus associations. These explanations are out of the scope of this project and should be researched further.

Beetles in the north may also be better adapted to cooler summer temperatures as suggested by Bentz et al. (2001). Her study found that northern beetles developed faster, but were smaller. As I did not have a way of measuring beetle sizes because I sampled trees from which mountain pine beetle had already emerged, it is possible that even though there were many more beetles emerging from my north central sites, they were smaller, and hence the phloem was thicker relative to beetle size in the north than in the south.

3.5.2 Dbh and Pupal Chamber Density

My finding that brood density and total brood per tree increased with increasing dbh in both regions was analogous to previous studies (Reid 1963, Cole and Amman 1969). The productivity in north central trees was much higher than that previously reported for more southern populations. Reid (1963) found that trees 20-24 cm dbh averaged 366 brood/m^2, 25-30 cm dbh trees averaged 560/m^2, and trees greater than 30 cm dbh averaged 1065/m^2 (Figure 18). He measured only one tree in each of the 30-35 cm and 35-40 cm dbh classes, and trees were only sampled up to 1.5 meters along the tree bole. I took measurements at three equidistant points up the entire attacked surface of the bole, but when comparing my lower segment samples with those of Reid(1963) (Figure 18), his data matches more closely to my southern populations than to the north central populations. The small sample size for the largest dbh classes in Reid (1963) may cause these data points to be unrepresentative, but he had adequate sample sizes for the 20-25 and 25-30 cm dbh classes. Since the actual height above ground at which the sample was taken varied with the attack height on the tree, the measurements for the larger trees were from higher on the bole than for the same sized trees in Reid (1963). Consequently, my data may actually have underestimated brood density relative to Reid's (1963) measurements.

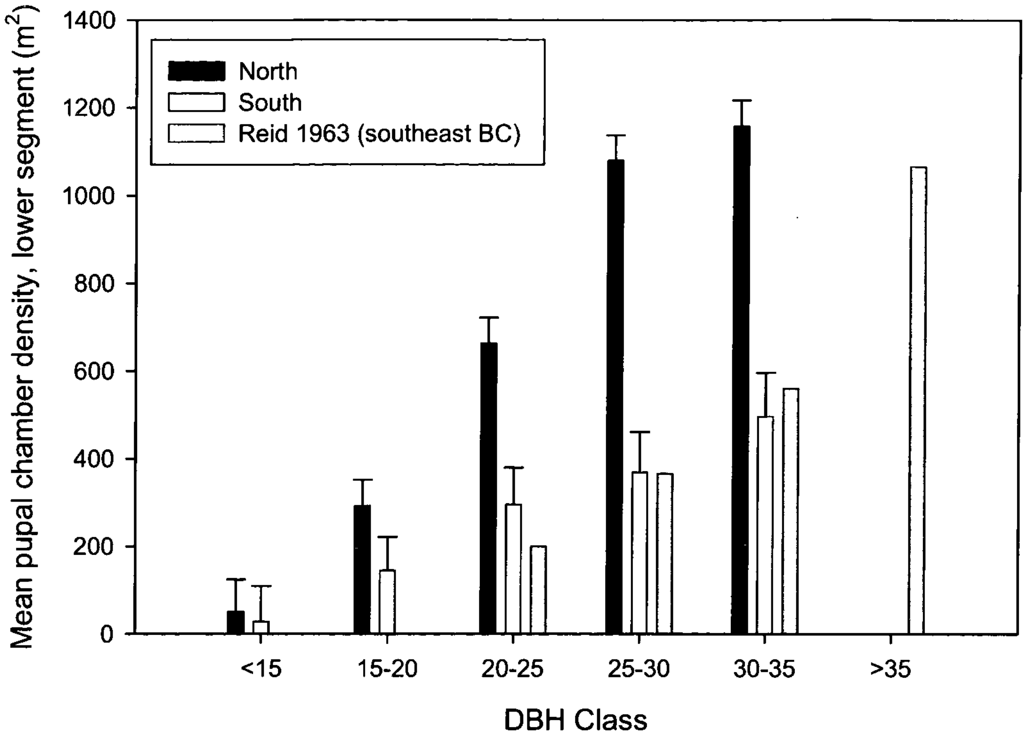

Figure 18. Brood density comparisons between my two regions and data from Reid (1963). Vertical bars represent standard error, and are not practical for the data from Reid (1963) due to the two largest dbh classes having only one sample tree.

3.5.3 Dbh and Pupal Chamber: Gallery Start Ratio

My findings that the number of pupal chambers produced per gallery start increases with increasing diameter in both my north central and southern trees is in concurrence with the literature. The number of pupal chambers produced per gallery start , however, is much higher in the north central trees (Figure 10), particularly in the 25-30cm and >30cm dbh classes. This is especially interesting because these larger trees have more surface area and higher attack heights than those in the southern sites; therefore the number of pupal chambers being produced in the north central trees is exponentially higher than in the southern trees. It is also interesting to note that since gallery start density was not related to productivity (see DBH section in results) intraspecific competition was not a determining factor in the higher pupal chamber: gallery start ratios in the north central trees.

The equation for the regression line for the north central data is y = 0.3209x – 3.3886 (where "x" is the dbh). The threshold dbh for a hypothetical 1:1 emergence ratio for the north central sites is 13.7 cm. The regression line equation for the southern data is y = 0.1336x – 1.1646. Using this equation, the threshold dbh for a hypothetical 1:1 emergence ratio is 16.2 cm.

Although the dbh threshold of a hypothetical 1:1 ratio of gallery starts to the number of pupal chambers was much lower in the north (13.7cm), the southern threshold of 16.2 cm was also much lower than the 25.4 cm proposed by Safranyik (1974). However, Safranyik (1968) found that trees with large crown volume produced the greatest number of beetles. My study did not take crown volume into account, but it may have played a role in influencing overall pupal chamber production as well as pupal chambers per gallery start ratios.

3.5.4 Relative Height

Reid (1963), Safranyik (1968), and Klein et al. (1978) all found that pupal chambers production decreases with increasing height up the tree bole. The trends from both my north central and southern trees agree with these previous studies (see Figures 11 and 12). This may be explained by the fact that phloem and outer bark thickness decreases with increasing height, and this is directly related to the amount of pupal chambers produced (Amman 1972).

My north central trees had higher productivity at higher levels up the tree than did my southern trees, likely because the north central sites were in a wetter Biogeoclimatic zone as well as an area where historically the climate was unsuitable for mountain pine beetle reproduction and development (see section 3.5.2.).

Another interesting pattern with my data is that there was no decline in pupal chamber densities from the middle segments to the upper segments in southern populations whereas there was in the north. This may be attributed to the upper segments occurring above the start of the crown in the south, whereas the lower and middle segments were usually located below the crown (ie., there was a regional difference in tree architecture). Greater shading from branches in the crown may have reduced moisture loss and heat in the southern sites, leading to higher pupal chamber production relative to the middle segment.

3.5.5 Absolute Height

As mentioned above, previous studies have shown a decrease in pupal chambers production with increasing height up the bole. Although there was substantial variation in my data, the trend (albeit weak) was similar to other studies (see Figures 17 and 18). The strongest relationships were in the two largest dbh classes, and the greatest differences between regions were also in the highest dbh classes (Fig. 16). There was not a large difference in the influence of height above ground on productivity, although in the largest two diameter classes, productivity seemed to increase slightly from the mid-range heights to the upper-range heights. This trend was also seen in the data for relative heights, and may be attributed to greater shading from the crown reducing moisture loss thus promoting higher beetle productivity.

When this is compared to the results from chapter 2, (*Lodgepole pine tree characteristics affecting mountain pine beetle attack: a comparison between north central and southern B.C.*) it is interesting to note that the biggest regional differences in gallery start densities occur in the smallest dbh classes, and in the largest trees the gallery start densities do not differ much between regions. In addition, gallery start density added just an additional 0.5% and 0.6% of variation for the north and south, respectively. This provides evidence that in this study, gallery start density did not have a significant effect on productivity, thus intraspecific competition was not a factor. Therefore greater pupal chamber production densities in the north are not related to a difference in gallery start density, but most likely related to the nutritional value (suitability) of the host as discussed in more detail below.

3.5.6 Conclusion

Because the phloem thicknesses were similar among similarly sized trees (Figure 9) and I compared productivity between regions by similar diameter classes, two of the most influential tree characteristics for pupal chamber productivity do not explain the regional differences I found. As mentioned above, Miller and Keen (1960) suggested that the nutritional quality of the phloem varies between trees, and this may have been one of the contributing factors causing the difference. Further research on the variation in phloem nutrition between trees and regions is needed.

Another possible explanation for this difference is that the north central sites were all in the dry, warm subzone of the Sub-Boreal Spruce zone, while the southern sites were in the dry, mild subzone of the Engelmann Spruce Subalpine Fir zone. Although the dry, warm subzone is one of the driest in the Sub-Boreal Spruce zone, the dry, mild subzone of the Engelmann Spruce Subalpine Fir is drier, and this may have influenced the moisture content of the phloem and outer sapwood (Coupé et al. 1991, Meidinger et al. 1991). However, Amman et al. (1977) reported that drying is more severe in smaller diameter trees than in larger, but in my study the biggest difference in pupal chamber production between regions was in the larger diameter classes (Figures 10 and 12). The southern sites were at a higher elevation, but in terms of climate and length of the growing season, the areas were similar based on Hopkins Bioclimatic Law (Hopkins 1919). This was supported by the observation that lodgepole pine growing in the southern region at the same elevation as the north central sites were mostly in mixed stands with ponderosa pine (*Pinus ponderosa* Dougl.) in the Interior Douglas-fir zone. This zone is much drier and warmer than the Sub-Boreal Spruce zone, with fire-dependent even-aged lodgepole pine stands at higher elevations and ponderosa pine at lower elevations (Meidinger et al. 1991). Based on my results, one could argue that mountain pine beetle productivity in this zone may be altered more by temperature-induced factors than host-tree size.

Alternatively, the difference regional productivity may be attributed more to host tree differences due to years of co-evolution with mountain pine beetle. Based on the work of Carroll et al. (2004), the southern sites were in an area where mountain pine beetle and lodgepole pine have likely co-evolved, whereas the north central sites were not. This may provide substantiation for a hypothesis that the trees in the north were more suitable hosts for brood production, and mountain pine beetle was able to exploit this resource more easily. The evidence discussed here from previous studies suggests that since the tree characteristics I measured did not sufficiently describe the differences between regions (i.e., phloem thicknesses were similar between regions for similarly sized trees). Further research is needed to determine if historic climate may influence host suitability. Carroll et al. (2006) generated climatic suitability classes for different climatic normal periods, making such a study feasible.

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Chapter 4: Influence of Historic Climate and Biogeoclimatic Zones on Mountain Pine Beetle Productivity in Lodgepole Pine

Abstract

Invasive insects and insects expanding their range often show a higher realized reproduction than in their native range. I tested the hypothesis that the mountain pine beetle performs better in lodgepole pine growing in areas with previously unsuitable climatic conditions. I felled and sampled trees ≥25 cm diameter at breast height in four areas in each of two biogeoclimatic zones. In each biogeoclimatic zone, I chose three stands from historically climatically suitable and unsuitable areas, respectively. Gallery start density was not significantly different in any of the areas. Pupal chamber productivity was significantly higher in areas with historically low climatic suitability than in areas with historically high climatic suitability. I hypothesize that a lack of selection pressure against susceptible and suitable trees may be the explanation for this relationship.

Keywords: Climatic suitability class, lodgepole pine, mountain pine beetle, suitability, susceptibility, selection pressure

4.1 Introduction

The range of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) is not limited to the north by its primary host tree (*Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm.), which extends into the Yukon and the Northwest Territories. Instead, the northern limit of the mountain pine beetle is determined by climate and elevation (Safranyik 1978) with the range of climatic suitability encompassing the southern half of British Columbia and southwestern Alberta in Canada. In the United States, it occurs in 12 western states but is limited by elevation (Amman 1973).

Historically, the mountain pine beetle annually affects an average of 50,000 ha of forested lands in British Columbia alone (Wood and Unger 1996). Large epidemics occur periodically (Taylor et al. 2006), in which more than 80% of host trees over 10 cm dbh may be killed over large expanses (Safranyik 1988). However, in the current outbreak in British Columbia the area infested as of 2007 has reached approximately 10.3 million[4] hectares (Westfall and Ebata 2008). It has also spread into areas further north and at higher elevations than recorded previously.

Presumably due to the extremely large population of beetles, smaller diameter trees (<10 cm dbh) and younger trees than usual are being attacked and killed in the current epidemic. Successful attacks have also been reported from interior hybrid spruce, *Picea glauca* (Moench) Voss x *Picea engelmannii* Parry ex. Engelm., (Huber et al. 2008). These somewhat extreme occurrences, along with my results with respect to pupal chamber production (Chapter 3) led me to hypothesize that mountain pine beetle may be more successful in lodgepole pine forests that have not experienced outbreaks in recorded history.

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[4] This figure includes "trace" amounts of infestation.

Research on the effects of climate change has led to the prediction that the mountain pine beetle's range will expand further north and to higher elevations at an increasing rate based on current climate change modeling (Logan and Powell 2001, Carroll et al. 2004). According to Houghton et al. (1990), temperatures are predicted to increase by 2.5 °C with a doubling of atmospheric CO_2. A 3 °C change in mean annual temperature corresponds to a 300-400 km latitudinal shift in isotherms, or 500 m in elevation (Hughes 2000). Range expansion in response to climatic change has been reported in Great Britain for birds (Thomas and Lennon 1999) and insects (Thomas et al. 2001). Over a 20-year time period, Thomas and Lennon (1999) reported an 18.9 km northward shift in the northern limit of several bird species, which they attribute to a period of climate warming. Thomas et al. (2001) reported approximately 3- to 15-fold increases in expansion rates of the silver-spotted skipper in Great Britain, and suggested that both ecological and evolutionary processes are most likely the cause.

Temperature decreases with an increase in latitude and/or elevation, and although factors such as topography and proximity to coastal areas may also have a profound effect on mean temperatures, latitude is the primary factor (Geiger et al. 1995). According to Lambert's Cosine Law (Geiger et al. 1995) the direct energy of the sun varies with the cosine of the latitude due to the curved surface of the earth. The equatorial regions get direct solar radiation up to 23.5° N/S latitude. The angle of the sun then gets increasingly oblique with latitude. A model of climate normals in British Columbia (Murphy 1996) suggests that for a one degree increase in latitude, there is a 1°C decrease in annual mean daily temperature. However, this is the average throughout the year, and may differ when only the growing season temperature means are considered.

Altitude also has a similar effect on temperature. Every 1°N latitude increase is roughly equivalent to 120 m increase in elevation while staying at the same latitude according to Hopkins Bioclimatic Law (Hopkins 1919). Safranyik (1978) found that this adjustment is remarkably similar to the equivalent range of mountain pine beetle in terms of altitudinal and latitudinal boundaries. For instance, near the northern limit of the beetle's range, the altitudinal limit for beetle survival is roughly 750 m above sea level, while at the southern most range the altitudinal limit is approximately 3650 m (Struble and Johnson 1955).

Based on work by Safranyik et al. (1975), Carroll et al. (2004) created a spatially explicit climatic suitability class (CSC) overlay for historic mountain pine beetle populations within British Columbia. This classification takes into account historic climatic conditions (i.e., 30-year climate normals), along with factors such as elevation, slope and aspect. When overlaying these historic data on current mountain pine beetle infestations, Carroll et al. (2004) reported an expansion in the range of benign habitats, as well as an increase (at an increasing rate) in the number of infestations since 1970 in previously climatically unsuitable habitats. They suggest that with the predicted warming trends associated with climate change, the range of mountain pine beetle will expand further north and to higher elevations than currently reported.

The current outbreak spans most of both low and high historical climatic suitability class ranges in British Columbia, allowing a comparison of populations in these CSCs. No such comparison has been made previously. Increased knowledge of the importance of CSCs on mountain pine beetle population dynamics may aid in future management of the lodgepole pine resource in British Columbia, and potentially help to avert future outbreaks of the magnitude seen today.

4.2 General Objective

The objective of this study was to investigate potential differences in mountain pine beetle productivity among biogeoclimatic subzones and historic climatic suitability classes in British Columbia. More specifically, I tested the hypothesis that in areas where the climate was historically optimal for the mountain pine beetle, host trees were less suitable for reproduction today than in areas where the beetle has not reached epidemic levels in the past.

4.3 Methods

4.3.1 Study Sites

Sampling was conducted in two regions during the summer of 2005, and in two additional regions during the summer of 2006. In 2005, trees were sampled in the Prince George Forest District (approx. 53.9° N, 123.5°W) and in the Rocky Mountain Forest District (approx. 49.5°N, 116.2°W) (Chapters 2 and 3). Sites in the Prince George Forest District were in the Sub-Boreal Spruce dry-warm subzone (Meidinger et al. 1991) and in "very low" and "low" climatic suitability classes (i.e., unsuitable for mountain pine beetle) based on 1921-1950 climate normals (Carroll et al. 2004). The 1921-1950 period was selected, since this period is representative of historical CSCs, i.e., climate conditions occurring prior to the current rapid warming trend. Sites in the Rocky Mountain District were in the Engelmann Spruce-Subalpine Fir dry-mild subzone (Coupé et al. 1991) and in "high" and "extreme" CSCs (i.e., highly suitable for mountain pine beetle) based on 1921-1950 climate normals. Based on present day climatic conditions (using 1981-2010 normals), both the Prince George and Rocky Mountain Forest District sites were in “high” and “extreme” CSCs.

In 2006, sampling was conducted in the Columbia Forest District (approx. 51.1°N, 116.3°W) and the 100 Mile House Forest District (approx. 52.0°N, 121.2°W). Sites in the Columbia Forest District were in the Engelmann Spruce - Subalpine Fir dry-cool subzone (Coupé et al. 1991) and in “very low” and “low” historic CSCs using the 1921-1950 normal period (Carroll et al. 2004). Sites in the 100 Mile House District were in the Sub-Boreal Spruce dry-warm subzone (Meidinger et al. 1991) and in “high” and “extreme” historic CSCs. Based on present day CSC (1981-2010 climate normal) the sites in the 100 Mile House Forest District remained “high” or “extreme”, while they were “low” for the Columbia Forest District sites (Table 1).

Table 1. Selection matrix of Biogeoclimatic zone (BEC), Forest District, and historic Climatic Suitability Class (CSC); using the 1921-1950 normal period.

BEC	Forest District	Historic CSC	Current CSC
SBSdw	(2005) Prince George	low/very low	high/extreme
	(2006) 100 Mile	high/extreme	high/extreme
ESSFdm/dk	(2006) Columbia	low/very low	low/very low
	(2005) Rocky Mountain	high/extreme	high/extreme

Sites were selected by conducting an intersection of three spatial data layers using a geographic information system. These layers were historic CSC, biogeoclimatic (BEC) subzone, and recent mountain pine beetle infestation as recorded from aerial surveying (Figures 1a and 1b). Polygons in which this intersection was equal to or greater than 10 hectares in area were considered for sampling.

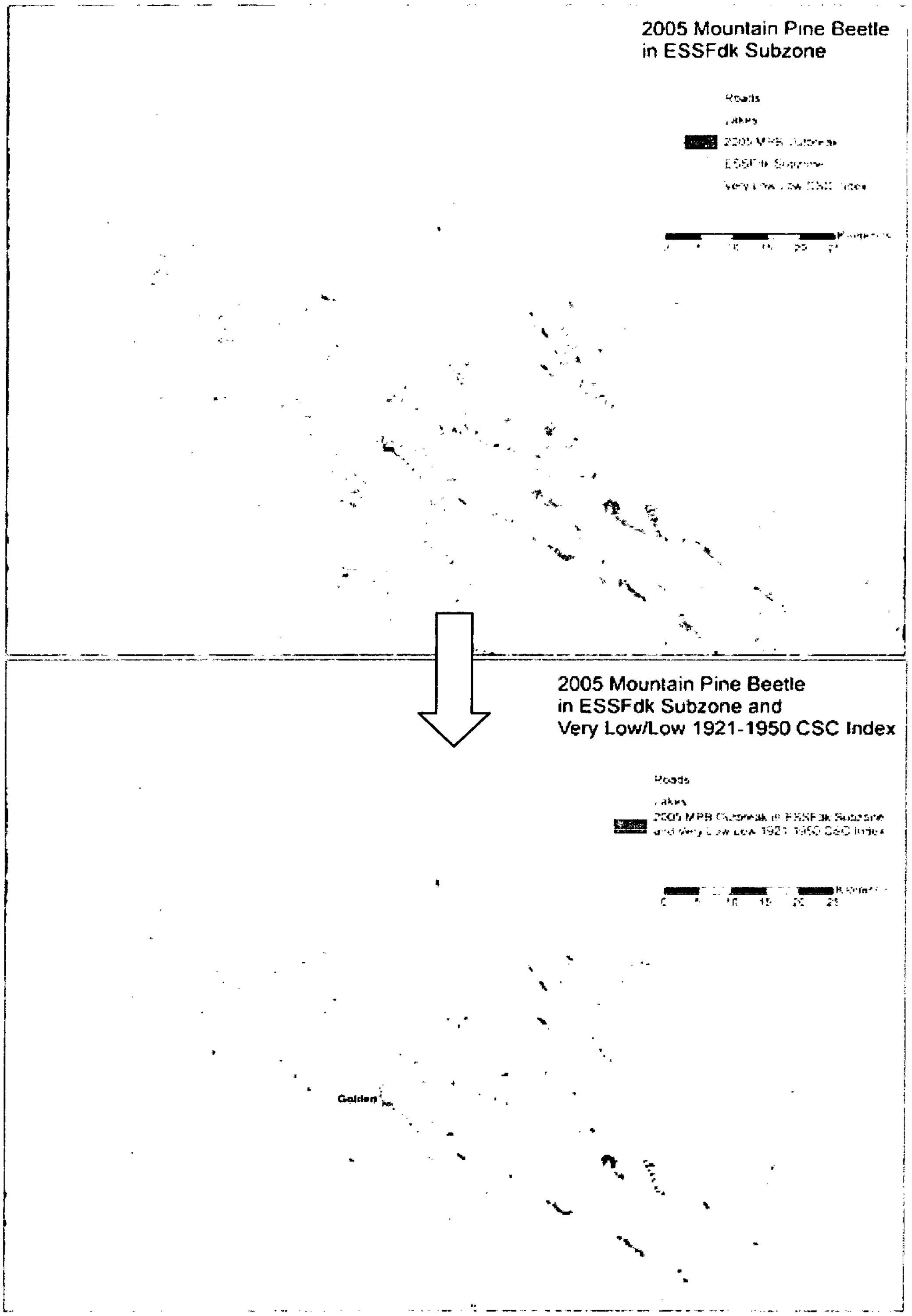

Figure 1a. GIS intersection of low and very low climatic suitability classification (1921-1950 normal period), dry-cool subzone of the ESSF biogeoclimatic zone, and recent (2003-2005) mountain pine beetle infestation for Golden region, with small box in lower figure showing study area (maps created by Gurp Thandi, CFS).

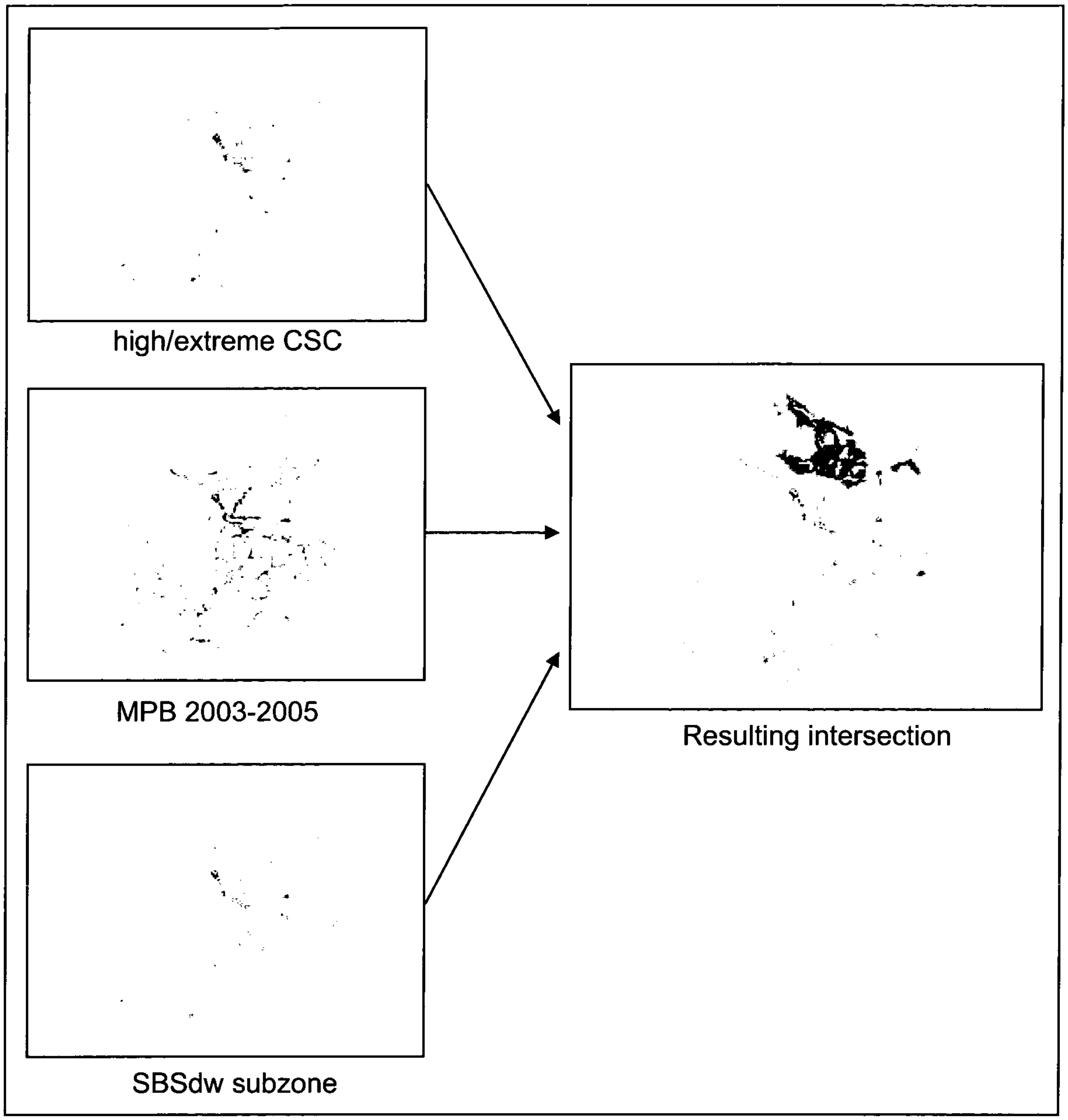

Figure 1b. GIS intersection of high and extreme climatic suitability classification (1921-1950 normal period), the dry-warm subzone of the SBS biogeoclimatic zone, and recent (2003-2005) mountain pine beetle infestation for 100 Mile House region (maps created by Gurp Thandi, CFS).

4.3.2. Site Characteristics

Species composition was considered comparable for all four regions, with lodgepole pine dominant (60 – 99 %) at all sites (Table 2). Percent mortality was highest in the 100-Mile House area (100 Mile House Forest District) (69%), followed by Prince George (Prince George Forest District) (67%), Kimberley (Rocky Mountain Forest District) (55%), and Golden (Columbia Forest District) (28%).

Table 2. Summary data for the stands sampled in all four regions (2005 and 2006). Percent mortality is the % killed of available lodgepole pine in the stand.

FOREST DISTRICT	ELEV. (m)	YEAR SAMPLED	MEAN RING COUNT	% PINE	MPB MORTALITY (% PINE)
Prince George	950	2005	113	75	45
Prince George	850	2005	132	79	61
Prince George	883	2005	89	97	43
Prince George	765	2006	148	82	86
Prince George	898	2005	146	88	67
Rocky Mountain	1500	2005	112	91	80
Rocky Mountain	1756	2005	103	92	41
Rocky Mountain	1473	2005	109	99	43
100 Mile House	976	2006	120	90	62
100 Mile House	956	2006	120	99	73
100 Mile House	1003	2006	122	94	69
Columbia	1870	2006	152	81	14
Columbia	1640	2006	160	60	35
Columbia	1775	2006	138	63	36

4.3.3 Stand selection and sampling

Five stands in the Prince George District and three in the Rocky Mountain District were sampled in the summer of 2005 (Chapters 2 and 3). In both Districts, these stands were lodgepole pine leading, 80 years or older, and of similar density. All stands were at least 10 hectares in area and a minimum of 1 km apart. Stands were selected in areas in which the mountain pine beetle epidemic was judged to be in the final stages and, therefore, the majority of the beetle population had left the stand. Particular emphasis was placed on selecting stands with similar local beetle populations.

A minimum of 8 randomly selected, variable-radius plots per stand were surveyed using a prism with a basal area factor (BAF) of 4. A baseline was established at a randomly selected angle from a point of commencement. Transects off the baseline were then put in at randomly selected distances by selecting numbers from a random number table between 80 and 150 m. In each plot, tree species, diameter at breast height (dbh), and attack status were recorded for each tree over 7.5 cm dbh.

Three stands in the 100 Mile House District and three in the Columbia District were sampled in 2006. A timber cruise was performed to report on the percent mortality, diameter distribution, and species composition of each stand. These plots were established using randomly selected distances from points where trees were felled. From each of these points, transects were put in at 90°, 180°, 270°, and 360°. A plot was established at a random distance along any or all of these bearings, as long as they fell within the stand. A minimum of 4 plots was established per stand[5].

4.3.4 Sample-tree Selection

In 2005, a minimum of 2 trees were selected to be felled for intensive sampling at each plot. To maintain an equal representation of diameters, six trees from each of the following five diameter classes were selected if available: <15 cm, 15-20 cm, 20-25 cm, 25-30 cm, and >30 cm (only data from trees from the 25-30 and >30 cm classes were used in this chapter as these were the only size classes sampled in 2006). If the desired tree size was not available from within the plot, the closest tree to the plot center in the desired diameter

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[5] Only 4 plots per stand were sampled in 2006 because I was mainly interested in felled tree parameters and the plot data was used only for determining percent mortality in the stand. In 2005 the plot data was also collected for a concurrent study (Björklund et al. 2009).

class was felled along the transect to the next plot. Trees selected for intensive sampling were at least 50 m from edges of stands, lakes, or any open area to minimize edge effects. At least one dominant or co-dominant tree was selected from within the plot so that an age count could be recorded from the stump.

In 2006, transects were put in at randomly selected angles and trees were selected at randomly selected distances between 80 and 150 m. A total of five trees in each of the 25-30 cm and >30 cm classes were selected per stand. The three closest trees to each point which met the following criteria were selected for felling: dbh of 25-30 cm or >30 cm; beetles had completed life cycle and emerged from tree; no major wounds, cat faces or forks; and a minimum of 50 m from edges of stands, lakes, or any open area to minimize edge effects. A ring count was made at the stumps of all felled trees.

4.3.5 Intensive Sampling

The attack height, defined as the distance from the base of the tree to the highest pitch tube and/or gallery start, was measured on each tree. The attacked portion was cut into 3 equal segments, and the diameter at the midpoint of each segment was measured. The sampling unit was a 15x30 cm rectangle (Safranyik 1968) cut in the bark at the midpoint of each of the three segments. This allowed the absolute height above ground of each sampling point to be calculated from the overall attack height. Each segment was sampled for gallery start density, exit hole density and pupal chamber density on the north[6] aspect of the bole.

Gallery start density was obtained by peeling off the outer bark to reveal each gallery and its starting point, and this number was multiplied by 22.22 to obtain density per square

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[6] Both the north and south aspects of the tree bole were measured during the summer of 2005. Early analysis showed that gallery start densities and productivity levels were similar regardless of aspect (for both regions), so for 2006 I sampled only the north aspects. Therefore, for this chapter only the data from the north aspects was used for the Prince George Forest District and the Rocky Mountain Forest District, while in chapters 2 and 3 I used the average of the north and south aspects of the bole.

meter. Pupal chamber density was obtained by peeling off the outer bark to reveal each individual pupal chamber, and this number was multiplied by 22.22 for the density per square meter.

Mean gallery start density was calculated for each tree from the segment means. The gallery start total for each tree was calculated by multiplying the mean gallery start density by the total surface area of the attacked portion of the bole. Mean pupal chamber densities were calculated using the same method.

4.3.6 Data Analysis

A between-subjects, nested design two-by-two factorial ANOVA was conducted to analyze the effects of historic climate (CSC) and biogeoclimatic subzone (BEC) on mountain pine beetle gallery start density. Stands were nested within each treatment. A Levene's test of equality of error variances was conducted and showed that the assumption of homogeneity of regression variance was met (P=0.420).

A between subjects two-by-two factorial ANOVA with stands nested within each treatment was also used to analyze the effects of CSC and BEC on mountain pine beetle productivity. Homogeneity of regression variances was tested using a Levene's test (P=0.177).

To test the effects of CSC and BEC on the overall mean number of pupal chambers produced per attacking gallery start , another two-by-two factorial nested ANOVA was performed. Homogeneity of variances was not met for untransformed data (P<0.05). A square root transformation of the data satisfied a Levene's test of homogeneity of variances (P=0.774).

The level of significance was set at α=0.05 for all statistical tests. Data were analyzed using SPSS 13.0 (SPSS Inc., Chicago, IL, USA). Graphs were created using SigmaPlot 9.0 (Systat Software, Inc., Port Richmond, CA, USA).

4.4 Results

4.4.1 Gallery Start Density

Gallery start density did not differ significantly between historically low/very low CSCs and high/extreme CSCs (*F*=10.17, df=1,3, *P*=0.061), although the trend was for slightly higher densities in regions of high/extreme historical suitability (Figure 2). The sites in the Sub-Boreal Spruce dry-warm subzones also did not have significantly different mean gallery start densities from sites in the Engelmann Spruce – Subalpine Fir dry-cool subzones (*F*=2.43, df=1,3, *P*=0.239).

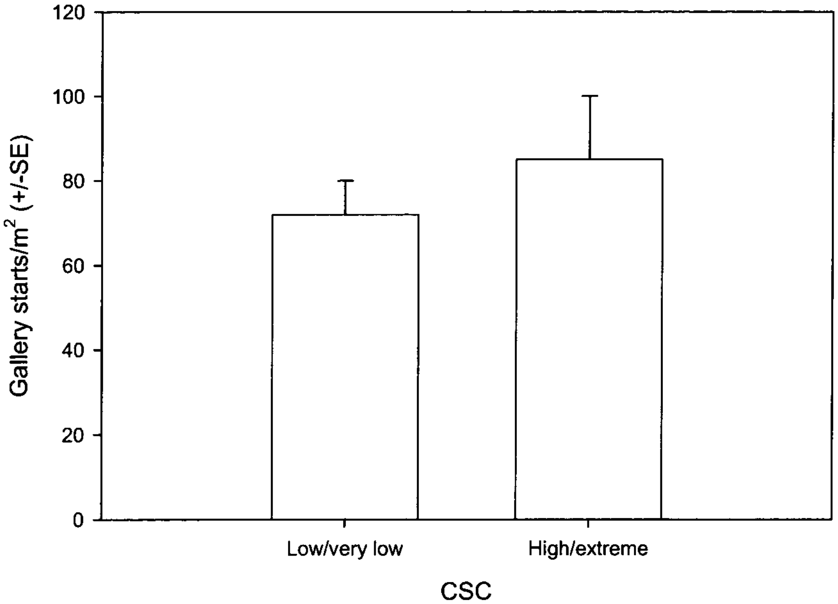

Figure 2. Mean gallery start density for sites in low and very low historical climatic suitability classes vs. those in historically high and extreme climatic suitability classes. Vertical bars represent standard error.

4.4.2 Pupal Chamber Density

Areas in which the historical climate suitability was low had significantly higher pupal chamber densities than areas with high historic suitability (*F*=22.72, df=1,3, *P*<0.05). Pupal chamber density in regions in the Sub-Boreal Spruce dry-warm subzones did not differ significantly from regions in the Engelmann Spruce – Subalpine Fir dry-cool subzones, i.e., in different biogeoclimatic zones but high historic climatic suitability (*F*=5.30, df=1,3, *P*=0.128) (Figure 3). The interaction effect of CSC and BEC was significant (*F*=32.43, df=1,3, *P*<0.05) because there was a difference in mean pupal chamber densities between these biogeoclimatic zones with low historic suitability.

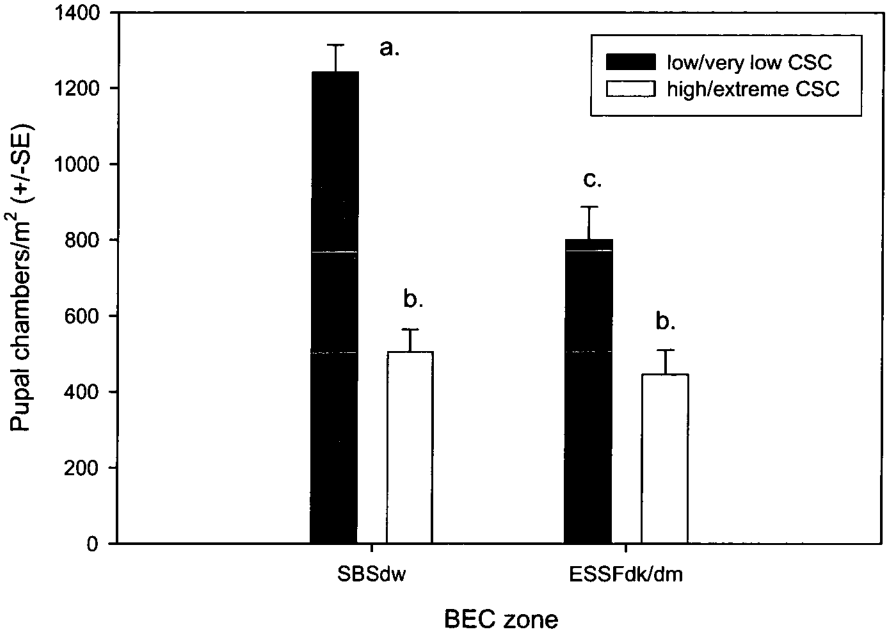

Figure 3. Comparison of mean pupal chamber densities between sites in the Sub-Boreal Spruce dry-warm subzones and sites in the Engelmann Spruce – Subalpine Fir dry-cool/dry-mild subzones for both low/very low and high/extreme historical climatic suitability classes. Vertical lines represent standard error.

4.4.3 Pupal Chamber: Gallery Start Ratio

The ratio of the number of pupal chambers produced per gallery start was significantly higher in regions with historically lower suitability for mountain pine beetle than areas with higher historic suitability (*F*=44.38, df=1,3, *P*<0.01) (Figure 4). The effect of BEC was not significant (*F*=2.67, df=1,3, *P*=0.234). The interaction effect of CSC and BEC was also not significant (*F*=1.1, df=1,3, *P*=0.404).

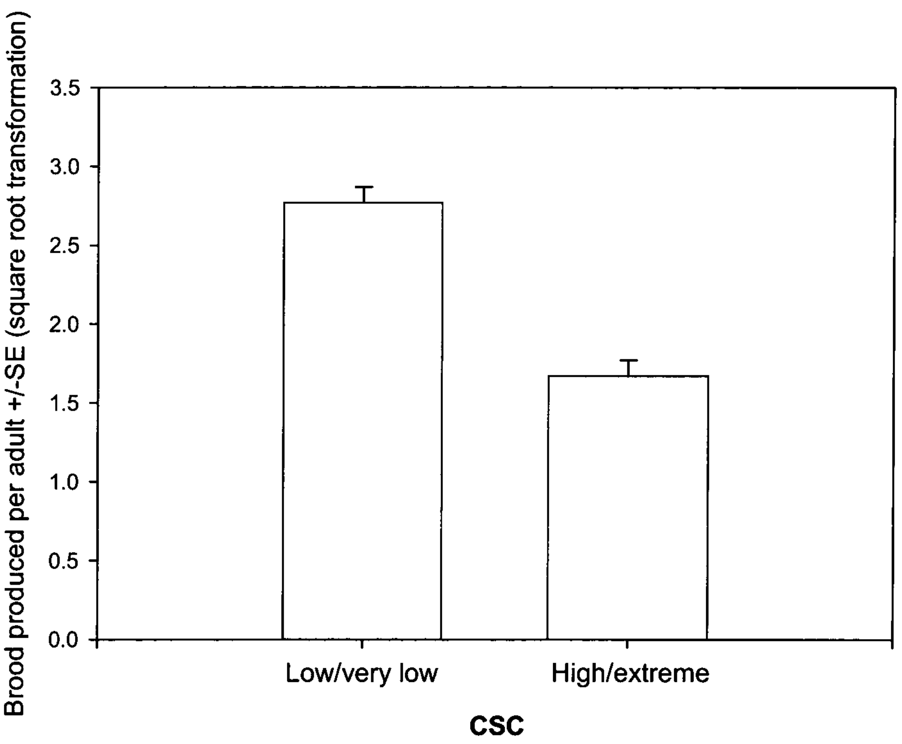

Figure 4. Mean number of pupal chambers produced per gallery start in sites of low and very low historical climatic suitability vs. sites with historically high and extreme climatic suitability for mountain pine beetle success (square root transformation of data). Vertical bars represent standard error.

4.5 Discussion

4.5.1 Site Characteristics

Although the percent lodepole pine mortality in the Columbia Forest District was much lower than the other three regions, there was no difference in gallery start density (see

Figure 2). Consequently, at the tree-level, beetle pressure may be considered to be similar in all four regions. The mean elevation for the sites in Columbia Forest District was higher than in the Rocky Mountain District, and normally this would be a cause for lower productivity (Amman 1973); however, the opposite was true. In addition, all three of the other sites are in present-day[7] high/extreme CSCs, while the Columbia sites are still in low/very low CSCs. Therefore, the productivity that was observed in the Columbia District would have likely been even higher, and similar to the Prince George District sites, had the climate been more suitable. The fact that the productivity was as high as it was in low/very low CSCs suggests that current climatic conditions are not limiting, but that variation in beetle pupal chamber productivity is instead likely mainly influenced by host tree characteristics, e.g., the suitability of available genotypes.

The fact that historic climatic suitability affected mountain pine beetle productivity, while BEC subzone did not, suggests that areas in which mountain pine beetle epidemics have not been historically present may have more suitable trees for mountain pine beetle reproduction. This is also supported by my results that gallery start densities did not differ significantly between CSCs or BEC subzones.

4.5.2 Co-evolution

The term “coevolution” was coined in 1965 (Ehrlich and Raven 1965) to describe “those interactions between organisms of different species in which evolution in one member of an interacting pair elicits an evolutionary response from the other member” (Mitton and Sturgeon 1982). Coevolutionary adaptations are recognized as an ever-present phenomenon,

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[7] The present-day CSCs are based on the 1981-2010 climate normal, as opposed to the historic CSCs which are based on the 1921-1950 climate normals.

and have been shown between plants and pollinators (Powell and Mackie 1966, Ramirez 1970) as well as predators and their prey (Sheppard 1962).

The coevolution between bark beetles and their host trees is an ancient one, and can be traced back to the Triassic Period (Sturgeon and Mitton 1982). The relationship between mountain pine beetle and lodgepole pine can be viewed as a predator-prey adaptation (Berryman et al. 1985). In areas where mountain pine beetle and lodgepole pine have coevolved (e.g., Rocky Mountain and 100 Mile House sites), the most susceptible and suitable trees may have been selected against over time. Mountain pine beetles must kill their host to survive; therefore, during outbreaks the most susceptible trees are taken out of the gene pool. In addition, the most suitable trees would produce the most pupal chambers, generating higher intensity outbreaks, i.e., a higher selection pressure. The resulting stands would thus be made up primarily of genotypes that were not attacked. Although the most susceptible and suitable trees have been selected against, the remaining genotypes could still be suitable enough for sustaining outbreaks, as seen in the Rocky Mountain and 100 Mile House Districts. The higher suitability of trees in areas with historically low climatic suitability may explain why the current outbreak in north central BC is largest on record.

4.5.3 Phloem Nutritional Value

The higher pupal chamber productivity in trees in areas with historically unsuitable climate can be due to higher susceptibility (weaker defense) or higher suitability (higher quality resources for insects and their associated fungi). My results showed that phloem thickness did not differ between the CSC classes, so the quantity of nutrients per volume of phloem tissue may have been higher in lower CSC classes. Phloem compression may differ among trees depending upon their growth rates, and therefore the amount of actual phloem tissue may differ in trees with the same recorded phloem thickness (Cabrera 1978). Alternatively, coevolved trees may have polyphenols (e.g. tannins, phenylpropanoids, etc.) that reduce the digestibility of the available nutrients (Hemingway et al. 1977). This was not tested in this study but recent research (E. Clark[8], unpublished data) indicates a weaker secondary resinosis response in north central trees than in southern trees.

From an evolutionary point of view, trees with the highest nutritional value in their phloem tissue should be more pre-disposed to out-compete trees with lower nutritional value, due to more vigorous growth rates and higher success in regeneration (Amman et al. 1988, Schmidt 1988). While it may be argued that competition between trees would be a higher selective pressure than from periodic mountain pine beetle outbreaks, this difference in phloem nutrients may be negligible from a between-tree standpoint. However, it may be different enough from a mountain pine beetle perspective to effectively cause the differences seen in mean productivity in my results.

4.5.4 Impact of Warmer Temperatures on Prince George Trees

It has been shown in provenance trials in B.C. that productivity in lodgepole pine is reduced when planted in areas with a higher mean annual temperature than where its genetic parents were located (O'Neill and Yanchuk. 2005, Wang et al. 2006). This would mean that in the sites where the CSC has gone from low to high in the past 80-100 years (slightly less than the mean age of the trees), the lodgepole pine would theoretically have reduced productivity. This may partially explain why the beetle productivity was significantly higher in Prince George than in the Golden sites, because the CSC rating changed from low to high in Prince George (over the past 80-100 years), while in Golden it remained low during this same time period.

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[8] Graduate Student, University of Northern British Columbia, Prince George, BC

4.5.5 Range Expansion: A Similarity to Exotic Species?

Although many animals tend to be relatively specialized at the extreme margins of their geographic range (Thomas et al. 1999), my results suggest that mountain pine beetle is flourishing in marginal regions. A similar situation was reported in Thomas et al. (2001), where several insect species in England have increased their variety of habitat types and dispersal tendencies.

In my study, I found that mountain pine beetle has higher productivity in forests where it has not existed at epidemic levels in recorded history than in forests where it has been recorded to have had many periodic outbreaks in the past. Therefore, these forests that have not seen historic outbreaks could be considered "inexperienced" or "naïve" to mountain pine beetle. This situation may be likened to that of emerging organisms invading new ecosystems and becoming more successful there than the native species. Such a situation is illustrated by *Cercospora* needle blight, which has infested native pine forests in India, and where it is a common pest in radiata pine (*Pinus radiata*) plantations (Bright 1998). In New Zealand and Chile, exotics have become a major threat to the established plantations, and exotic pests in Uruguay have become so successful in radiata pine the use of plantations has been abandoned (Hammond 1995).

There is evidence to suggest that exotic and emerging pests are more destructive than native pests (Liebhold et al. 1995, Niemelä and Mattson 1996). Emerging species (and native species expanding their range into novel ecosystems) may be so successful because they are in new ecosystems in which trees have not evolved specific defense mechanisms, and where there are fewer natural enemies. Commonly, successful invasions are associated with environmental stresses such as global warming, changing climate, habitat modification and fragmentation of habitat (Krcmar-Nozic et al. 2000). An example of this is the dramatic colonization of North American habitats by exotic European phytophagous insects, in which Niemelä and Mattson (1996) suggest that the exotic insects are much better competitors than the native species. In many of these cases, European insects are more productive because while they are in a climate and ecological system similar to their native range, their native enemies and competitors are not present. In addition, host availability is usually much higher in the colonized territory (Niemelä and Mattson 1996). Insect productivity is positively related to the host plant's geographical range as well as to the average local abundance of plants within that range (Strong et al. 1984), and invasive pests usually are most successful when there is low diversity, limited intra-system competition, and soil and climatic conditions similar to the invasive species' native conditions (Krcmar-Nozic et al. 2000).

Although the mountain pine beetle is native to BC, it could be considered as invasive/emerging because it is moving into and inhabiting areas for which we have no records of previous outbreaks at epidemic levels (Krcmar-Nozic et al. 2000). It did, however, occupy some of these areas at endemic levels (Lewis and Hrinkevich 2008), but the populations would have been so small that the associated native predators would not have high enough populations to affect epidemic populations of mountain pine beetles. In addition, trees would not have evolved defensive mechanisms because beetles in the endemic stage exist mainly in dead and dying trees, and the population is relatively static (Safranyik and Carroll 2006). Since this emersion into a new ecosystem is very similar to the situation with exotic species, it is not unreasonable to attribute some of the success that mountain pine beetle has in naïve forests to the same causes.

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5. Conclusions

The objective of this study was to increase my understanding of mountain pine beetle – lodgepole pine interactions, with particular reference to geographic variation during the epidemic population phase. The general purpose was to determine if there are significant differences in the insect – host interactions among differing ecological and latitudinal extents of the current outbreak, and if so, whether this is related to latitude or the fact that mountain pine beetle has not been recorded in these systems historically.

The mountain pine beetle, *Dendroctonus ponderosae* Hopk., has been studied in great detail over a large geographical range in the past 50-60 years. Amman and Cole (1983) did much of their work in Utah and Wyoming, Raffa and Berryman (1983) were in Washington and Northern Idaho, Berryman (1976) worked in Idaho and Montana, Mitchell and Preisler (1991) studied the beetle in central Oregon. In Canada, Reid (1962a, 1962b, 1963) did much of his work in southeastern British Columbia, while Safranyik (1968, 1974) studied mountain pine beetle from across its range in BC.

The information published in the literature to date covers many different geographic regions, and there are definitely differences due to climate, elevation and forest variables. However, the trend that mountain pine beetle usually selects large, apparently healthy trees in a stand first remains true across all studies. During the current "hyper-epidemic" in British Columbia, the outbreak has extended further north than previously recorded, and it has been at a higher intensity. Beetles in the north central sites are also utilizing more surface area on the trees for reproduction, which leads to faster population growth. This, along with a favorable climate and the large, continuous forest type of mature lodgepole pine in north central BC, has led to the explosive development of the outbreak. These conditions provided an opportunity to study the insect under somewhat unusual circumstances.

The main purpose of this study was broken down into three specific objectives: 1) compare and contrast beetle attack dynamics in north central sites (Prince George Forest District) with that of southern sites (Rocky Mountain Forest District) as a function of host characteristics (susceptibility); 2) compare host suitability in relation to pupal chamber production for the two regions as a function of host characteristics (suitability); and 3) test the hypothesis that trees in areas of low historic climatic suitability (Carroll et al. 2004) for mountain pine beetle will have significantly higher pupal chamber production than those of high historic suitability.

The original hypothesis in this study was that during the current outbreak in north central BC, smaller diameter trees than ever before were being attacked and producing brood. I set out to investigate if there were some tree characteristics such as age, growth rate, bark roughness, phloem thickness, or dbh significantly affecting attack and pupal chamber productivity parameters at differing heights along the bole. Results from the southern BC sites (Chapters 2 and 3) corresponded well with reports from the literature (chapters 2 and 3). Results from north central BC differed in that diameter did not significantly affect attack (gallery start) densities. Gallery start densities on small diameter (<15 cm dbh) trees were significantly higher in north central BC than in southern BC. Gallery start density declined with relative height in the south, but not in north central BC. Gallery start densities were significantly higher on small trees, and extended much further up the tree bole, in north central BC compared to southern BC.

Pupal chamber productivity at my southern sites was similar to productivity reported in the literature, whereas productivity was higher in the north. Diameter accounted for 52.3 % and 42.8 % of the variation in pupal chamber production (pupal chamber density) in north central and southern BC, respectively. Gallery start density added less than 1%, indicating that gallery start densities were not generally high enough to generate significant intraspecific competition. Regression analyses indicated that in the south, a ratio of 1:1 or greater emerged pupal chambers per gallery start occurred in trees larger than 16.2 cm dbh, whereas in the north, this ratio was achieved at 13.7 cm dbh. Pupal chamber densities in north central trees were as high or higher than in the most productive part of the southern trees (the lower third) regardless of relative height, indicating significantly higher host tree suitability in north central trees.

The influence of dbh on phloem thickness was about the same for both regions, and in both regions there was a significant increase in phloem thickness with increasing dbh. In addition, phloem thicknesses did not differ significantly between regions, but the means within two of three diameter classes were slightly higher for southern trees. This was somewhat unexpected given the higher densities of brood produced in the north central trees, and that Amman (1972) showed that phloem thickness was the most important factor in brood production.

My results indicated that north central trees are more suitable for brood production than southern trees. The biggest difference between regions was that many more beetles were being produced in the larger diameter trees in the north than the same diameter classes from the south. I hypothesized that this is in part due to a lack of selection pressure on north central pine populations, since these stands have been in climatically unsuitable areas up until recently. To test this hypothesis, I chose two additional sites in the same biogeoclimatic (BEC) zones but opposite historic climatic suitability classes (CSCs).

The results from the second summer of field sampling suggested that differences in historic climate rather than BEC zones were responsible for the higher productivity numbers in the north. I felled and sampled trees ≥25 cm diameter in four areas in two biogeoclimatic zones. In each biogeoclimatic zone, I chose three (five in one area) stands from historically climatically suitable and unsuitable areas, respectively. Gallery start density was not significantly different in any of the areas. Pupal chamber productivity was significantly higher in areas with historically low climatic suitability than in areas with historically high climatic suitability. Also, beetles utilized more surface area on trees in historically low CSCs, resulting in higher reproduction rates and faster population growth. I hypothesize that a lack of selection pressure against susceptible and suitable trees may be the explanation for this relationship.

In areas where mountain pine beetle and lodgepole pine have coevolved (e.g., Rocky Mountain and 100 Mile House regions), the most susceptible and suitable trees may have been selected against over time. Mountain pine beetles must kill their host to survive; therefore, during outbreaks the most susceptible trees are taken out of the gene pool. In addition, the most suitable trees would produce the most pupal chambers, generating higher intensity outbreaks, i.e., a higher selection pressure. The resulting stands would thus be made up primarily of genotypes that were not attacked. Although the most susceptible and suitable trees have been selected against, the remaining genotypes would still be suitable enough for sustaining outbreaks, as seen in the Kimberley and 100 Mile House regions. The higher suitability of trees in areas with historically low climatic suitability may explain why the current outbreak in north central B.C. is larger than ever recorded.

5.1 Future Research and Considerations

Although this research suggests that lodgepole pine in regions with historically poor mountain pine beetle climatic suitability produce higher numbers of beetles than those with good historical climatic suitability, more research is needed in testing the biological process behind these patterns.

The fitness of beetles produced in areas of historically poor climatic suitability should also be investigated, e.g., beetle size, fat reserves, and sex ratios could be measured and compared to beetles from areas with a historically suitable climate. The numbers of beetles may not be important if they are unable to fly and reproduce as successfully as other beetles.

One interesting outcome from my results is that the influence of dbh on phloem thickness was about the same for both regions, and in both regions there was a significant increase in phloem thickness with increasing dbh. In addition, phloem thicknesses did not differ significantly between regions, but the mean phloem thickness within two of three diameter classes were slightly higher for southern trees. These were unanticipated results given the higher densities of pupal chambers produced in the north central trees, and that Amman (1972) showed that phloem thickness was the most important factor in pupal chamber production. It has been reported that the nutritional quality of phloem may vary between trees (Miller and Keen 1960, Reid 1963), and in this case the phloem in the north central trees may have had higher nutritional quality than in trees in the southern sites. Other potential explanations may be that beetles in the north may be smaller (Bentz et al. 2001), and/or that trees in the north may have a lower defense. Both of these explanations are out of the scope of this project and should be investigated further.

There is a commonality between North Central B.C. (Prince George area), Central Idaho (Stanley area), and Northern Colorado (Fraser/Winter Park area). In all of these areas there is anecdotal evidence that winters are not as cold as they used to be. I feel that similar studies to what I have done in British Columbia should be done in these U.S. locales. More specifically, further investigation is needed in other areas where mountain pine beetle epidemics are at unprecedented levels and whether these are happening in areas of low climatic suitability. For example, in the southern Rockies, range expansion entails mountain pine beetle moving up in elevation rather than latitude as in my study. At higher elevations, other tree species such as whitebark pine (*P. albicaulis* Engelmann) are becoming increasingly susceptible to mountain pine beetle and the effect of a large beetle epidemic in this species are critical to grizzly bear habitat in addition to other ecological concerns (Logan and Powell 2001).

5.2 Management Implications

Forest managers need the most recent and relevant information in order to manage forests effectively, especially given increasing societal focus on multiple values. With the current mountain pine beetle epidemic that is simultaneously occurring not only in British Columbia and Alberta, Canada, but also in the United States in areas such as Central Idaho, Southern Wyoming and Northern Colorado, there is a wide variety of forest management objectives involved. From the B.C. interior, where timber harvest is the main objective, to the Colorado Rockies, where wildfire and outdoor recreation is the main concern, forest managers need to have current information on the biology and population dynamics of mountain pine beetle in order to manage forests effectively and in a timely manner.

Although no one knows for sure what climate change may bring, forest managers also need to think about how a changing climate may affect future forest health conditions. My research has suggested that areas where it was previously too cold for mountain pine beetle populations to grow into large epidemics may now be more suitable for eruptive beetle epidemics than in areas historically suitable for the beetle. This knowledge may be applied in future decision making in regard to harvesting in areas further north and at higher elevations where it is still too cold for successful mountain pine beetle reproduction. If forest managers can harvest highly suitable areas before they are attacked by beetles the size and intensity of future outbreaks may be mitigated.

It is interesting to note that if mean annual temperatures continue to increase in the Prince George region as expected, forest managers may be wise to take this predicted increase in temperature into consideration when choosing stock for replanting, and use seed from warmer regions (Wang et al. 2006) where mountain pine beetle has co-evolved with lodgepole pine (seedlings will have similar genetic makeup as trees from historically high/extreme climates).

In the past, forest managers were told that as a "rule of thumb" mountain pine beetle attacks the largest trees and will rarely attack smaller trees (i.e., <20cm/8 in.) (Hopping and Beall 1948, Cole and Amman 1969, Safranyik et al. 1974, Safranyik 1988) in large quantities, and that if it did hit such smaller trees, the pupal chambers produced would be minimal. However, results from my research have shown that during these episodes of "hyper-epidemics" it is not uncommon for trees <15cm (<6 inches) to be attacked.

Furthermore, my research (Chapter 3) showed that in the southern sites (areas of high historic suitability), a 1:1 or greater emerged pupal chambers per gallery start ratio occurred in trees larger than 16.2 cm dbh (Safranyik (1974) reported 25.4 cm), whereas in the north (areas of low historic suitability), this ratio was achieved at 13.7 cm dbh.

The results from this research may be helpful for forest managers prioritizing stands for harvest. The message for forest managers here is that they not only need to prioritize stands based on diameter classes, but also need to take historic CSCs into consideration. It may also be useful to incorporate the results from areas with low historic CSCs into current susceptibility and risk-rating systems (Shore and Safranyik 1992, Shore et al. 2000).

Because trees in areas of low historic suitability are utilized more efficiently by the beetle, there is more surface area for reproduction. In turn, higher reproduction leads to faster population growth. Forest managers should use this information when prioritizing stands for harvesting during mountain pine beetle outbreaks or the onset of incipient populations. Beetle populations may be kept to a minimum if stands with the lowest historic suitability are harvested first.

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