

**NORTHERN RANGE LIMIT MOUNTAIN PINE BEETLE (*DENDROCTONUS
PONDEROSAE*) OUTBREAK DYNAMICS AND CLIMATE INTERACTIONS IN
MIXED SUB-BOREAL PINE FORESTS OF BRITISH COLUMBIA**

by

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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

June 2012

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Abstract

Insect outbreaks are some of the most destructive processes of forest change with long-term economic and ecological effects that can be severe. For native insects that have co-evolved with their host forests it is important to develop and implement management strategies that are consistent with the basic ecology of the ecosystems being affected. This requires a sound ecological understanding of the disturbance regime and its function, which can only be gained through long-term stand histories appropriate to the scale of the process. This is becoming increasingly important in light of changing climate conditions which have already influenced disturbance regimes and the spatial distribution of insect ranges with unknown consequences.

The objectives of this study were to develop a long-term record of mountain pine beetle (MPB) outbreaks near the northern limit of the species' range and to examine the interacting factors driving that disturbance regime. Using a combination of dendrochronological methods to reconstruct stand and outbreak history together with long-term local and large-scale climate data, I developed an integrated model of outbreak dynamics for north-central BC where little is known about the role of MPB in forest stand dynamics or the influence of climate on outbreak development. Using a 200-year outbreak reconstruction I determined that host susceptibility and mortality patterns had distinctly different characteristics than those described further south. Climate was more important than forest structure in determining outbreak frequency and severity, and persistent warm temperature anomalies, including the large-scale climate patterns driving these trends, were the most important direct climate drivers of outbreak development. Over short time scales,

host stress preceded outbreaks, but long-term periods of vigorous tree growth were also important for outbreaks to develop. Differences between this study and others suggest that outbreak risk management and predictive models must consider regional differences in forest structure, host-climate relationships and climatic pressure on beetle populations. Given that regional host susceptibility criteria are met, low-frequency climate patterns such as PDO and ENSO are probably the most important outbreak drivers across the province. Recent climate changes have already altered the historical regime, and ongoing warming will likely change many of the interactions described here.

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Hrinkevich, K., and K. J. Lewis. 2012. Northern range limit mountain pine beetle outbreak dynamics in mixed sub-boreal pine forests of British Columbia. *Ecosphere*: 2(10):116.

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Acknowledgments

My dissertation research would not have been possible without the continuous and generous support of my supervisor, Dr. Kathy J. Lewis, who taught me much more than I ever expected to learn in an academic endeavor. From the moment I arrived at UNBC, Kathy provided me with an entirely new perspective on academia, encouraged and allowed me to fumble my way through some innovative and non-traditional methods of study that from the onset neither of us was sure were possible or even rational (especially those models I developed in the hospital tethered to an IV), and showed me that balancing life with an academic career was not only possible, but could be rewarding as well. I can't thank her enough for the confidence she entrusted in me to take this project in the direction of my choosing, and for the patience and countless opportunities outside the study itself she provided or condoned that at the end of the day were just as important in completing this process and for my development into the self-assured, well-rounded person I leave this program as. I am honoured to have had the chance to work with Kathy and look forward to our continued collaboration in the future, particularly when it involves fishing.

I thank the other members of my graduate committee, Drs. Scott Green, Lori Daniels, Brad Hawkes, and Rene Alfaro for their contributions and insightful comments on earlier drafts, as well as for the extra time many have spent outside of official committee business teaching me about dendrochronology and throwing ideas around about disturbance ecology, entomology, climate change, and just in general about where life can lead from here. I am also grateful to Dr. Rosemary Sherriff for taking the time to serve as my external examiner; I can't imagine a better fit for this project look forward to future discussions about the overlapping components of our work.

I have been fortunate to have the support of many field and lab assistants, among them Rurik Muentner was an amazing worker, theorist and friend through the most trying field season of the project, without whom I don't know that I would have tracked down as many of the sites as I did, sampled so efficiently and extensively, and transported as much 'data' (i.e. heavy pieces of wood) from the middle of nowhere back to the lab. I also thank Doug Thompson for his willingness and knowledge to introduce me to the northern-interior forests of British Columbia and to pinch hit whenever I found myself in need of a field assistant to drop everything for a week to come camp in the rain with me. Doug was also a tremendous help in the lab and during the analysis and writing phases, always willing to talk tree rings with me. I thank all the other members of the tree ring lab who assisted, talked shop, and simply put up with the sounds of sanding and the beeping of the Velmex for so long: Chris Konchalski, Kennedy Boatang and Sean Sweeny, you were a great crew to conspire with in a lab that required detail-oriented people with excellent taste in music.

Thank you to the Takla First Nation for sharing the beauty of their territory and allowing me to do much of my sampling within their lands, and to Terry Teegee for helping to facilitate access. I am also tremendously indebted to many people outside of this project

who helped me to maintain my sanity, stay focused and calm, and remember that life is meant to be celebrated with the people who inspire you, put up with you on your bad days, make you smile and encourage you to fulfil your dreams. Thank you Sharon Hunter, Sonja Ostertag, Jose Delgado-Guevara, Heidi Knudsvig, Stacey McCarthy, the Chilcotes, and all you dendro fanatics out there I've known for years thanks to NADEF and AAG. A special thank you to Margaux Shilling; I could have never finished this without your love and support and look forward to repaying the favor with a lifetime of the same.

Funding for this research was provided by the Government of Canada through the Mountain Pine Beetle Program, a three-year \$100 million program administered by Natural Resources Canada, Canadian Forest Service. Additional support was provided through a fellowship from the Pacific Institute for Climate solutions and NSERC.

1. Introduction

1.1 Context

Forest disturbances are important processes that shape the composition, structure and functional components of the ecosystem through the damage or removal of individual trees in a stand and the alteration of the growing space for the surviving and newly established occupants (Oliver and Larson 1996). Disturbances can be endogenous, arising from within the stand such as insect and pathogen outbreaks, or exogenous, originating from outside the stand as in cases of flooding and fire. They can be natural or human created, biotic or abiotic and can range from stand-replacing events to minor interruptions temporarily suppressing the growth of select individuals. Often, it is the interaction of multiple disturbance agents through time that shapes the past, present and future successional trajectory of a forest system (Rogers 1996).

The social, economic and ecological effects of forest disturbances can be large and long term. In North America, insect and pathogen outbreaks are the most destructive processes of forest change, affecting nearly 20.4 million hectares per year with an economic impact of over 2 billion dollars per year in the United States alone, almost 6 times the cost associated with forest fires (USDA 1997, Dale et al. 2001). In addition to timber losses (Parkings and McKendrick 2007), outbreaks influence wildlife habitat (Chan-McLeod 2006), fire behavior (Jenkins et al. 2008), carbon storage (Kurz et al. 2008) forest structure and stand dynamics (Shore et al. 2006), property and recreation values (McGregor and Cole 1985) and watershed quality through hydrologic impacts (Redding et al. 2008). Despite these effects, where native insects are concerned that have co-evolved with the host forest, outbreaks are considered normative events (Mattson 1996) because of the important role

they play in the natural cycle of forest development and regeneration (Logan and Powell 2005). For forest managers, this means it is essential that mitigation strategies are consistent with the basic ecology of the ecosystems (Romme et al. 2006) to ensure that management objectives do not negatively impact other natural components of the system. To do so requires a sound ecological understanding of forest disturbance processes and their function.

A major limitation to understanding forest disturbance processes is that the temporal scale of forest change often exceeds the scope of recorded history. Because trees can survive for many centuries and the disturbance interactions that shape stand development and susceptibility to future disturbance begin at the time of stand-initiation (Veblen et al. 1994), long-term histories are necessary for developing effective sustainability goals under an ecosystem management paradigm (Christensen et al. 1996). One of the most useful methods for reconstructing past disturbances is dendrochronology which uses the natural record of environmental variability stored in the annual rings of trees to develop stand histories (Speer 2010). The great value of dendrochronology lies in the practice of crossdating (Douglas 1941) which allows the precise dating of tree ring-derived time series with an annual resolution that can extend as far back in time as there are temporally-overlapping wood samples available, live or dead. Using this approach, dendrochronologists have reconstructed multi-century records of insect outbreaks (Hadley and Veblen 1993, Zhang and Alfaro 2002, Berg et al. 2006, Hrinkevich and Lewis 2012), fire (Baisan and Swetnam 1990, Brown and Swetnam 1994, Stephens et al. 2003), foliar pathogens (Welsh et al. 2009) and climate (Jacoby and D'Arrigo 1989, Diaz et al. 2001, Davi et al. 2003, Trouet and Taylor 2009), establishing links between these components through patterns of long-term interaction (Veblen et al. 1994, Zhang et al. 1999, Heyerdal et al. 2002, Grissino-Mayer et al. 2004,

Axelsson et al. 2009, Sheriff et al. 2011). The specific relationships between climate, insect and other forest disturbances often vary depending on species life history strategies, physiological tolerances and host ecology (Dale et al. 2001, Bentz et al. 2010), so management strategies that incorporate as much understanding of the effects that forest stand dynamics and climatic variation have on outbreak dynamics greatly improve our ability to mitigate risk (Taylor et al. 2006).

The importance of climate in the population dynamics of forest insects is well established, however, rising concerns over the impacts of climate change on forest disturbance processes have increased attention on defining specific climate-outbreak relationships (Bentz et al. 2010). These concerns arise from the fact that climate can influence the timing, frequency, intensity, extent and duration of disturbances (Dale et al. 2001), and disturbances can greatly accelerate or amplify the effects of changing temperature and precipitation on forest composition and structure (Overpeck et al. 1990, Swetnam 1993, Swetnam and Lynch 1993) when compared with the direct effects of a changing climate on tree species distributions that are more likely to occur over hundreds of years (Loehle and LeBlanc 1996, He et al. 1998). Insects, in particular, are extremely sensitive to climatic variation because, as poikilotherms, virtually every aspect of the life cycle is influenced by temperature. Some consequences of rising temperatures on insect herbivores have already been documented, including genetic adaptations to shifts in seasonal timing (Bradshaw and Holzapfel 2006) and range expansions into formerly unsuitable habitats (Battisti et al. 2005). Indirect climatic effects that are mediated through other organisms such as the host plant or community associates may also alter the balance of external pressures on insect populations that influence colonization and reproduction success (Bentz et al. 2010). In order to predict

the effects that climate change will have on insect disturbance regimes we need long term data that will allow us to identify and decouple climatic effects from the stand-dynamics components of the system to determine how these factors interact. This should result in an integrated risk model accounting for the major drivers of the disturbance regime that can inform forest management decisions in response to environmental changes.

1.2 Study objectives and rationale

The broad objectives of this study are to develop a landscape-scale disturbance history for the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins (Curculionidae: Scolytinae)) in north-central British Columbia (BC) near the northern extent of the beetle's range and to examine the long-term interactions between MPB outbreaks, climate and host forest stand-dynamics, including other disturbance agents influencing the outbreak cycle. The MPB is an aggressive bark beetle native to western North America whose populations periodically increase to outbreak levels capable of causing tree mortality over many thousands of hectares, and it is considered the most destructive biotic disturbance agent of mature pine forest (Furniss and Carolin 1977, Safranyik and Carroll 2006). In BC lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) is the primary host although most pine and occasionally other species such as Engelmann spruce are also attacked (Furniss and Carolin 1977, Unger 1993). Lodgepole pine-dominated stands cover approximately 14 million hectares of forestland in BC and account for roughly 25% of the provincial timber supply (BC Ministry of Forests 1995) so the socio-economic and ecological impacts of MPB epidemics can be severe. Currently western Canada is experiencing the largest and most

devastating MPB epidemic on record that has affected over 17.5 million hectares of forest land in British Columbia (BC) (BC Ministry of Forests, Lands and Natural Resource Operations 2011) and has recently become established on the eastern slopes of the Rocky Mountains and in west-central Alberta (Cullingham et al. 2011).

Our current understanding of MPB outbreak dynamics is based almost wholly on research from climatically optimal habitats where infestations have historically been most severe, but recent changes in climatic conditions are causing marginal environments to become increasingly susceptible to outbreaks (Bentz et al. 2010). Some of the most dramatic changes are expected to occur at the northern range limit where climatic susceptibility has been historically low (Carroll et al. 2004). A major concern here is that host availability is not limiting and climatic changes could provide MPB access into previously unaffected pine forests to the north and the boreal forest to the east that extends across the county from Alberta to Nova Scotia (Cullingham et al. 2011). With the exception of the Forest Insect and Disease Survey (FIDS) records that began aerial surveys in 1959 and some written accounts of historical outbreaks in north-central BC dating back to 1948 (Wood and Unger 1996), there is very little empirical evidence about outbreak dynamics near the northern range limit. It is unclear whether outbreak regimes respond similarly to the factors driving epidemics in the better studied, climatically optimal parts of the range or if universal management principles apply across the province. Broad structural and compositional differences between the northern-interior and central-interior forests suggest this may not be the case, and the interactions between stand dynamics and climate on MPB disturbances in the north is unclear. What is certain is that if current warming trends continue, climatically marginal areas will become increasingly important MPB habitat and serve as primary sources for

range expansion. Outbreak management in these areas will likely become a priority as this occurs, which will require a sound ecological understanding of the MPB disturbance regime and the major factors driving outbreak development. This study will provide the long-term records necessary to describe the interactions between MPB, climate, and stand dynamics on an ecologically appropriate time scale for the northern-interior pine forests of BC. It will also serve as baseline information for evaluating existing and future susceptibility to MPB under the prevailing climate change scenarios and may help in managing range expansion into adjacent forests that share more structural similarities with my study area than with the better-studied pine forests to the south.

1.3 Background information on the mountain pine beetle

1.3.1 Life cycle and population processes

The MPB life cycle, described in detail by Safranyik and Carroll (2006), consists of four stages: eggs, larva, pupa and adult, all of which occur beneath the bark of the host tree except during the dispersal phase of mature adults. Populations are typically univoltine, producing one generation per year that begins in late July to mid-August when dispersing adults mate and females deposit eggs into galleries excavated in newly colonized host trees. Eggs hatch within a week of oviposition and larvae immediately begin feeding on the phloem tissue of the inner bark by excavating larval mines perpendicular to the parental gallery. Larvae pass through four instars, gaining cold-hardiness as they develop (Amman 1973). MPB overwinter as late instar larvae and complete development in the spring once temperatures begin to warm. By June they pupate, developing into teneral adults between

late June and early July. Teneral mature for an additional two weeks, feeding on the inner bark and on spores of blue stain fungi lining the pupal chambers to support flight muscle development (Reid 1958) and to pick up the microorganisms necessary for successful colonization and reproduction in their new hosts (Safranyik et al. 1975).

The timing of emergence is temperature-dependent and usually peaks between mid-July and mid-August (Safranyik and Carroll 2006). Following emergence, beetle flights may be short- or long-range, although the large majority of dispersals are within-stand (Safranyik et al. 1992). Above-canopy long-distance dispersal is probably more important once locally-available host trees have been depleted (Safranyik and Carroll 2006). Once a host is selected, usually through a combination of random landings, visual cues and direct assessments of suitability after landing (Raffa and Berryman 1982, Pureswaran and Borden 2003), the initiation of the egg gallery by the pioneer female prompts a series of chemical interactions that attracts a mate and results in the production of aggregation pheromones that instigate a mass attack (Safranyik and Carroll 2006). For colonization to succeed, the attacking beetles must overwhelm the host tree defenses which involve the production of constitutive and induced secondary resins (Berryman 1972) to slow the attack and either expel the beetles from the tree or confine and kill them in lesions of dead tissue produced during the induced resinosis (Safranyik and Carroll 2006). MPB rely on two strategies to overcome this response. First, the aggregation pheromones produced by early attacking females act to rapidly concentrate attacks that can exceed the resistance capacity of the selected tree (Safranyik et al. 1975). Second, the fungal spores acquired during adult maturation in the pupal chambers of the former host are inoculated into the new host upon attack, penetrating the living cells of the phloem and xylem quickly (Safranyik et al. 1975) and disrupting the

production of defensive resins (Safranyik and Carroll 2006). Successful colonization results in the death of the host tree and the production of a new brood for attack the following year.

1.3.2 Epidemiology

There are four distinct phases in the MPB population cycle that are primarily defined by the strength of the interactions between population size, stand resistance, and distribution of MPB infestations on the landscape. Endemic populations are the most common phase, persisting at very low levels in a stand in numbers too small to successfully kill a single large-diameter tree and restricted to low-quality hosts with little defensive capacity (Safranyik and Carroll 2006). Generally, after stand resistance peaks, usually around the time of crown closure for lodgepole pine (Farnden 1996), stands can maintain steady endemic MPB populations in the low-vigour individuals that are competing for resources as the stand undergoes self-thinning (Yoda et al. 1963). The combination of low host quality, patchy host availability, and small population sizes usually limits endemic populations from growing larger, but any decrease in host resistance or increase in MPB population size can allow an incipient-epidemic infestation to develop which is defined by the capacity of the population to successfully mass-attack a single large-diameter tree in the stand (Safranyik and Carroll 2006). Consecutive years of favorable climate for beetle survival combined with a period of stress or damage to the host tree are generally cited as drivers of the sustained increases in beetle population size out of the endemic phase (Safranyik et al. 1974, Thomson and Shrimpton 1984, Carroll et al. 2004).

Incipient-epidemic populations attack primarily large-diameter trees and experience a sustained yearly population growth which is reflected by infestation patterns consisting of

clumps of attacked trees that establish throughout individual stands (Safranyik and Carroll 2006). Once these spot infestations begin to coalesce and new infestations disperse at a landscape scale, the epidemic phase has begun in which MPB populations become increasingly resilient to large losses in their numbers, the size and severity of the infestation grows annually and the large-diameter component of the affected stands are severely depleted (Safranyik and Carroll 2006). Epidemic populations eventually collapse due to a depletion of suitable hosts or an unseasonably cold event during the late fall or early spring that drastically reduces the number of beetles surviving to colonize new hosts (Safranyik and Carroll 2006). The post-epidemic phase simply describes the decline of the residual MPB population back to endemic levels through various pathways of reduced brood survival (Safranyik and Carroll 2006) that may also include some additional pine mortality caused by secondary bark beetle species that survived the MPB collapse (Safranyik et al. 1974).

1.4 Conceptual model for describing outbreak dynamics

Disturbances, although variously defined, generally refer to discrete events involving a particular agent disrupting the structure of an ecosystem or community that alters resource availability and/or the physical environment (White and Pickett 1985). In contrast to a disturbance event, such as an insect outbreak, a disturbance regime refers to the spatial and temporal dynamics of repeated disturbances over longer time periods, including characteristics such as disturbance frequency, return interval, size, intensity and severity (Turner 2010). Disturbance histories such as those developed using dendrochronology provide the long term ecological perspective appropriate for describing disturbance regimes,

however, this is only part of the information necessary to understand the dynamics driving the regime. For insect disturbances, outbreak dynamics refers to the long-term interactions between the endogenous and exogenous elements involved in rapid insect population fluctuations, particularly the factors that trigger and terminate outbreaks and define the outbreak regime (Rose and Harmsen 1981). In this paper, I combine a reconstructed MPB outbreak history with an analysis of the long-term ecological interactions driving the disturbance regime to describe the outbreak dynamics of MPB in north-central BC, focusing primarily on the factors that trigger the reconstructed outbreaks.

In order to describe outbreak dynamics, it is useful to examine the disturbance system using the conceptual model originally developed for plant diseases by Stephens (1960) referred to as the disease triangle. The disease triangle represents the occurrence of a biotic disturbance, in this case a plant disease, as the obligate interaction between a susceptible host, a virulent pathogen, and a favorable environment for disease development (Stephens 1960, Agrios 2005). The same concept applied to an insect disturbance states that outbreak development absolutely depends on the relationships between a susceptible host, an insect agent and a suitable climate to support population growth. The long-term interactions between these three necessary causal factors define the outbreak dynamics that provide a more complete understanding the ecological process as a whole (Figure 1.1). For MPB, these interactions are fairly well-defined based on observations of individual outbreaks, although less is known about the long-term dynamics, particularly at the northern extent of its range.

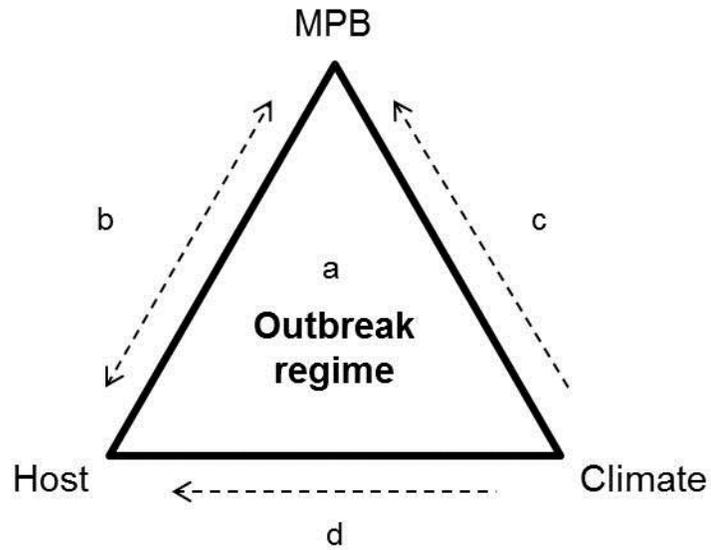


Figure 1.1. Conceptual model of outbreak dynamics adapted from Stephens (1960) showing the three necessary causal factors of an insect outbreak and the interactions between factors (b, c, d) that over longer time scales determine the outbreak regime (a) for a given area.

1.4.1 MPB-host interactions

There are a number of important MPB-host interactions related to the conflicting requirements for what defines a suitable host and a susceptible host. Suitable hosts refer to those trees with characteristics, usually size-related, that are capable of supporting MPB population growth, while susceptibility depends on the defensive capacity of the tree and is often age-related. MPB prefer large trees within a stand because many of the characteristics associated with tree size influence brood production and survival. In general the thicker bark and thicker phloem of large trees enhance survival and attack success by producing larger broods and larger beetles with faster life cycles and greater relative emergence rates (Safranyik and Jahren 1970, Amman and Cole 1983, Safranyik and Carroll 2006) as a result of the greater quantity and probably nutritional quality of the resource (Safranyik and Carroll 2006) and the additional protection from temperature extremes, natural enemies and sapwood drying (Reid 1963, Safranyik et al. 1974). The minimum diameter of trees for successful attack and survival of MPB is usually around 10 cm (Safranyik and Carroll 2006), however, Safranyik et al. (1974) found that only trees larger than 25.4 cm diameter produced enough emerging beetles to sustain an outbreak. In risk modeling, stand averages greater than 20.5 cm diameter are generally considered susceptible (Safranyik et al. 1975, Cole and Amman 1980), assuming this structural threshold coincides with a reduction in tree defenses.

Large trees are normally the most vigorous and resistant to attack (Shrimpton 1973) until approximately 60 years, at which time stand resistance begins to decline rapidly because the normal process of stand aging results in mature trees competing for resources (Safranyik et al. 1974). By the time stands reach 80 to 100 years, defensive capacity is low

enough that they are considered highly susceptible to MPB outbreaks (Safranyik and Carroll 2006). Because stand age is a major determinant of outbreak risk, any factors that influence age distributions also influence stand susceptibility, which is why fire cycles are often included in outbreak risk models (Taylor et al. 2006). There is also an upper limit for age-related susceptibility which Taylor and Carroll (2004) constrained to 160 years when modeling stand level outbreak risk in BC, citing this as the age at which thinning phloem associated with senescence began to adversely affect MPB population growth. In climatically optimal regions, the size, severity and periodicity of outbreaks is considered highly dependent on the age and size structure of the host forest (Alfaro et al. 2004, Axelson et al. 2009), but it is unclear what role forest structure plays in marginal climates.

1.4.2 Climate-MPB interactions

Virtually every aspect of the MPB life cycle is controlled by temperature, and accordingly much attention has been given to describing the individual controls at various stages of development and population phases. Carroll et al. (2004) and Safranyik and Carroll (2006) provide detailed summaries of the specific climatic thresholds used to define outbreak suitability, most of which relate to survival probabilities based on the ability to maintain univoltine life cycles and seasonal synchrony (Logan and Powell 2001). Annual and seasonal heat accumulations influence developmental rates and the timing of emergence and peak flight (Reid 1962, McCambridge 1971) which largely control the potential for winter survival and mass attack success (Safranyik and Carroll 2006). Cold tolerance is probably the most well-studied climate interaction, in large part because it is the single greatest cause of MPB mortality (Cole 1981) and as such one of the most important controls of population

growth and outbreak potential. Seasonally varying cold-tolerance thresholds based on larval development rates (Wygant 1940) can profoundly influence MPB population dynamics and winter temperatures are consistently cited as the dominant climate driver in climate-outbreak modeling studies (e.g. Aukema et al. 2008, Fauria and Johnson 2009).

1.4.3 Climate-host interactions

Climate-host relationships are probably the least well-understood interactions influencing MPB outbreak dynamics. These indirect effects on MPB populations that are mediated by the host tree are almost always discussed as a decrease in host-resistance brought on by climate-induced water stress (Carroll et al. 2004), but the mechanisms of this are unclear because of complications with other climate feedbacks and regional ecosystem differences (Bentz et al. 2010). There is little consistency among climate-outbreak interaction studies as to the role of drought and host stress in MPB outbreak dynamics, yet enough evidence exists supporting the effect (e.g., Shrimpton and Thompson 1982, Thompson and Shrimpton 1984, Trzcinski and Reid 2009) that it is included as an explanatory variable in almost all climate suitability analyses. In this paper, I challenge the assumption that precipitation alone is a universally appropriate proxy for host stress and present an alternative method for examining climate-host interactions in relation to MPB outbreaks.

1.5 Organization of this paper

The first objective of this study is to reconstruct a landscape-scale disturbance history for MPB in north-central British Columbia (BC) where the outbreak regime is expected to be highly sensitive to climatic variability and likewise highly susceptible to the effects of climate change. Based on that reconstruction my additional objectives are to examine the long-term interactions between MPB outbreak history, climate and forest stand dynamics, including other disturbance agents that influence MPB, in order to define the major drivers of outbreak dynamics in this system and to aid in the development of predictive models for assessing and managing future risk. Based on the outbreak dynamics model described and illustrated in Figure 1.1, this study contains four component parts: (1) the outbreak reconstruction, (2) the MPB-host forest interactions, (3) the climate-MPB interactions, and (4) the climate-host interactions. Because these components are highly interrelated, rather than divide the study into four data chapters and discuss each component separately, I present the information as two larger chapters that, from an ecological perspective, provide a more comprehensive and cohesive representation of MPB outbreak dynamics in north-central BC.

In Chapter 2, I develop a multi-century reconstruction of MPB outbreaks at a landscape-scale in north-central BC (Figure 1.1a) and use the characteristics of the disturbance regime to examine interactions between MPB and the host forest (Figure 1.1b), particularly the stand dynamics that are associated with outbreaks. This analysis includes information about the role of fire and other disturbance agents operating in the system, host selection and stand susceptibility, changes in outbreak severity, and the successional trajectory of this forest given the historic disturbance regime and with respect to expected

climate changes. I compare these results with those from other studies to address regional differences and the implications of these for management. In Chapter 3, I examine the direct climate drivers influencing the timing of the reconstructed MPB outbreaks, including both local and large-scale climate patterns with known relationships to MPB population dynamics (Figure 1.1c) as well as the indirect climatic effects on outbreak timing that are mediated by the host tree (Figure 1.1d). For the indirect effects I examine climate-tree growth relationships first to determine how local climate influences host trees, and then analyze the relationship between the host climate response and outbreak timing to determine specifically how climate-driven tree-growth variability influences MPB outbreak development. By combining the two climate interactions I provide a comprehensive explanation of the major climate influences on MPB in north-central BC that addresses the relative importance of both direct and indirect effects, and compare those relationships to climate-outbreak models developed in other parts of the province to explore regional differences. Lastly, I discuss the implications of the climate interactions for developing predictive climate-outbreak risk models. Chapter 4 presents a synthesis of all the results, integrating the roles of host forest dynamics and climate in a comprehensive discussion of the interrelationships driving outbreak dynamics in north-central BC. I also discuss the overall implications of these findings for MPB management in BC, currently and with respect to climate change and the future of this disturbance system. Lastly I address future directions this research could take to improve our understanding of MPB outbreak dynamics in BC that should aid in risk management and the development of predictive disturbance models in order to mitigate the ecological and economic effects that future epidemics may have.

2. Historical outbreak dynamics and forest structure at the northern range limit for mountain pine beetle in British Columbia

2.1 Abstract

Recent widespread mountain pine beetle (*Dendroctonus ponderosae*) (MPB) outbreaks in western North America have caused unprecedented tree mortality across much of the beetle's known historic range and into novel habitats near the range margins. Our current understanding of outbreak dynamics and their relationship to forest structure is based almost wholly on research from climatically optimal habitats where infestations have historically been most severe. As range expansion continues, marginal habitats may become increasingly susceptible to outbreaks, yet little is known about the factors driving outbreak development in these forest types or how the disturbance regime differs. This study uses dendroecology and forest structure analysis to reconstruct historic outbreak dynamics at the northern MPB distribution limit in British Columbia to extend the disturbance record beyond the scope of documented history and to evaluate the long-term relationships between stand structure, host suitability, and regime characteristics at the range margin. I sampled 22 sites with evidence of past infestations, and using mortality dates, survivor growth releases, and tree vigor analyses I reconstructed five probable outbreak periods predating the current epidemic. At least two of these events fit the profile of large epidemics occurring in the 1900s-1910s and again in the 1940s-1950s, with evidence of two 19th century infestations and chronic localized mortality beginning around the 1980s. Stand age appears to be the most important factor limiting outbreaks prior to 1870, indicating a strong relationship with fire history at centennial time scales. Outbreak cycles were comparable to those reported in other locations, yet beetle preference for larger and older trees suggests that provincial

susceptibility models may not accurately represent northern outbreak risk, particularly in older stands. Following stand maturation, host availability does not appear to limit outbreak severity or recurrence. Here density-independent factors associated with additional climate pressures are likely more important. With enhanced climate suitability, outbreak scale and severity will likely increase dramatically in this landscape which is currently not limited by host distribution. My reconstruction can inform management strategies as this occurs and outbreaks move into previously uninfested forests that share many structural and ecological similarities with my sites.

2.2 Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Curculionidae: Scolytinae)) (MPB) is a native bark beetle of western North America. It is an aggressive species whose populations periodically increase to outbreak levels capable of causing tree mortality over many thousands of hectares, and is considered the most destructive biotic disturbance agent in mature pine forests (Furniss and Carolin 1977, Safranyik and Carroll 2006). Most pine species are susceptible to attack, but in British Columbia (BC) the most common host is lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) which covers approximately 14 million hectares of forestland and accounts for roughly 25% of the provincial timber supply (Taylor and Carroll 2004). Currently, British Columbia is experiencing the most severe outbreak on record, affecting over 10.1 million hectares at the peak of the infestation in 2007 (Westfall and Ebata 2007). Widespread and ongoing mortality of pine forests is also occurring throughout the western United States in numerous

outbreaks that began building in the late 1990s (Gibson et al. 2008). In addition to extensive timber loss, the combined socio-economic and ecological impacts of MPB epidemics can be severe. Beetle-related mortality may influence fuel distribution and fire behavior, successional trajectories, carbon storage, watershed quality, wildlife composition, and recreational values (Safranyik et al. 1974, McGregor and Cole 1985, Jenkins et al. 2008).

Despite a co-evolved insect-host relationship based on normative outbreaks that are central to lodgepole pine disturbance ecology (Mattson 1996), current evidence suggests the natural cycle of disturbance and forest development is shifting towards unprecedented infestations throughout North America, including movement into novel habitats with potentially devastating consequences (Logan et al. 2003, Logan and Powell 2005). Some of the most dramatic changes are expected at high elevation and high-latitude sites near the beetle's range limits where changing climatic conditions have enhanced the potential for beetle survival and reproduction (Carroll et al. 2004), yet we have very little empirical evidence describing these effects. It is unclear whether outbreak dynamics in marginal environments respond similarly to the factors driving epidemics in the better studied, climatically optimal parts of the range or if universal management principles apply across the province. What is certain is that if current warming trends continue, climatically marginal areas will become increasingly important MPB habitat and serve as primary sources for range expansion. Outbreak management in these areas will likely become a priority as this occurs, particularly at the northern limit which borders a nearly continuous supply of previously uninfested lodgepole pine and jack pine (*Pinus banksiana* Lambert) to the north and east across the continent.

There are a number of factors that can influence MPB population dynamics and allow normally endemic populations to erupt to epidemic levels. These include cross-scale processes (Raffa et al. 2008) that increase the availability or susceptibility of host trees (Shore and Safranyik 1992, Taylor and Carroll 2004) or favor beetle population growth (Safranyik and Carroll 2006). In general, the distribution of mature healthy pine trees with thick phloem determines host availability, while climate suitability, primarily as it relates to developmental temperatures, governs beetle success (Safranyik and Carroll 2006). Outbreak dynamics, specifically the timing, frequency, scale and severity of infestations, are determined by interactions between the two (Royama 1992), and vary with geography (Cole and Amman 1980). Other disturbance agents also commonly interact with outbreak regimes (Rogers 1996). In BC, fire history affects the availability and susceptibility of host trees for MPB (Parker et al. 2006) and is a key driver of the forest structure-outbreak relationship. Because the temporal scale of these interactions can extend for centuries, managing for major epidemics requires an examination of long term disturbance histories to understand the ecological significance of these processes. Currently, documented evidence of historical MPB activity in British Columbia is limited to ground surveys dating back to 1910, province-wide aerial surveys beginning in 1959 (Wood and Unger 1996), and a small number of dendroecological reconstructions conducted primarily in the southern interior region of the province (e.g. Alfaro et al. 2004, Axelson et al. 2009). In the north, little information exists detailing outbreak history prior to the 1940s, and it is unclear whether outbreak models developed further south accurately describe the disturbance regime here. Broad compositional and structural differences between BC's northern and southern interior lodgepole pine forests suggest that this may not be the case. Before we can begin to assess

the influence of climate or implications of climate change, benchmark data describing the outbreak cycle and its relationship to forest structure is critical for developing risk models and management strategies suitable for marginal environments.

Dendroecology is a useful tool for reconstructing forest disturbance histories that pre-date written records. It has been successfully used to study the disturbance dynamics of defoliators (Swetnam and Lynch 1993, Speer et al. 2001, Zhang and Alfaro 2002) foliar pathogens (Welsh et al. 2009), and a number of bark beetle species (Veblen et al. 1991b, Stuart et al. 1989, Berg et al. 2006). For MPB, evidence of past outbreaks can be found directly through the dating of pine mortality events and indirectly in the accelerated radial growth response of surviving individuals in the affected stand. This indirect approach has been used in a variety of forest types to study MPB outbreaks where mortality data is limited (Heath and Alfaro 1990, Veblen et al. 1991a, Campbell et al. 2007, Axelson et al. 2009). A number of additional dendroecological approaches can support of these reconstructions, which are strongest when multiple lines of evidence converge on a particular interpretation. The purpose of this study was to use dendroecology to reconstruct the long term outbreak dynamics of MPB at the northern extent of the beetle's range in BC in relation to stand and host susceptibility. Specifically, my objectives were to: (1) describe forest structure and composition in the context of stand history, particularly the patterns of establishment and disturbance influencing outbreak ecology; (2) characterize MPB-related mortality relative to host selection (tree age, size, and vigor) and stand susceptibility and outbreak severity; and (3) reconstruct the timing, frequency, and magnitude of historical MPB infestations beyond the scope of written records using pine mortality, survivor growth releases, and host vigor estimates as proxy evidence. I compared my results with studies conducted in the southern

interior of BC and the Rocky Mountains in the US to evaluate differences associated with forest type and geographic location, and examined changes observed in the regime over time. The relevance of these results is discussed in the context of provincial risk modeling, outbreak management strategies and range expansion scenarios consistent with projected climate changes.

2.3 Methods

2.3.1 Study Area

The study area is located in north-central British Columbia, at the northwest corner of the Sub-boreal spruce (SBS) biogeoclimatic zone, with sites located in the SBSmc2 and SBSwk3 subzones (Meidinger and Pojar 1991). It is roughly bounded by Takla Lake to the north, Stuart Lake to the east, and Babine Lake to the west and south (Figure 2.1). This region, northwest of Fort St. James, also represents the most active area for documented outbreaks in the north (Safranyik et al. 1974). The Forest Insect and Disease Surveys (FIDS) records describe at least one major outbreak predating the current one in this region between the 1940s and the 1960s, in addition to numerous smaller infestations, with some stands being classified as chronically infested (Wood and Unger 1996). The regional climate of the Fort St. James area is characterized by short, warm summers (15.3°C average July temperature) and cold, snowy winters (-11.3°C average January temperature), with moderate average annual precipitation (487.1 mm), just under half falling as snow (Environment Canada 2010). These climate normals are typical for SBS forests in British Columbia.

Upland coniferous forests dominate the landscape, with hybrid white spruce (interior spruce) (*Picea engelmannii* Parry x *P. glauca* (Moench)) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) leading late successional stands, and lodgepole pine and trembling aspen (*Populus tremuloides* Michx.) establishing as seral associates. Other common tree species include paper birch (*Betula papyrifera* Marsh.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and black spruce (*Picea mariana* (Mill.) B.S.P.). SBS forests occur at low to mid-elevations (500-1300 m) across the entire study area, with patches of Engelmann Spruce – Subalpine fir (ESSF) forest types occupying higher elevations. I restricted sampling to lower elevation SBS forest types where lodgepole pine plays a more dominant role. Stand histories in SBS forests can vary greatly because of multiple, often concurrent, disturbance agents acting within the same stands. Fire and mountain pine beetle are the most prominent mortality agents, although fire in this system occurs on much longer time scales with cycles of at least 100 years to over 6000 years, and typically results in stand-replacing events rather than selective thinning (Wong et al. 2004). For my specific subzones sampled, fire cycles have been found to be 125 years in the SBS_{mc} subzones of the Lakes and Morice Timber Supply Areas (Steventon 2001) and up to 500 years in the willow variant of the wet cool subzone (SBS_{wk1}) (DeLong 1988). Also important in the SBS, although less likely to kill its host, the two-year cycle budworm (*Choristoneura biennis* (Freeman) (Lepidoptera: Tortricidae)) is a major insect defoliator of interior spruce and subalpine fir that has caused up to eight large outbreaks in my study area during the past two centuries (Zhang and Alfaro 2002, 2003).

2.3.2 Site Selection

Candidate stands for field sampling were identified using FIDS records (Wood and Unger 1996) and forest cover maps to select sites within known historic outbreak regions that were conifer-dominated, 120+ year-old stands likely originating as seral lodgepole pine. During ground surveys I screened candidate stands for signs of probable MPB outbreak history that included the presence of standing dead or downed pine with visible pitch tubes, J-shaped parental galleries, lateral larval galleries and/or exit holes in the remaining tree bark, as well as indirect structural evidence including a pine-dominated mortality distribution and size structure indicative of a MPB-dominated disturbance history. This structural criterion compensated for the degradation of direct evidence over time as a result of weathering, decomposition, and secondary beetle attack, and limited the effect of any confounding canopy disturbances targeting other species. Ultimately I selected 22 sites (Figure 2.1) for the disturbance history, and 4 additional sites distributed across the study area showing no evidence of past disturbance to serve as a control representing the regional climate-tree growth response of pine for my study area. Control sites were mature open-canopy lodgepole pine-dominated stands growing on steep or well drained rocky slopes with no downed trees, fire scars or other signs of tree damage or pathogen activity. Many of the trees in these sites, however, were recently dead from the ongoing MPB outbreak, estimated to have died within 1-3 years based on needle color and retention.

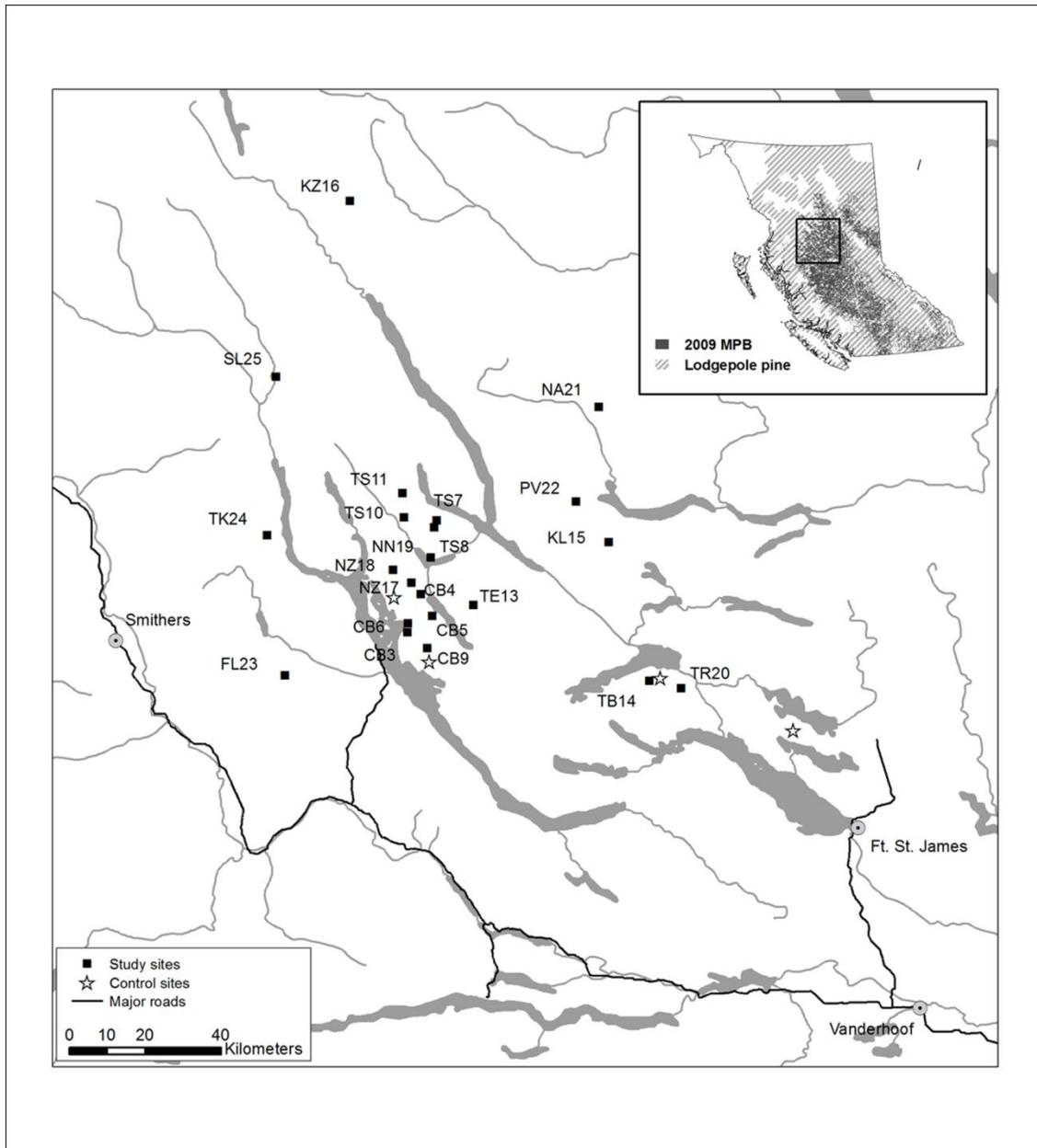


Figure 2.1. Detailed site and study area locations within British Columbia relative to the 2009 cumulative mountain pine beetle outbreak extent and lodgepole pine distribution.

2.3.3 Data Collection and Analysis

At each control site, I selected up to 20 of the largest, presumably oldest pine trees and collected 2 increment cores at 0.3 meters height. Within the outbreak sites I established variable-sized rectangular plots to sample all standing and downed trees greater than 10 cm diameter at breast height (DBH). Plot size varied (300-625 m²) with stand density and dead pine distribution to ensure suitable representations of stand structure (minimum 20 live trees) and mortality (minimum 5 dead pine). In cases of extensive canopy thinning due to the current MPB outbreak, recently dead standing pine (needles present) were included to meet the 20 live tree minimum. I cored all living trees at 0.3 meters and recorded species, DBH and canopy position. Dead standing trees were inventoried similarly, but only pine were cored and any evidence of mortality agent noted. At 12 sites I cored additional trees outside plot boundaries to improve sample sizes, for a cumulative total (all sites) of 45 spruce, 9 subalpine fir, and 11 pine sampled out of plot. For all downed trees originating within the plot I recorded species and DBH, noted cause of death, and cut cross-sections from all pine with wood intact enough to determine mortality dates. At 13 sites I collected additional cross-sections (46 total) from downed pine outside of the plot to increase sample sizes. All stems smaller than 10 cm were inventoried in 50 m² circular subplots centered at the corners of the rectangular plots which were averaged into standardized stems per hectare for each site. Stems were inventoried in the following classes: 4-10 cm diameter trees, saplings that were at least 1.3 m in height and less than 4 cm diameter, and seedlings that were less than 1.3 m tall. I tested for differences in recruitment for each class, including canopy trees greater than 10 cm, which were associated with the number of MPB outbreaks reconstructed

for that site using ANOVAs or Kruskal-Wallis means comparisons tests depending on whether the requirements for parametric statistics were met.

I mounted and sanded all cores and cross-sections following standard dendrochronological procedures (Stokes and Smiley 1968), and used the list method (Yamaguchi 1991) to visually crossdate each sample. Annual rings were measured using a Velmex system and the program COFECHA (Holmes 1983) used to assist in correcting and verifying the dating of all live and dead trees. Within sites I developed mean standardized chronologies for each species represented by 10 or more trees using the program ARSTAN (Cook and Holmes 1986) to fit a horizontal line through the mean of each series to emphasize deviations from mean growth, especially periods of sustained growth release that could be linked to canopy disturbances (Veblen et al. 1991a).

To determine the timing and scale of growth releases I used the program JOLTS (Holmes 1999, unpublished, University of Arizona) to analyze each time series with a moving windows procedure that calculates the difference between two adjacent sections of the series at annual increments and flags any years where the differences exceed a user-specified threshold value. Release detection criteria were formulated using guidelines established in similar studies (e.g. Rubino and McCarthy 2004, Berg et al. 2006, Axelson et al. 2009), with some differences to account for additional disturbance signals observed in my mean chronologies, namely growth responses to repeated two-year cycle budworm outbreaks in spruce and fir. For these species I used sites with strong MPB signals, i.e. synchronous pine mortality pulses, to calibrate detection parameters that identified growth releases associated with known canopy mortality events while avoiding periods of growth recovery following budworm defoliation. First I combined spruce and fir at each site into a single data

set based on high correlations between chronologies (Pearson $r = 0.452 - 0.801$, all $p < 0.001$) to strengthen the common signals I was interested in isolating (MPB and budworm) and limit the effects of species-specific responses. I then fit a spline curve with a frequency response period of 20 years over each series and tested 10 year windows of forward to backward spline values for years with a doubling of radial growth. The spline helped to remove the effects of sudden, short-term suppression/recovery events, while the 10 year window and 200% release threshold ensured that flagged events would be sufficiently longer and higher in magnitude than typical budworm recoveries (Zhang and Alfaro 2002) or responses to inter-annual climate variability. The length of the final release chronologies was determined by the interval containing at least 5 recording trees.

Releases in the standardized pine chronologies were smaller and less consistent than in the spruce and fir, not surprising given lodgepole pine's seral role and canopy-dominant position in these stands. To improve detectability of pine releases I isolated the disturbance signal in each series from baseline growth using the program OUTBREAK (Holmes and Swetnam 1996, unpublished, University of Arizona) to subtract my control pine chronology (undisturbed sites) from the pine collected at the outbreak sites. This produced corrected index series emphasizing only deviations from baseline growth unique to the disturbed sites. This is common practice in outbreak reconstructions for defoliators such as the two-year cycle budworm (Zhang and Alfaro 2003), larch sawfly (Girardin et al. 2001) and western spruce budworm (Campbell et al. 2006) which use a non-host species to remove the influence of climate. My method differed in that I was able to use same species as a control because canopy mortality events can be readily identified in the field. I developed the final control chronology using ARSTAN (Cook and Holmes 1986) to fit a negative exponential

curve to 72 series (50 trees) selected for the strongest regional agreement. All series were truncated to 1800 consistent with the recommended common signal strength ($EPS > 0.85$) for chronology development (Cook and Kairiukstis 1992). I ran the OUTBREAK-corrected pine series through JOLTS using a 10-year running mean procedure and the same release magnitude (200% increase) used for spruce and fir. All JOLTS results were quality checked at the individual site level against known mortality dates, then combined into a composite data set for a landscape-scale analysis.

For all pine definitively identified as beetle-kill I calculated radial growth increments for the 10-year period prior to death as an indication of tree vigor at the time of attack. Tree vigor can be a useful indicator of MPB population pressure because it is positively related to phloem thickness and host resistance (Cole 1973). Therefore, mortality in vigorous trees can indicate population buildup into an outbreak phase. Conversely, endemic phase mortality should be limited to weakened trees exhibiting slower radial growth. Each growth increment was standardized by tree diameter to account for differences in tree size following the methods of Bloomberg and Morrison (1989). Periodic growth was expressed as a percentage of total tree size at the beginning of the period using the following equation: $(x_i / r - x_i) * 100$ where x represents the sum of the ring widths for the interval i years and $r - x_i$ equals the radius of the tree at the beginning of the interval. I used the mean 10-year periodic growth rate for all living pine trees as my baseline for comparison.

2.4 Results

Species composition and stand structures varied in the relative distribution of live pine, spruce and subalpine fir (Table 2.1), however, the dead component of each stand was consistently and predominantly large diameter pine ($M = 29.1$ cm, $SD = 9.5$) (Figure 2.2). Mean DBH for positively identified beetle-killed trees ($n=168$) was slightly higher ($M = 33.7$ cm, $SD=8.2$). Live pine had a similar size distribution ($M = 29.0$ cm, $SD = 8.3$). Sites experienced between 22-100% pine mortality, accounting for up to 74% of the total mortality observed at a given site (Table 2.1). I collected a total of 963 increment cores and 199 cross-sections, including 327 dead pine. I did not find any fire scars that could be sampled for fire dates. Mean live pine age was 212 years ($SD=44$) and ranged from 138-352 years. Mean pine age (at coring height) at the time of death for all samples and in confirmed beetle-kill only was 185 years ($SD=47$) and 194 years ($SD=43$), respectively, and ranged from 70-353 years (Figure 2.2). My earliest reconstructed mortality occurred in 1835. I developed 54 standardized chronologies, and stand development followed a similar pathway at each site, colonized initially by single-cohort, fast-growing pine, followed by spruce and fir establishment soon after (Figure 2.3). Repeated suppressions consistent with the two-year cycle budworm outbreaks described by Zhang and Alfaro (2002) were prevalent in the spruce and fir chronologies. The majority of stands established in the mid to late 1700s with the exception of two 17th century initiations and one in the early 1800s (Table 2.1).

Establishment dates for all live trees > 10 cm diameter (Figure 2.4) show an age distribution ranging between 59 and 352 years old with pine and spruce dominating the older age classes and subalpine fir dominating the more recent establishment events. The timing of fire events, estimated by the stand establishment dates of the sites (Table 2.1) is consistent

with the pulses of pine establishment, the last of which occurred in the 1820s. Very low pine recruitment continued until the 1860s, after which time no new pine trees established. Subalpine fir and spruce establishment were continuous throughout the record, but subalpine fir became much more successful around the mid-1800s when pine and spruce establishment began to decline. Stem densities by site which include all the regeneration size classes (Figure 2.5) show canopy trees, small trees that were below diameter threshold for aging, sapling and seedling densities ranging from 425-1475 stems per hectare, 50-3300 stems per hectare, 50-8500 stems per hectare and 300-17550 stems per hectare respectively. Subalpine fir almost wholly dominates the stem classes smaller than those aged. The results of the ANOVA and Kruskal-Wallis tests (Table 2.2) showed no significant differences at any canopy level in stem density relative to the number of reconstructed outbreak events a site had experienced.

Within individual sites I observed synchronous and asynchronous pine mortality (Figure 2.3). Synchronous pulses occurred throughout the 1940s-1950s, 1980s, and again in 2006-2007. Stand level growth releases generally followed within 1-4 years, but the characteristics varied between sites and between species with spruce and fir exhibiting consistently higher magnitude growth responses than pine. Release duration was also variable, with periods of sustained high growth rates ranging from approximately 20 to over 100 years based on visual assessment of the site chronologies. Incremental pine mortality over many different years was more common than large pulses within sites and relative to these events stand-level growth releases were less clear, not surprising as plot averages can mask the response by smaller proportions of survivors. The JOLTS analysis identified the strongest and most consistent responses at each site, resulting in the detection of 1-2 major

release periods (>40% trees recording) at each site (Figure 2.4). Twentieth century major releases generally corresponded to at least one mortality date and were recorded by both pine and the non-host species, though not always at similar magnitudes. In some cases major non-host releases coincided with known two-year cycle budworm outbreaks, but there was no consistent response within sites to repeated defoliation events.

Table 2.1. Site inventories showing the distribution and dating of live (L) and dead (D) (pine only) trees ≥ 10 cm diameter at breast height in each plot and the total number of dated samples used to build the final site chronologies (C), including any additional trees sampled outside plot boundaries. The only other species present was trembling aspen, which were inventoried at two sites for a total of 4 trees, none of which had cores intact enough for dendrochronological processing.

Site	Lodgepole Pine				Interior (Black †) spruce			Subalpine fir			
	L (n)	D (n)	D (%)	C (n)	Master	L (n)	C (n)	Master	L (n)	C (n)	Master
CB3	18	5	23 ‡	29	1779-2006	7	17	1784-2007	13	17	1884-2007
KZ16	23	18	69	34	1786-2007	17 †	17 †	1828-2007	8		1821-2007
SL25	5	5	21 ‡	10	1808-2007	10	13	1814-2007	13	12	1845-2007
TS7	11	14	52	15	1807-2006	0			28	27	1869-2006
CB5	10	14	56	31	1780-2006	2		1846-2006	5		1901-2006
CB4	10	15	68	31	1780-2006	6		1792-2006	6		1837-2006
TE13	8	13	37	22	1684-2007	5	13	1693-2007	24	24	1684-2007
FL23	5	9	39 §	18	1824-2007	12	14	1826-2007	7	14	1839-2007
TK24	5	10	38	16	1743-2007	7	11	1766-2007	47	47	1748-2007
TS8	4	9	82	11	1783-2006	4		1795-2006	18	18	1863-2006
NA21	4	9	27 ‡	16	1654-2007	4	11	1678-2007	29	29	1733-2007
CB6	3	10	48	18	1780-2006	3		1809-2006	11	11	1867-2006
PV22	5	21	45	27	1788-2007	18	18	1800-2007	18	15	1805-2007
TS11	2	10	50	10	1787-2006	4	10	1797-2007	51	48	1864-2006
NZ18	3	15	61	15	1753-2007	10	10	1774-2007	31	31	1820-2007
CB9	2	19	73	12	1762-2006	2		1790-2006	36	35	1859-2006
NN19	1	10	42		1780-2003	6		1792-2007	25	23	1879-2007
NZ17	1	14	37	20	1748-2007	8	10	1786-2007	15	16	1778-2007
TB14	1	22	54	21	1764-2002	3	12	1825-2007	37	36	1825-2007
KL15	1	28	68	28	1778-2007	9	12	1786-2007	22	20	1786-2007
TS10	0	13	68	10	1781-1973	11	11	1785-2006	16	16	1884-2006
TR20	0	34	74	28	1780-2007	0			29	29	1787-2007
Total				431	1654-2007		202	1678-2007		486	1684-2007

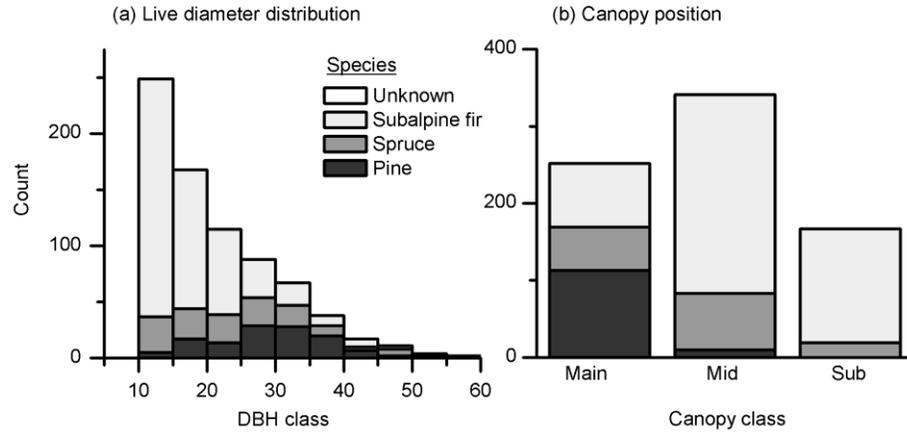
Notes: Master chronology length indicates earliest and latest dated rings, but chronologies were only built for sample sizes ≥ 10 . Blank cells indicate sites with too few dated trees for chronology development. Pine mortality (D) is summarized as total number dead trees (n) and as a percentage of total plot mortality (all species). Pine led mortality in all sites except where noted.

† Interior spruce found in all sites except KZ16 which was entirely black spruce

‡ Unknown (unidentified) species led total mortality

§ Subalpine fir led total mortality

LIVE TREES



DEAD TREES

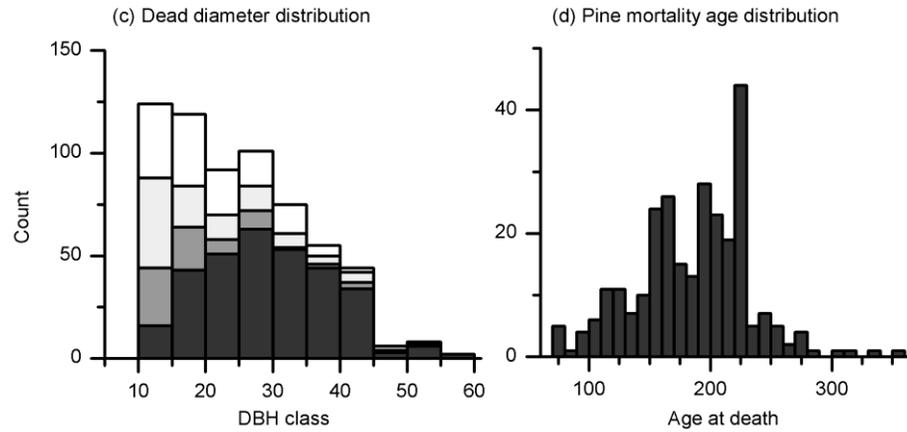


Figure 2.2. Composition and structure summarized for all trees ≥ 10 cm DBH. Live (a) and dead (c) diameter distributions show relative composition at 5cm size class intervals. Canopy distribution for living trees only (b) shows compositional differences between the dominant and codominant (main), intermediate (mid) and suppressed (sub) canopy classes. Mortality age distribution for dead pine only (d) shows age at the time of death (at sample height) for all pine with intact pith and outer ring dates in 10 year age classes.

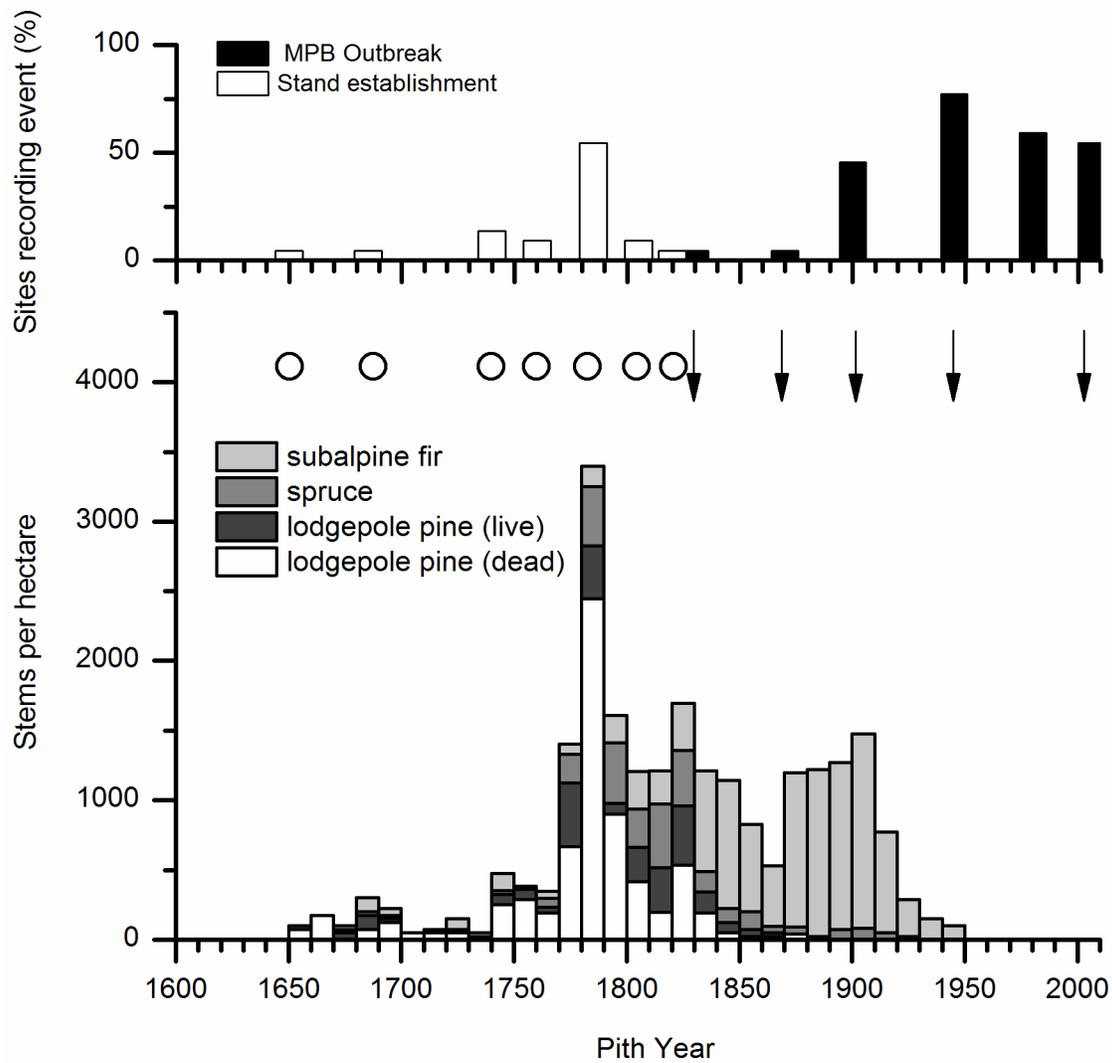


Figure 2.3. Establishment dates for all living trees greater than 10 centimeters diameter and all dead pine from all sites combined (bottom graph). Open circles approximate the timing of fires in my study area and are based on stand-initiation dates. Arrows indicate the timing of mountain pine beetle outbreaks reconstructed by this study. The proportion of sites recording each event is shown in the top graph.

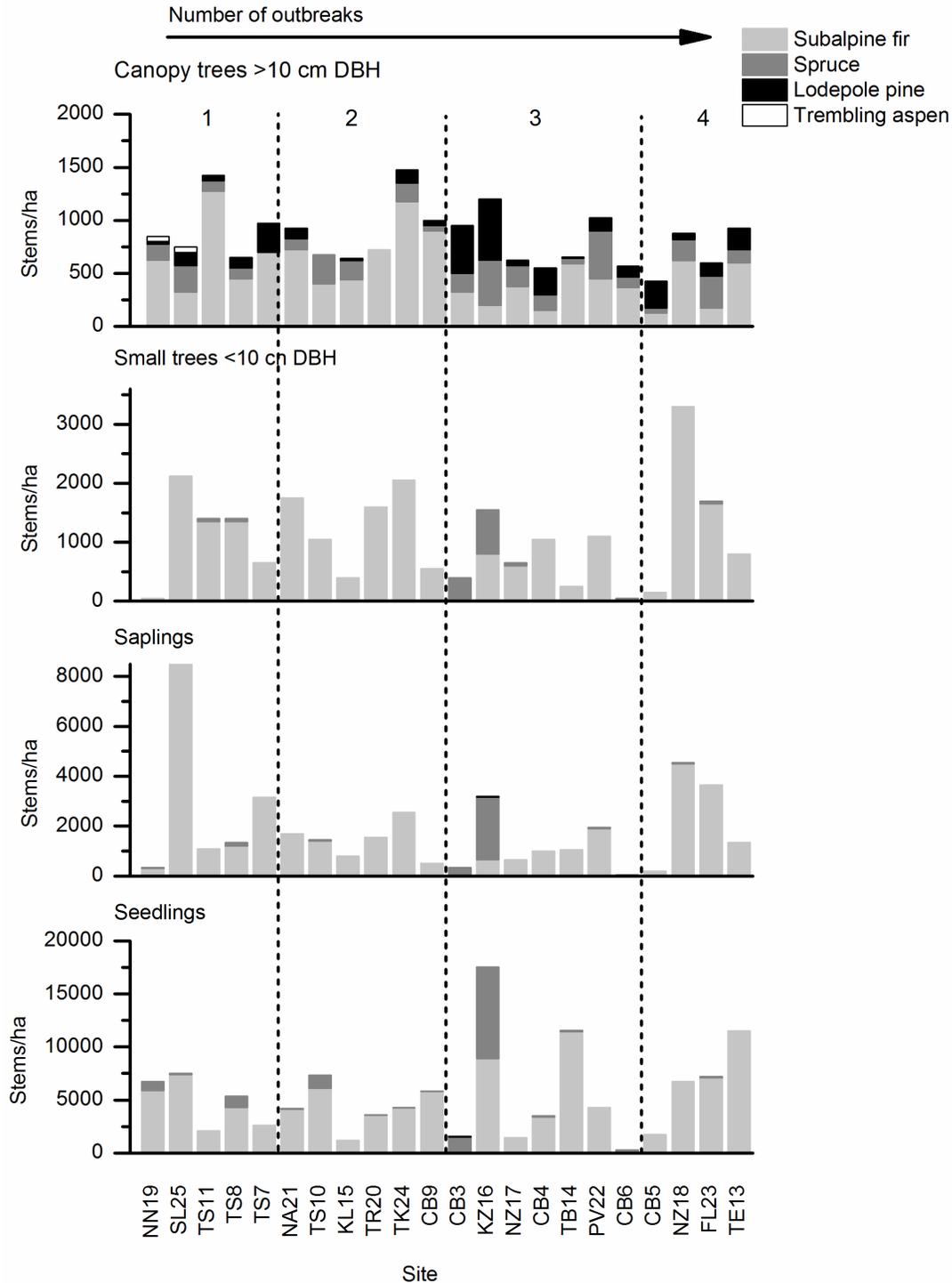


Figure 2.4. Stem densities at each site for all canopy levels ordered left to right by number of outbreaks experienced in that site. Number of outbreaks was determined using the pine mortality and survivor release data to determine whether mortality events occurred at that site during the reconstructed outbreak periods. All spruce were interior spruce except for site KZ16 which was entirely black spruce.

Table 2.2. Stem density summaries by canopy class and number of outbreaks that occurred. Results of the ANOVA and Kruskal-Wallis means comparisons results are listed for each test of stem density differences between the groups defined by number of outbreaks.

Canopy class	M (SD)^a	M 1 (SD)^b	M2 (SD)^c	M3 (SD)^d	M4 (SD)^e	*F_{df}	p
Canopy tree	840 (274)	930 (302)	907 (313)	796 (259)	708 (237)	0.636 _{3,18}	0.602
Subcanopy tree	1092 (811)	1125 (796)	1233 (673)	721 (535)	1488 (1365)	0.849 _{3,18}	0.485
Sapling	1864 (1906)	2890 (3300)	1425 (722)	1178 (1078)	2438 (2010)	*1.811 ₃	0.613
Seedling	5375 (4108)	4860 (2424)	4417 (2085)	5750 (6396)	6800 (3990)	0.283 _{3,18}	0.837

^a Mean stem density for all sites with standard deviation in parentheses

^b Mean stem density for sites experiencing one outbreak with standard deviation in parentheses

^c Mean stem density for sites experiencing two outbreaks with standard deviation in parentheses

^d Mean stem density for sites experiencing three outbreaks with standard deviation in parentheses

^e Mean stem density for sites experiencing four outbreaks with standard deviation in parentheses

* All results are from ANOVA tests except for the sapling group which used a Kruskal-Wallis test

In the composite data set I observed up to 5 periods predating the current outbreak with coincident growth release, pine mortality, and above average tree vigor estimates indicative of MPB canopy disturbances (Figure 2.5). Across all years, annual mortality ranged from 0-24 events occurring in up to 8 sites concurrently, and release percentages ranged from 0-43.3% of trees recording an event in either species group at a maximum of 22 sites. The most widespread event, based on number of sites recording, occurred in 1945 and the most severe, based on highest mortality, in 2006. Despite a declining sample depth for reconstructed mortality further back in time, mortality events match the timing of growth releases in the 1830s, late 1860s-1870s, 1900s-1910s, 1940s-1950s, and the 1970-1980s. Non-host releases are out of sync with pine releases in the 1970s and to a lesser degree in the 1870s and 1940s. I believe this to be an artifact of the detection procedure that occurs when canopy thinning occurs in close succession with two-year cycle budworm defoliation/recovery events. Although the moving windows procedure is calibrated to ignore short, low magnitude growth fluctuations occurring independently, it is unable to decouple the compounding effects of coincident responses resulting in slightly skewed timing or magnitude of the flagged event. For this reason, the timing of pine releases probably more accurately approximates outbreak timing.

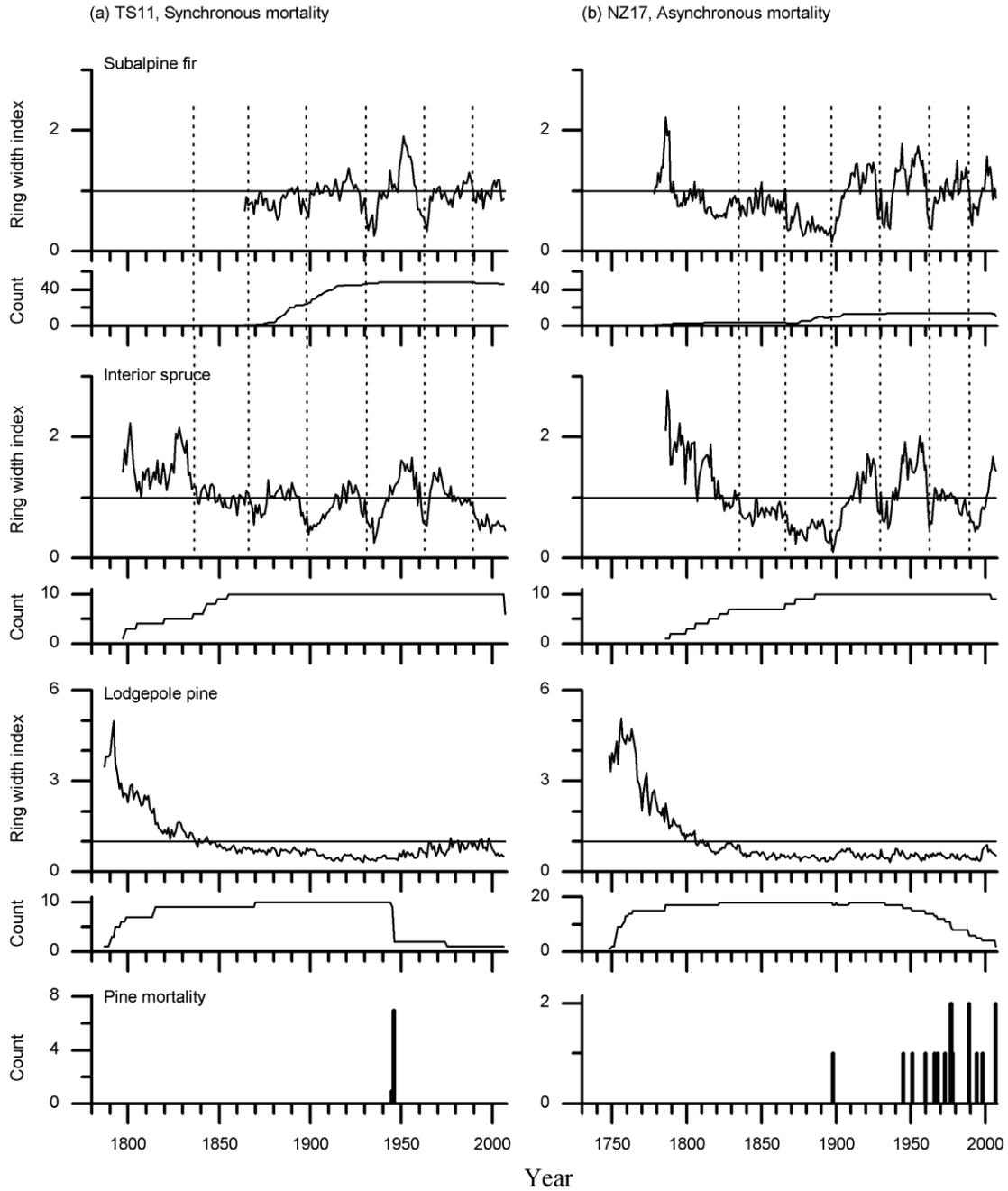


Figure 2.5. Standardized chronologies for lodgepole pine, interior spruce and subalpine fir from two sites exhibiting (a) synchronous pine mortality (site TS11) and (b) asynchronous pine mortality (site NZ17). Reference lines for each chronology represent mean index values, with sample depths drawn below each species. Dashed vertical lines indicate periods of two-year cycle budworm outbreaks identified by Zhang and Alfaro (2002, 2003).

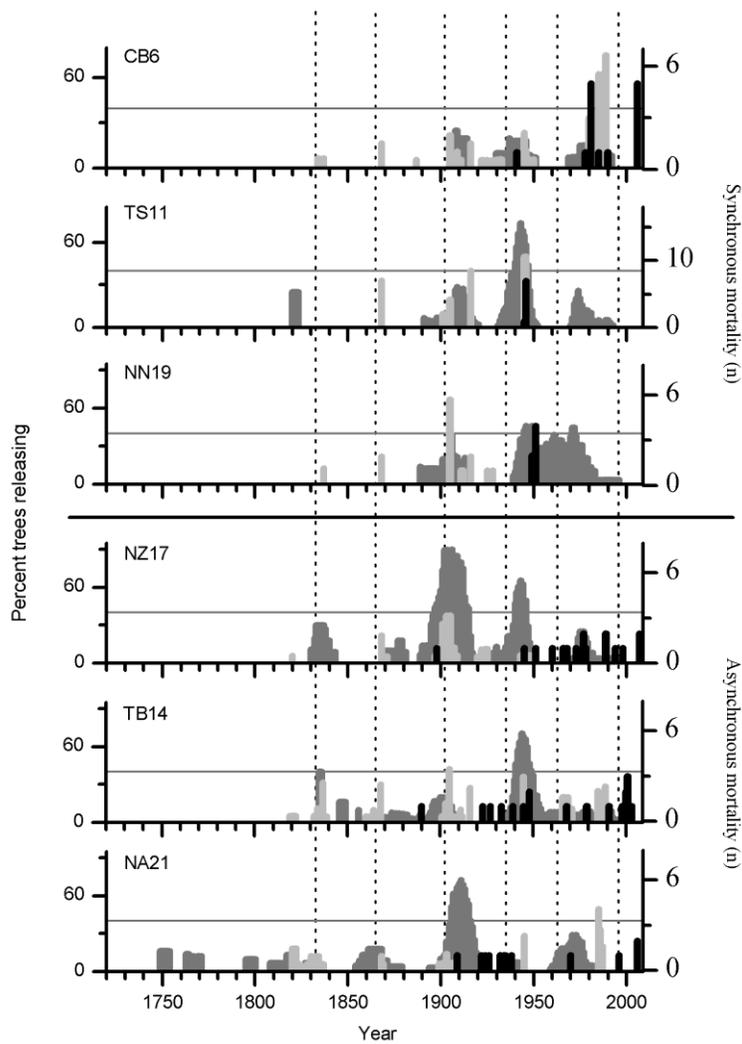


Figure 2.6. JOLTS results from selected sites representing synchronous and asynchronous mortality patterns. Black bars show pine mortality, dark (light) grey bars show the percentage of non-host (pine) trees experiencing a doubling of growth or greater for that year. Reference lines are drawn at 40% to delineate major release events. Dashed vertical lines indicate periods of two-year cycle budworm outbreaks identified by Zhang and Alfaro (2002, 2003).

Standardized ten year periodic growth increments at the time of death for beetle killed pine ($M = 2.31\%$, $SD = 1.66$) exceeded the mean live pine growth increment ($M = 3.38\%$, $SD = 2.29$) in the 1900s, 1940s-1950s, and fairly regularly from the late 1970s onward (Figure 2.5d), each corresponding to a release and/or mortality period identified above. Lower than average radial growth increments were recorded relatively continuously, but occurred exclusively during the 1920s, 1930s and the 1960s during periods of comparatively low release and mortality. Across the length of the entire record (1800-2007), landscape-scale outbreak events occurred on average every 29.6 years. There appeared to be a shift towards larger events around the 1870s when release percentages more than double for pine, though that increase was not observed in the non-host record until the turn of the century. I observed a similar shift in recent years when mortality levels exceeded the highest on record, however, release data is unavailable for comparison after 1997 because of the ten-year window used in the JOLTS calculations.

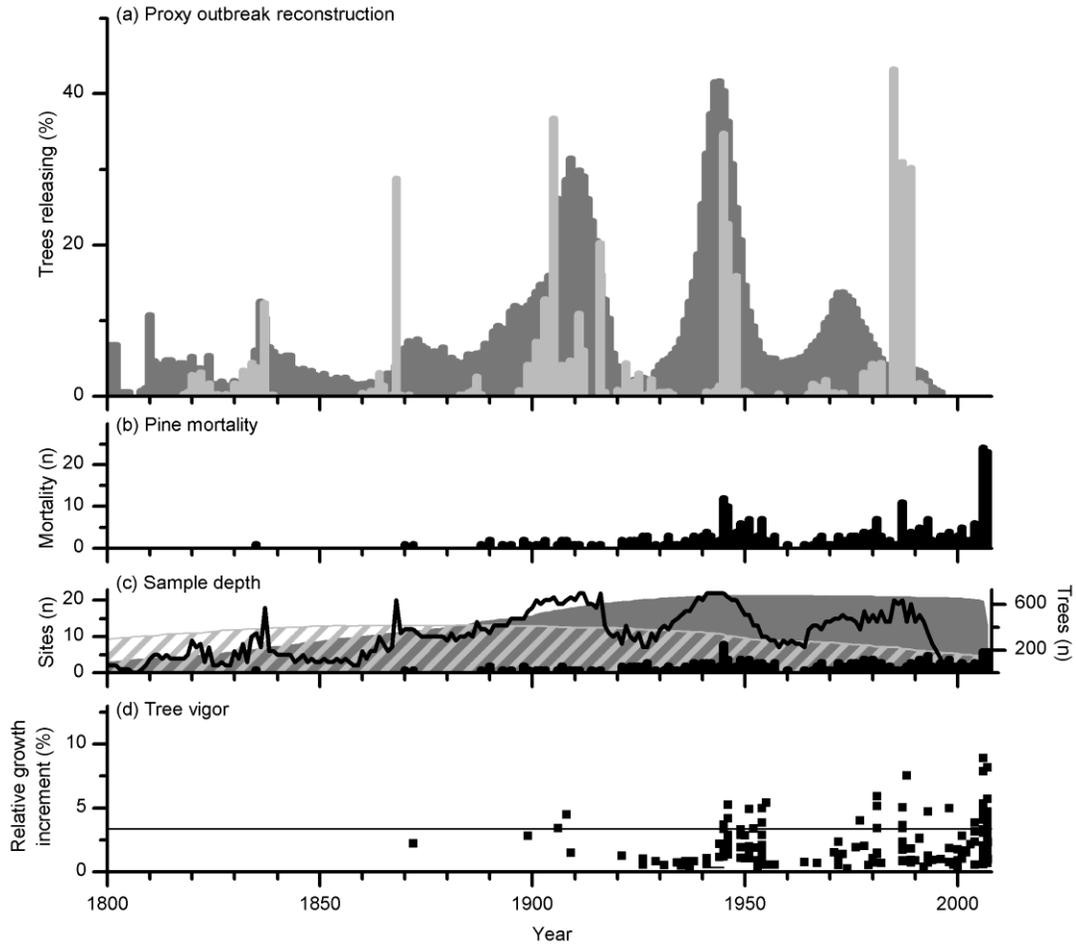


Figure 2.7. Landscape scale outbreak reconstruction based on composite data for all sites. Proxy reconstruction (a) shows the timing of pine (light grey bars) and non-host (dark grey bars) growth releases relative to (b) pine mortality events. Sample depth figure (c) shows the number of surviving pine (hatched light grey fill) and non-host (solid grey fill) trees used to calculate release percentages, the number of sites at which trees were releasing (black line), and the number of sites recording pine mortality (black bars) annually. Ten year relative growth increments standardized by tree size (d) represent tree vigor at the time of death for all confirmed beetle-killed pine trees. Reference line represents the mean ten year standardized growth increment for all living pine trees, above which I consider pine mortality to be occurring in healthy trees.

2.5 Discussion

2.5.1 Stand history

The establishment patterns and species compositions observed are typical for sub-boreal forests of north-central BC, consisting of single cohort seral pine stands giving way to shade-tolerant stands dominated by spruce and/or subalpine fir. The structure of the tree strata below the canopy (< 10 cm DBH) indicates that subalpine fir will ultimately dominate the landscape in the absence of another pine or spruce establishment event. Fast early growth rates for pine and spruce suggest these stands originated following stand-replacing fires (Veblen et al. 1991b). In the majority of sites, fires probably occurred during the mid- to late-18th century, with the exception of two stand initiations occurring earlier in the 1600s and two in the early 1800s. The stand age similarities for most sites in the study area suggest that infrequent, large severe fires are important, but over much longer time periods than MPB outbreaks. The prevalence of fire-intolerant subalpine fir in the smaller diameter classes and a lack of fire scar evidence suggests that fire has been absent from these stands since initiation. Under a typical stand-replacing fire regime, long fire-free intervals such as this are likely a prerequisite for outbreaks to develop. Age distributions of the living trees and stem densities for all trees, saplings and seedlings suggest that pine, and to a lesser degree spruce, persistence in these stands is dependent on the return of fire. Because we specifically targeted older sites in order to reconstruct MPB outbreaks, these statements about the relationship between fire and MPB only apply to remnant stands that have escaped more recent fires and not to the fire cycle for the landscape as a whole. The MPB outbreaks reconstructed following stand maturation did not appear to have any influence on regeneration patterns, either by causing pulses of tree establishment (Figure 2.3) which are

commonly linked to outbreaks in the southern-interior of BC (Axelson et al. 2009, Axelson et al. 2010) or through the alteration of stand densities at any canopy level (Figure 2.4, Table 2.2) even through repeated outbreaks. Rather, recruitment in these mixed-species SBS stands in the absence of fire appears to be a function of continuous regeneration by shade-tolerant species where composition ultimately depends on the competitive advantage of higher recruitment rates by subalpine fir.

With MPB, evidence for repeated two-year cycle budworm outbreaks was pervasive in my non-host chronologies and I suspect that both disturbance agents have a strong and widespread influence on stand development over similar time scales. Methodologically, the persistence of both signals in the tree-ring record introduces some problems for decoupling outbreak history, but ecologically this interaction may be an important component of outbreak and stand dynamics and should be explored further. Regardless of defoliation history, I know from the composition and structure of dead trees that my sites experienced selective pine mortality, eliminating the need to differentiate between mortality processes affecting other species. Direct beetle evidence on more than half of the dead pine sampled suggests that for two centuries MPB has been the most influential mortality agent affecting these stands.

2.5.2 Host selection, stand susceptibility and outbreak severity

On average, beetle killed pine trees in my study area were larger than the 25.4 cm DBH threshold defined by Safranyik et al. (1974) as necessary to sustain an outbreak, and comparatively large living pine today suggest that stand averages, at least for pine, have

exceeded the 20.5 cm DBH minimum used to define size structures at risk for an outbreak (Safranyik et al. 1975, Cole and Amman 1980) for much of the past century. Early outbreaks in the 1800s were probably less skewed towards larger diameter trees because the stands that had reached susceptible ages were younger. Smaller trees may have limited these early outbreaks from developing into larger events, because the more recent preference for larger than average trees suggests that beetle populations here may not be able to buildup and maintain epidemic population sizes in hosts that are considered to be in susceptible size classes elsewhere. Furthermore, the persistence of large diameter living pine in age ranges that closely match the age ranges of dead pine indicates that outbreak severity has historically been low and limited by some factor other than host availability, contrary to the density-dependent theories proposed in climatically optimal regions (Cole and Amman 1980, Alfaro et al. 2004). This is consistent with the asynchronous mortality pattern observed resulting in the incremental removal of pine from the canopy in multiple, low severity events rather than large, devastating outbreaks. Amman and Baker (1972) attribute higher proportions of large diameter pine trees at higher elevations to increased host survival, presumably related to the adverse effects of temperature on beetle success. The higher latitude of my study area likely has a similar effect. Larger trees provide a number of advantages over smaller diameter trees for northern beetle populations subject to greater climatic pressure. Most of these can be attributed to thicker bark and thicker phloem which have been shown to enhance survival and attack success by producing larger broods, larger beetles, faster life cycles and greater relative emergence rates (Safranyik and Jahren 1970, Amman and Cole 1983, Safranyik and Carroll 2006).

Pine mortality in this area is also skewed towards older trees than those typically considered susceptible to beetle attack. Taylor and Carroll (2004) constrained age-related susceptibility to between 80 and 160 years when modeling stand level outbreak risk in BC, the upper limit representing the age at which thinning phloem associated with senescence is thought to begin adversely affecting population growth. My mortality dates for confirmed beetle kill averaged 194 years and up to 353 years, suggesting that these northern pine stands remain susceptible to beetle attack long after provincial models suggest. Above average periodic growth increments in many of the beetle killed pine indicate that these infestations are not endemic populations restricted to weakened trees in the stand. Rather, beetle success in vigorous trees suggests that these older pine stands can support epidemic populations. The relatively continuous mortality observed in less vigorous trees also suggests these stands maintain a nearly continuous supply of endemic beetle populations. The prevalence of large, old pine trees available likely enhances the stability of these populations between outbreak phases relative to post-outbreak stand structures dominated by smaller diameter, vigorous young pine that is much less favorable for beetle survival and reproduction. This has dramatic implications for climate change impacts in the region because beetle populations here may be able to respond more quickly and successfully to increasingly favorable conditions, with potentially greater risk for large epidemics to develop if high-latitude endemic populations function more like incipient-endemic populations held in check by more continuous exogenous pressures.

2.5.3 *Outbreak regime*

Between 1800 and 2007, I reconstructed six periods of MPB disturbance occurring in the 1830s, late 1860s-1870s, 1900-1910s, 1940s-1950s, 1980s, and the epidemic underway at the time of the study. Survey records confirm the timing of a widespread, severe infestation in the 1940s-1950s, as well as numerous, chronic infestations occurring throughout the 1980s and 1990s until the current outbreak began building in the 2000s (Wood and Unger 1996). My proxy data extends the record 140 years describing three additional release periods consistent with the known outbreak response, although the degradation of direct mortality evidence prior to 1900 requires cautious interpretation of these events as MPB outbreaks. The two-year cycle budworm signal in the non-host chronologies may have influenced the release analyses for these species, though conservative thresholds and supporting evidence from other sources suggest the filtering procedure was successful in identifying canopy disturbance events. To reduce the effect of any timing errors, I limit my discussion to a decadal resolution and use direct pine mortality evidence wherever possible to describe outbreak details.

The current outbreak is the most severe on record, but the scale, severity, and mortality characteristics of the 1900-1910s and the 1940-1950s events also fit the profile of large epidemics (Amman and Schmitz 1988, Safranyik and Carroll 2006). The 1980s saw abundant mortality, but these were localized infestations until the 2000s. Steady population pressure from the 1980s could have contributed to the unprecedented mortality of the 2000s. Consistent with the growth release data, I suspect that prior to 1870, outbreaks would have been small-scale, low-severity disturbances that failed to coalesce across the landscape, such as the 1830s event. Based on stand ages from all my plots, landscape-scale susceptibility

would have occurred around 1860-1870 (Raffa and Berryman 1982), establishing reasonable potential for outbreaks to grow large around this time. My landscape-scale outbreak return cycle of approximately 30 years agrees well with the 20 to 40-year cycle described by Amman and Schmitz (1988) and the 42 and 36-year cycles observed in south-central BC (Alfaro et al. 2004, Axelson et al. 2009), however, unlike these studies, stand age and size structure in the northern interior is probably less important for controlling outbreak periodicity. Rather, the mortality and stand development patterns reconstructed here suggest that following stand maturation, density-independent factors such as climate suitability are the dominant influence limiting outbreak development.

2.5 Conclusions

My outbreak reconstruction at the northern limit of the MPB range served two purposes: first, to lengthen survey records to an ecological time scale appropriate for examining long term disturbance processes and interactions; and second, to provide an outbreak susceptibility profile for forests that are distinctly different from those found in climatically optimal parts of the range. Differences between my study and others highlight the importance of geography and forest structure in modeling outbreak risk in marginal habitats, especially in response to climate change projections for these sensitive zones. Rising outbreak severity demonstrated in recent years suggests this area is already experiencing an altered disturbance regime, and ongoing range expansion into structurally similar, previously uninfested forests to the north and east calls for a better understanding of outbreak dynamics in these types of environments. This is particularly true with respect to susceptibility models developed in other parts of the province which may underestimate outbreak risk in the north, especially in older stands with a large proportion of pine

remaining. Although the effects of climate change can only partly be addressed by this study as I did not include any information about past climate in the reconstruction, my results suggest that historically unfavorable climate has been more important than stand structure in regulating outbreak development. This is probably due, in part, to long fire-free intervals allowing large cohorts of mature pine to persist across extensive areas. As climate becomes more suitable, I expect outbreak severity will continue to increase throughout the northern range margin following the distribution of available hosts, which are currently not limiting in the landscape. My reconstruction may help to forecast outbreak potential and develop timber management plans accordingly as this occurs.

3. Local and large-scale climate interactions with a multi-century record of mountain pine beetle outbreaks in north-central British Columbia

3.1 Abstract

Phytophagous insect populations are extremely sensitive to climatic variation at virtually every stage of their life cycle. Recent unprecedented outbreaks of bark beetles across western North America and rising concerns of the effects that climate change may have on future disturbance regimes has increased attention on the specific links between climate and outbreak development. The objectives of this study were to examine the direct and indirect effects of known climatic drivers on mountain pine beetle outbreaks near the northern limit of the species range where the disturbance regime is expected to be extremely sensitive to climatic variation, yet very little is known about specific climate responses here.

Using a 200-year outbreak history available for the study area I examined the long-term relationships between outbreak timing and the known local and large-scale climate drivers using superposed epoch analysis (SEA) to determine which factors were most important in outbreak development. I examined the indirect climatic effects mediated through the host tree-climate response by including a climate-sensitive host chronology developed using dendrochronological methods as a climate variable in the analysis. Lastly I looked at climate suitability for the study area as defined by existing models to visually assess the individual climate parameters and support the results of the SEA tests.

My results indicated that persistent positive winter temperature anomalies and the large-scale patterns of climate variability that drive them (the Pacific Decadal Oscillation and El Niño–Southern Oscillation) were the most important predictors of when outbreaks will occur. Extreme cold events and the large-scale patterns associated with them (the Arctic

Oscillation and Pacific North American pattern) showed no skill for predicting outbreaks, but this does not discount the importance of minimum temperatures in influencing inter-annual population dynamics. Short-term host stress was an important precursor to outbreak development, however, differences in geography and species responses to climatic variability dictate that a precipitation may not be a universally acceptable proxy for host stress. Over longer time periods, prolonged host vigor was significantly related to outbreak development, suggesting that healthy trees may provide certain advantages in marginal environments subject to greater climatic pressures.

3.2 Introduction

The importance of climate in the population dynamics of phytophagous insects is well established, however, recent widespread epidemics and rising concerns over the impacts of climate change on forest disturbance processes have increased attention on the specific links between climate and outbreak development (Dale et al. 2001, Bentz et al. 2010). Climatic effects can be direct or indirect and can influence insect herbivore physiology, behavior or success at virtually every stage of the life cycle. The most well-studied direct effects are temperature-driven, primarily because poikilotherms are extremely sensitive to thermal conditions and, relative to other types of climatic variation, projected increases in global temperature are expected to have the most dramatic influence on population dynamics (Bale et al. 2002). Some consequences of rising temperatures have already been documented, including genetic adaptations to shifts in seasonal timing (Bradshaw and Holzapfel 2006) and range expansions into formerly unsuitable habitats (Battisti et al. 2005). Indirect effects include any climate-induced changes that are mediated through other organisms such as the

host plant or community associates. Over short time scales the most important indirect effect is often associated with a decrease in host resistance brought on by climate-induced water stress, but the mechanisms of this are not well understood and often complicated by interactions with other critical feedbacks or by regional ecosystem differences (Bentz et al. 2010).

Forest insects capable of attacking and reproducing in healthy trees are key drivers of ecosystem change because of their ability to dramatically influence tree mortality rates. In the western United States and Canada, the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins (Curculionidae: Scolytinae)) is a native bark beetle that experiences periodic population eruptions responsible for landscape-scale mortality in mature pine stands. Timber losses have important economic and social impacts (Parkins and McKendrick 2007), but outbreaks can also have significant ecological effects on wildlife habitat (Chan-McLeod 2006), fire behavior (Jenkins et al. 2008), carbon storage (Kurz et al. 2008), and hydrology (Redding et al. 2008). Currently western Canada is experiencing the largest and most severe MPB epidemic on record that has affected over 17.5 million hectares of forest land in British Columbia (BC) (BC Ministry of Forests, Lands and Natural Resource Operations 2011) and MPB has recently become established on the eastern slopes of the Rocky Mountains and in west-central Alberta (Cullingham et al. 2011). Situated at the northern extent of the beetle's range, MPB populations in BC are expected to be particularly sensitive to climatic variation and have received much attention over the previous decade in an effort to define the role of climate in outbreak dynamics and develop predictive models for future susceptibility across the expansive host range to the north and east.

Climate suitability models originally developed by Safranyik et al. (1975) to assess beetle habitat suitability and later adapted for spatio-temporal analyses (Carroll et al. 2004, Moore et al. 2005) combine three categories of variables critical to the climate-outbreak relationship to estimate outbreak risk. These categories include variables to describe heat accumulation as it pertains to developmental rates of individual beetles and population synchrony, cold mortality potential during the overwintering period, and host stress which includes any climatic factors linked to changes in host defensive capacity. The specific variables may differ depending on the spatial and temporal scope of the model. Detailed laboratory and field observations have identified threshold values for each parameter that are used to quantify favourability. Heat accumulation thresholds define the temperature cues necessary to synchronize life cycle processes with critical seasonal events in order to maximize reproductive success (Logan and Powell 2001). Examples include the minimum temperature requirement for flight that triggers emergence and promotes mass attack (McCambridge 1971) or the cumulative number of degree days specified for specific periods that initiate egg hatch and ensure developmental rates sufficient for overwinter survival and a univoltine life cycle (Carroll et al. 2004). Cold mortality thresholds define the seasonally varying tolerances of MPB larvae to winter temperatures (Logan et al. 1995), below which survival rates have limited potential to sustain epidemics (Safranyik and Carroll 2006). Winter temperature suitability can be assessed by counts of days below the temperature curves developed by Wygant (1940) that detail the frequency and timing of extreme cold events or by seasonal and monthly averages that represent overall winter temperature trends. Host stress thresholds are less specific than the temperature requirements defined for MPB development and survival. Typically host stress is defined by some measure of water deficit

over two or more years, usually early growing season precipitation totals that are below a long-term average although other indices have also been used to approximate precipitation variability (Carroll et al. 2004). A more direct indicator of host stress can be measured using the radial growth of host trees prior to attack, where reduced growth represents a reduced capacity for a defensive resin response and consequently lowered host resistance (Safranyik et al. 1974).

More recently large-scale patterns of climate variability with atmospheric teleconnections in western Canada have become a focus of MPB climate suitability studies because of the potential for improving ecologically relevant climate predictions over larger areas and longer time scales than local variables allow (Stenseth et al. 2003). Linking large-scale climate indices to outbreak dynamics can reduce the complexity associated with individual climate variables by providing a more generalized probability of when suitable conditions occur. The benefit of these relationships is that, as we improve predictions of phase shifts, we may also increase our ability to forecast the probability of MPB outbreaks occurring. The dominant climate indices with biologically-relevant links to MPB ecology in BC include the Pacific Decadal Oscillation (PDO), the El Niño – Southern Oscillation (ENSO), the Arctic Oscillation (AO), also known as the Northern Annular Mode (NAM), and the Pacific North America pattern (PNA) (Stahl et al. 2006a, Fauria and Johnson 2009, Thomson 2009). The PDO is a climate pattern centered in the North Pacific Ocean that oscillates on a 20-30 year cycle and is generally expressed in western North America as winter (October-March) temperature anomalies and spring snowpack and streamflow anomalies, with warm (cool) phases linked to above (below) average temperature and below (above) average precipitation and snowpack in my study area (Mantua et al. 1997). Stahl et

al. (2006a) linked the frequency of MPB cold mortality events in BC with winters with strong negative PDO indices, suggesting climate favourability and potential for MPB expansion during positive and neutral PDO years. The PDO may also indirectly influence MPB success if host susceptibility is affected by PDO-driven climate trends, but this relationship has not been studied. ENSO phases, which are often assessed by the Southern Oscillation Index (SOI) to describe the warm El Niño (negative SOI) and cold La Niña (positive SOI) conditions associated with fluctuating sea surface temperatures in the equatorial Pacific, share similarities with PDO teleconnections in BC, but cycle over a much shorter time scale of 2-7 years (Shabbar and Bonsal 2004). BC winters are generally warmer (colder) and drier (wetter) following the onset of an El Niño (La Niña) event (Shabbar and Khandekar 1996, Shabbar et al. 1997), with the warm ENSO phase associated with significantly higher (lower) frequencies of warm (cold) spells and extreme warm (cold) temperature events (Shabbar and Bonsal 2004). The cold ENSO phase is generally associated with the opposite effects.

Interactions between large-scale climate indices can also influence climatic suitability for MPB outbreaks. For example, Bonsal et al. (2001) noted that ENSO temperature impacts were enhanced when in-phase with the PDO, consistent with the findings of Stahl et al. (2006a) who showed the highest probability for MPB cold mortality was associated with negative PDO winters that occurred during La Niña or neutral ENSO years. The PNA is a PDO-driven atmospheric circulation pattern that has been associated with significantly warmer January minimum temperatures in its positive phase during periods with above average NAM index values (Thomson 2009), which could also influence overwintering survival rates. Alone, AO phases, which describe the strength and location of

the westerly winds around the northern polar areas, show inconsistent relationships with winter temperatures (Zhou et al. 2001), but are important in regulating the occurrence of Arctic air flows to the south which can influence cold spell duration and warm spell frequency in BC (Shabbar and Bonsal 2004). Stahl et al. (2006a) attribute the highly negative AO indices of 1984/85 to the cold mortality events that ended the Chilcotin outbreak despite a positive PDO winter.

Much of what we know about climate suitability for MPB is based on detailed studies of individual climate components in a controlled setting, such as cold tolerance at various life stages (Logan et al. 1995), or observations of a set of climatic conditions surrounding single outbreaks, especially the Chilcotin outbreak that began in the 1970s in south-central BC (e.g. Thomson and Shrimpton 1984, Aukema et al. 2008). Some studies examine climate suitability independently of outbreak data using established climate drivers to classify outbreak risk based on historical climate profiles (e.g. Safranyik et al. 1975) or to examine the influence of large-scale ocean-atmosphere patterns on specific parameters of climate susceptibility such as winter temperature variability (e.g. Stahl et al. 2006b, Thomson 2009). Very few studies have compared long time series of MPB outbreak data directly against long-term climate data to investigate the consistency of these relationships through multiple outbreak events. This is in part because detailed outbreak histories for BC generally do not exist before 1959 when the Canadian Forest Service, Forest Insect and Disease Survey (FIDS) began conducting annual aerial overview surveys of these disturbances province-wide. Since this time only two major epidemics have been documented, the Chilcotin outbreak of the 1970s and 1980s and the present outbreak which began to develop in the 1990s, although there is evidence of another large epidemic in north-central BC that was in

decline around the time monitoring began and numerous smaller infestations throughout the 1980s (Wood and Unger 1996, Hrinkevich and Lewis 2011). Although the FIDS (1959-1996) and later BC Ministry of Forests annual forest health surveys (1999-present) provide nearly continuous MPB outbreak data since 1959, they have limited value for investigating low-frequency climate-outbreak relationships with patterns such as the PDO that have only undergone one phase shift during the survey period. Fauria and Johnson (2009) caution in their study linking PDO and AO to the aerial survey records that significant relationships observed over these short time series do not provide enough evidence to determine causality of the relationships observed. For PDO, this would require at least some replication of known phase shifts which would include an outbreak record at least as long as the instrumental PDO record (1901-present).

In this study I use a proxy MPB outbreak record covering the period 1800-2007 derived from tree-ring data (Hrinkevich and Lewis 2011) to examine long-term climate-outbreak relationships in north-central British Columbia. Specifically my objectives are: (1) to examine the interrelationships between the known climatic drivers of MPB population dynamics, host tree growth and outbreak timing, (2) to analyze climate-tree growth relationships in order to determine which climatic effects are mediated through the host trees, and (3) to evaluate existing models of climate suitability for MPB in the study area relative to outbreak history. My study addresses a number of gaps in existing climate-outbreak research, including a need for increased understanding of outbreak dynamics in climatically sensitive regions at the northern range limits where the effects of climate change are expected to be most severe. Furthermore, by using long-term data I provide additional evidence about the causal links between climate and outbreak development, particularly for

low-frequency patterns. Lastly, my use of a host tree growth chronology allows me to directly examine the relationship between climate-induced host stress and outbreak development rather than using indirect climate variables that may not accurately reflect changes in host susceptibility. Although climatic links to host stress were identified in early investigations of host-climate-outbreak relationships (Shrimpton and Thomson 1982, Thomson and Shrimpton 1984), more recent work typically assumes the same climate-tree growth relationships apply and uses a growing season precipitation variable to represent host stress. I question whether this assumption holds in pine ecosystems other than the Chilcotin plateau where they were developed and present an alternative method for examining the role of host stress.

3.3 Methods

3.3.1 Study area

The study area is located in the northern interior of British Columbia, at the northwest corner of the Sub-boreal spruce (SBS) biogeoclimatic zone (Meidinger and Pojar 1991). It is roughly bounded by three of BC's largest natural lakes, Takla, Stuart, and Babine to the north, east, and southwest respectively (Figure 3.1). Historically, this region near Fort St. James represents the most active area for documented MPB outbreaks at this latitude and lies close to the historic northern limit of the beetle's range in BC (Safranyik et al. 1974). Survey records report a major epidemic in the area in the 1950s followed by a period of chronic infestations beginning in the 1980s and building throughout the 1990s (Wood and Unger 1996), with ongoing infestations coalescing into the present epidemic during the mid-

2000s. An independent tree ring-reconstruction of MPB outbreaks in the study area (Hrinkevich and Lewis 2011) details these events as well as three additional outbreak periods, including one large epidemic in the early 1900s and two 19th century events.

The regional climate of the Fort St. James area is characterized by short, warm summers and cold, snowy winters (15.3°C and -11.3°C average July and January temperatures), with moderate average annual precipitation (487.1 mm) distributed relatively evenly throughout the year (Environment Canada 2010). These are typical climate normals for SBS forests in British Columbia. Upland coniferous forests dominate the landscape, characterized by late successional stands of hybrid white spruce (interior spruce) (*Picea engelmannii* Parry x *P. glauca* (Moench)) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt. Lodgepole pine (*Pinus contorta* Dougl. Var. *latifolia* Engelm.) and trembling aspen (*Populus tremuloides* Michx.) primarily lead seral stands. Other tree associates include paper birch (*Betula papyrifera* Marsh.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and black spruce (*Picea mariana* (Mill.) B.S.P.).

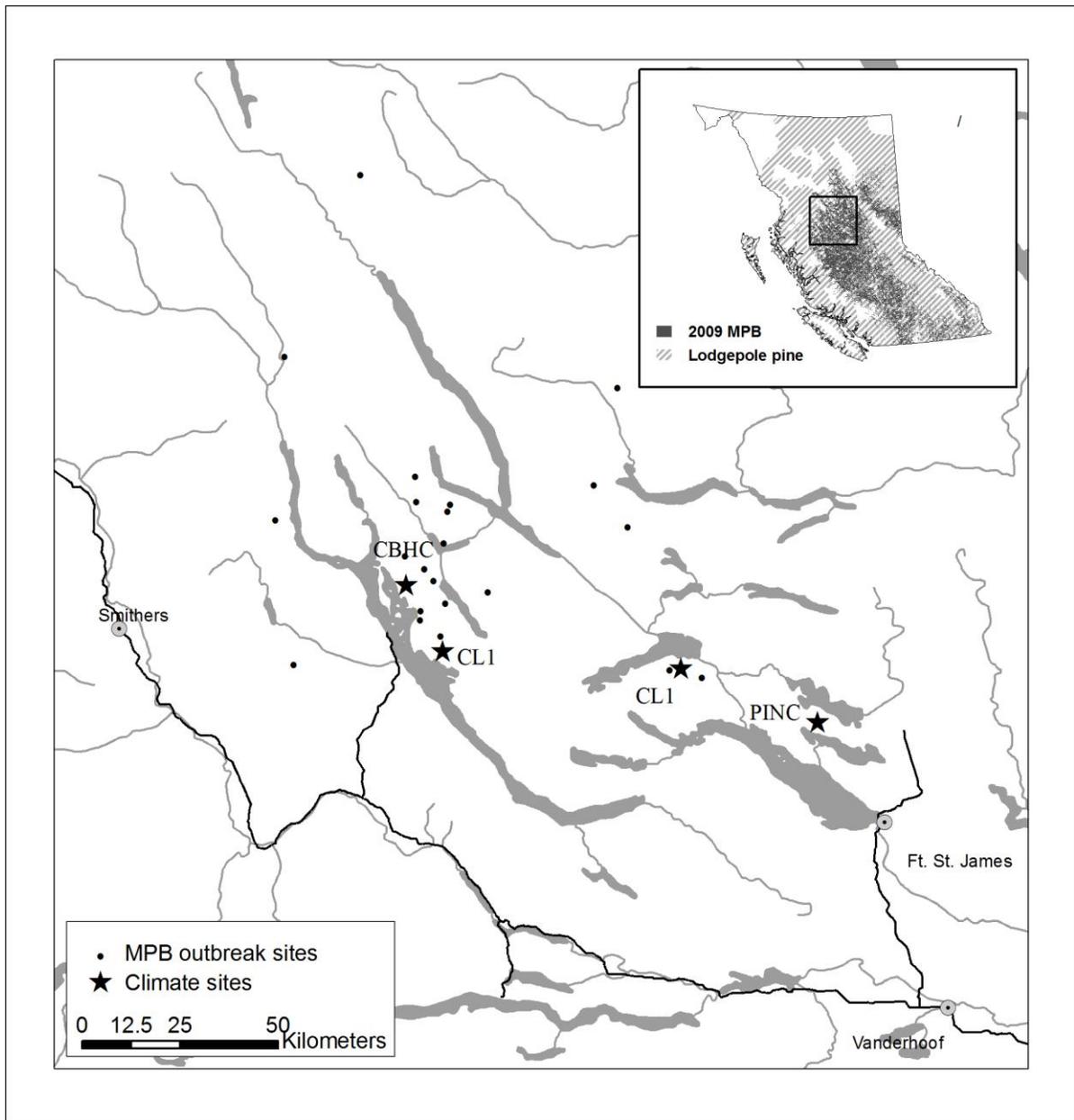


Figure 3.1. Study area map showing the locations of each of the climate sites used to compile the master climate chronology as well as the locations of the study sites used to develop the mountain pine beetle outbreak reconstruction. Inset shows location of study area in British Columbia relative to the distribution of lodgepole pine and the 2009 cumulative mountain pine beetle outbreak extent.

3.3.2 Chronology development

I sampled four sites distributed across the study area defined by the outbreak reconstruction (Hrinkevich and Lewis 2011) for my climate-tree growth analysis (Figure 3.1). To maximize the climate signal and limit any stand-level influences on tree growth, I selected only mature open-canopy, pine-dominated sites on steep or well-drained slopes that showed no signs of past disturbance, although some of the trees were recently dead or dying from the ongoing mountain pine beetle outbreak. Needle color and retention in these stands suggested attack dates within three years of the sampling date. I selected up to 20, but as few as 4 where availability was limited, of the largest trees at each site and extracted two increment cores from each, with the exception of site CB1 where only single cores were collected, resulting in a combined total of 82 cores from 58 trees.

Increment cores were mounted and sanded following standard dendrochronological methods (Stokes and Smiley 1986) until the cell structure of individual growth rings was clearly visible under a dissecting microscope. I used the list method (Yamaguchi 1991) to dot and visually crossdate cores from all the living trees with a known outer ring date, then used the living-tree marker years to assign calendar years to the dead series. I measured the annual rings of all samples using a Velmex measuring system and used the program COFECHA (Holmes 1983) to assist in correcting and verifying the dating of each series. Series with anomalous radial growth patterns were truncated or discarded to produce a final chronology with the highest series intercorrelation containing 67 cores from a total of 47 trees (Table 3.1). High intercorrelations among sites indicate a strong regional tree growth signal that applies across the study area. I developed a standardized mean chronology using the program ARSTAN (Cook and Holmes 1986) to first fit a negative exponential curve or a

linear regression to each series to remove the effects of age on tree growth and then to remove autocorrelation from each of the detrended series using the built-in autoregressive modeling function. The final chronology was computed using the residuals from the autoregressive modeling to obtain an estimate of mean growth for each year with serial persistence removed to enhance the common climate signal (Cook 1985). I confirmed that the master chronology maintained the recommended common signal strength ($EPS > 0.85$) for the entire period of record (Cook and Kairiukstis 1992).

Table 3.1. Descriptive statistics computed using the program COFECHA for individual climate sites used to compile the final chronology and for the master chronology

Site	N ^a	r ^b	MS ^c	Period ^d	Length ^e
CL1	5 (4)	0.650	0.262	1850-2005	156
CB1	17 (17)	0.684	0.299	1875-2006	132
PINC	36 (20)	0.653	0.249	1800-2005	206
CBHC	9 (9)	0.710	0.315	1850-2005	156
Master	67 (47)	0.633	0.269	1800-2006	207

^a Number of series in each chronology with the number of trees in brackets

^b Pearson's correlation coefficient calculated between all series in chronology

^c Mean sensitivity is an indicator of the relative variation in ring width in series

^d Period covered by each chronology

^e Total number of years in the chronology

3.3.3 Climate data

I obtained temperature and precipitation records from the nearest meteorological station in Fort St. James for the climate variables known to influence MPB population dynamics (Table 3.2). Monthly variables were compiled from the Adjusted and Homogenized Canadian Climate Data (AHCCD), a quality-controlled dataset of monthly averages that incorporates adjustments to the original station data to address changes in instrumentation and observation procedures over time (Environment Canada 2011). Variables based on daily temperature thresholds were compiled from the National Climate Data and Information Archive records available online from Environment Canada (http://www.climate.weatheroffice.ec.gc.ca/prods_servs/index_e.html#cdcd) and I used Wygant's (1940) cold mortality curves to calculate the number of days below the 50% and 100% mortality curves. I also calculated 2-5 year running means for each variable to examine relationships associated with more persistent climate conditions such as consecutive warm winters or prolonged droughts.

For the four dominant large-scale climate modes thought to influence MPB success in BC, I obtained data online from the National Center for Atmospheric Research, Climate Analysis Section (SOI, <http://www.cgd.ucar.edu/cas/catalog/climind/soi.html> and AO, <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>), the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) at the University of Washington (PDO, <http://jisao.washington.edu/pdo/>), and the World Data Center for Paleoclimatology, Boulder and the NOAA Paleoclimatology Program (PNA, <http://www.ncdc.noaa.gov/paleo/metadata/noaa-recon-8697.html>) (Table 3.2). Following Redmond and Koch (1991), I focused on winter climate associations with these indices when

North Pacific teleconnections are strongest. I defined winter SOI by the preceding June–November index values (Redmond and Koch 1991), PDO using December–February (DJF) means (Stahl et al. 2006a), and AO using mean December–March (DJFM) index values (Hurrell 1995). I used a reconstructed December–January (DJ) PNA index (Trouet and Taylor 2009) because the instrumental records available were too short (1948–2010) to coincide with a sufficient number of outbreak events for my analysis. As with the temperature and precipitation data, I also calculated running annual means for each index to examine lower frequency trends associated with outbreak development. I included 2–10 year averages for PDO, PNA and AO, and 2–5 year averages for SOI because of the shorter periodicity between phases.

Table 3.2. Climate variables known to influence mountain pine beetle population dynamics with commonly used threshold values for climate suitability modeling. Data sources for each variable are included. The rationale for including these variables in the analysis and the specific effects they represent in the population dynamics of MPB is described in detail in the text.

Category ^a	Climate Variable	Predicted threshold ^b	Period ^c	Source data
Heat Accumulation	August maximum temperature	≥ 18.3 °C (McCambridge 1971)	1895-2010 (4)	(Environment Canada 2002, 2011)
	Summer and annual degree days	> 305 dd > 5.5 °C (Aug 1 to end of growing season)	1895-2002 (3)	“ “
		> 833.3 dd > 0 °C (Aug 1 to July 31) (Carroll et al. 2004)		“ “
Cold Mortality	October-March minimum daily temperatures	Days above mortality curve (Wygant 1940)	1896-2001 (3)	“ “
	Winter (DJF) monthly temperature (mean/minimum)	DJF $>$ average (Fauria and Johnson 2009)	1896-2010 (4)	“ “
Host stress	Early growing season (AMJ) precipitation	2+ years $<$ average (Thompson and Shrimpton 1984)	1896-2010 (4)	“ “
	Radial growth (residual chronology)	Index values < 1 (Shrimpton and Thompson 1982)	1800-2006 (6)	(Hrinkevich and Lewis 2011)
Large-scale indices	PDO	DJF > 0 (Stahl et al. 2006a)	1901-2009 (4)	(Mantua et al. 1997)
	SOI	June-November < 0 (Redmond and Koch 1991)	1867-2009 (5)	(Trenberth 1984)
	AO (NAM)	DJF > 0 (Fauria and Johnson 2009)	1899-2011 (4)	(Hurrell 1995)
	PNA (reconstructed)	DJ > 0 (Thomson 2009)	1725-1999 (5)	(Trouet and Taylor 2009)

^a Major categories of climate variables thought to influence MPB outbreak dynamics

^b Predicted thresholds used to define climate suitability for MPB with source

^c Period indicates time covered by the data series. The number of outbreaks that occurred during that time period which were included in the SEA analysis are in parentheses.

3.3.4 Climate, tree growth and outbreak relationships

I calculated correlation and response functions using DendroClim2002 (Biondi and Waikul 2004) to test for relationships between my residual climate chronology and the instrumental temperature and precipitation data. These procedures calculate a sequence of coefficients between the annual tree-ring index values and a pre-defined set of monthly climate variables using Pearson's product moment correlations and principle components regression models, respectively, generating bootstrapped error estimates for significance testing. Comparing the results of both functions helps to minimize problems associated with collinearity in the climate predictors and the identification of spurious relationships (Blasing et al. 1984). I tested a 17-month window of mean and minimum temperatures and total precipitation beginning in May of the preceding year through the current December for the period 1912-2004.

To examine the relationships between the climate variables and the timing of MPB outbreaks, I used the proxy outbreak record developed by Hrinkevich and Lewis (2011) to identify event years that represented the first year of an outbreak in which large pulses of mortality well exceeded the baseline mortality levels observed between outbreak periods. I defined event years based on the best combination of data available for that period including direct evidence found in survey records and the reconstructed mortality dates, as well as indirect outbreak indicators such as tree vigor at the time of death and survivor growth releases as described in detail in the reconstruction. For the period 1800-2007 the six MPB event years included in this analysis were 1837, 1868, 1906, 1945, 1987, and 2006. I investigated current year and lagged relationships between the start of an outbreak (event years) and each of the climate variables of interest including the residual tree ring

chronology representing the host climate response (Table 3.2) using superposed epoch analysis (SEA). SEA is a compositing technique that calculates mean conditions in a response variable before, during, and after a set of events which have been superposed onto the variable such that all events occur at time zero and the annual variation surrounding each event can be summarized across the entire time series. It is widely used to study fire-climate relationships (Baisan and Swetnam 1990, Swetnam 1993, Grissino-Mayer and Swetnam 2000, Hessl et al. 2004), but has also been used to analyze climatic and tree growth variation associated with insect outbreaks (Nola et al. 2006, Pohl et al. 2006). I used an 8-year window surrounding each MPB event including the 5 years preceding and 2 years following the onset of the outbreak which allowed us to examine climate relationships that may be more important in the years building up to or immediately following a MPB population eruption than in the event year itself, such as a lagged response to winter temperature associated with slow population growth. I used the program EVENT (Holmes and Swetnam 1994) to compare my climate variables within the event window to a set of 1000 randomly selected event years used to calculate bootstrapped confidence intervals. Significant departures of actual from simulated means were evaluated at the 95% and 99% levels using the normal approximation of the means and percentile rank methods depending on the distribution of the input variables (Mooney and Duval 1993).

I examined climate suitability in the study area using the known favourability thresholds for MPB populations (Table 3.2) to visually assess which factors were most limiting in this region and how climate variability over time related to outbreak history. I plotted values for summer and annual degree days, August maximum temperature, standardized spring precipitation and number of days below the 50% and 100% cold

mortality thresholds for the complete period on record (1895-2002), using the threshold values to classify years as either suitable or unsuitable for each variable in the model. Precipitation suitability was defined by a two-year trend based on the current and previous year's standardized score so that only the second year of consecutive annual precipitation deficits was classified as favorable. I overlaid the reconstructed outbreak periods over all the climate variables as a reference, defining the starting years by the same criteria used to identify event years for the SEA and estimating the end of the outbreak period based on declining trends in tree mortality. The most recent outbreak that began in the area in 2006 was not included in the analysis because daily temperature data was only available through 2002.

3.4 Results

3.4.1 Climate-MPB outbreak-host tree growth relationships

The SEA results for the local climate variables were largely non-significant, with the exception of mean DJF temperatures that, at 5 year running averages, were significantly higher ($p < 0.05$) in the year of an outbreak (Figure 3.2a). I found no relationships over shorter time periods (< 4 years) or for minimum DJF temperatures at any frequency. August maximum temperature, summer and annual degree days, and April-June precipitation were also unrelated to outbreak timing at any lag or running average. I tested May-June temperature and May-June precipitation in addition to the original variables compiled because of the significant correlations between these variables and host tree growth, but

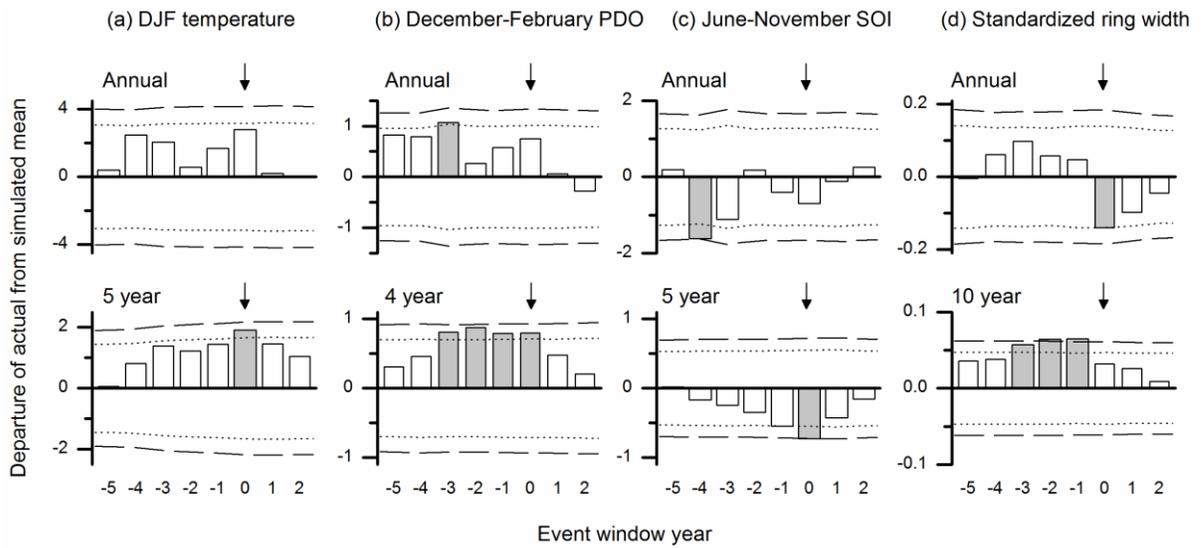


Figure 3.2. Superposed epoch analysis results for variables showing significant relationships to outbreak events. Variable names are listed across the top. The top row shows annual relationships between the variable and outbreak events. The bottom row shows representative examples of the lower frequency trends that were significantly related to outbreak timing, with the trend length indicated for each variable. Event window years represent the 8 years analyzed around the outbreak events, with year zero (indicated by an arrow at the top of each graph) corresponding to the year the outbreak occurred and negative (positive) numbers corresponding to years preceding (following) the event. Hashed lines represent 95% and 99% confidence intervals and shaded bars indicate significant relationships at that window position.

found no relationship with outbreak timing for either. Of the large scale indices tested, PDO and SOI showed significant relationships with outbreak timing, while PNA and the AO were unrelated at any lag or running average. PDO was consistently higher ($p < 0.05$) in the 3 years preceding an outbreak for short-term trends (1-3 year averages), with outbreaks occurring in years associated with 4-10 year trends of higher winter PDO (Figure 3.2b). SOI showed a pattern similar to that of the PDO, except with consistently lower index values associated with outbreaks. Below average annual SOI values occurred 4 years prior to an outbreak, with more prolonged negative trends occurring successively closer to the event year. Five year trends of SOI were significantly lower in the year of an outbreak (Figure 3.2c).

SEA results for the standardized tree ring chronology were more complex than those of the climate indices. Unlike the consistent associations observed for PDO and SOI at all running averages, the relationship between tree growth and outbreak timing reversed between the higher and lower frequency trends of the running means. In the year of the outbreak I observed significantly lower tree growth, with this effect persisting in the high-frequency ring-width signal (1-3 year running means) for two years after the start of the outbreak (Figure 3.2d). At lower frequencies (4-10 year running means) higher than average tree growth was consistently associated with the onset of an outbreak, beginning three years before the event and moving closer to the event year with progressively longer trends. Above-average tree growth over a period of four years preceded an outbreak by three years, while a 10-year trend preceded an outbreak by one year. These relationships are well-represented when annual and 5-year running means of the standardized tree ring index are plotted against the timing of outbreak periods, with a distinct punctuated period of low

growth occurring at the time of the outbreak start and longer-term persistent above-average tree growth occurring in the years preceding (Figure 3.3).

The correlation and response function results were comparable in the direction and magnitude of the relationships between monthly climate and tree growth. For ease of interpretation I present only the correlation results, noting any differences in the results of the two approaches. Tree growth was significantly positively related to winter temperature for November and March (Pearson $r = 0.262$ and 0.211 , $p < 0.05$), and to seasonal averages for November-March and December-February ($r = 0.253$ and 0.222 , $p < 0.05$) (Figure 3.3). Warm spring temperatures in May and June negatively influence tree growth ($r = -0.261$, -0.379 , $p < 0.05$), with some evidence for a similar effect in September, although this relationship is not supported by the response function. The strongest climate-tree growth relationship is for spring precipitation which shows significant positive correlations with ring width for May and June ($r = 0.399$ and 0.521 , $p < 0.05$).

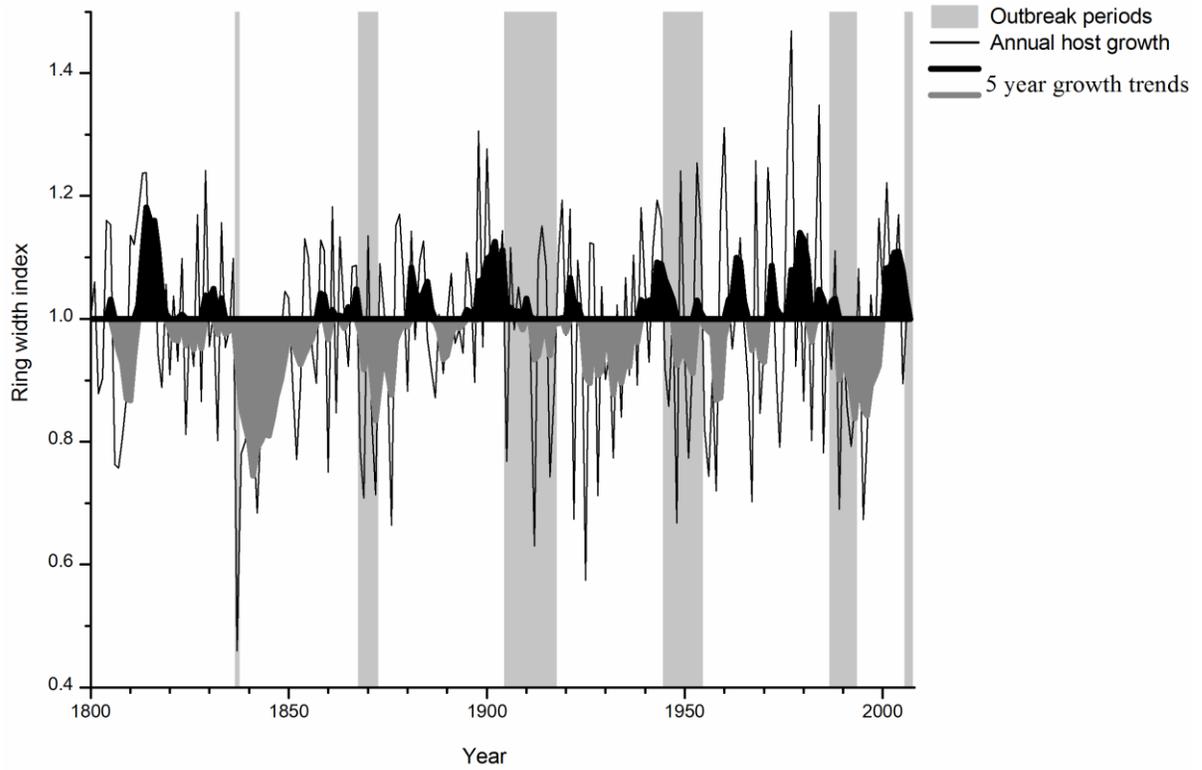


Figure 3.3. Annual and 5-year running means of the tree ring chronology used in the SEA analysis overlaid on the reconstructed outbreak periods. Distinct periods of punctuated host stress (below-average growth) occur at the start of each outbreak, while 5-year trends of persistent above-average growth precede the start of each outbreak.

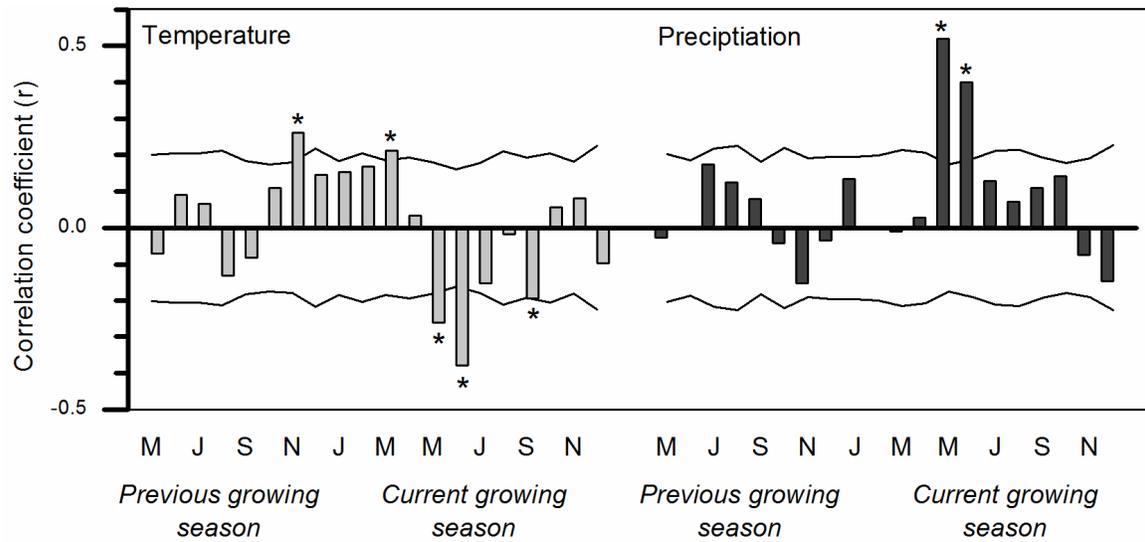


Figure 3.4. Climate-tree growth correlations between mean temperatures and total precipitation and my master residual climate chronology over a 17-month window beginning in May of the preceding year and ending in the December of the current year for the period 1912-2004. Asterisks indicate significant correlations for that month that were assessed using 95% confidence intervals (black lines).

3.4.2 *Climate suitability*

The climate suitability results are summarized for each variable based on the timing of suitable years relative to the reconstructed outbreak periods. Summer degree day totals were variable with respect to the heat accumulation threshold prior to the 1920s, but after the mid-1920s all but three years were above the minimum requirement. The extended period of unsuitable summer heat accumulation corresponded with the start of the 1900s outbreak, but the latter two outbreaks occurred during periods of extended suitability for this variable. Annual degree day totals were above the minimum suitability thresholds for all the years on record (1896-2002) and showed no consistent pattern of above- or below-average heat accumulation relative to outbreak timing (Figure 3.4). August maximum temperatures were also favorable throughout most of the period on record with the exception of two years in the early 1900s and a group of years beginning in 1955 that did not meet the maximum temperature threshold. Unfavorable August temperatures generally occurred between outbreaks and never coincided with the onset of one of these periods, although there was an extended period of August maximum temperature below 18.3°C that coincides with the estimated timing of the 1940s outbreak collapse. Precipitation was more variable around the suitability threshold than the heat accumulation variables and had a higher percentage of unfavorable years, but there was no consistent pattern relative to outbreak timing. Only the earliest outbreak began during consecutive years of below-average precipitation, although extended dry periods did occur during two of the reconstructed events. Of the six highly suitable periods defined by 3 or more consecutive dry years, half occurred between outbreak events and no dry periods persisted for longer than one year after 1983. Cold mortality days with temperatures below the 50% threshold were common throughout the record, ranging between 0-23 days/year (M=5.3, SD=5.2), with 19 years free from cold spells. Temperatures

below the 100% mortality threshold were less common, occurring between 0-13 days/year ($M=1.5$, $SD=2.6$) in approximately half of the years on record. Two of the three MPB events began in years with no cold mortality days. The earliest event, however, began in a year with 4 (1) days below the 50% (100%) threshold which are below average for the number of annual cold mortality events calculated over entire the time period. Above average numbers of cold mortality events occurred during each of the reconstructed outbreak periods.

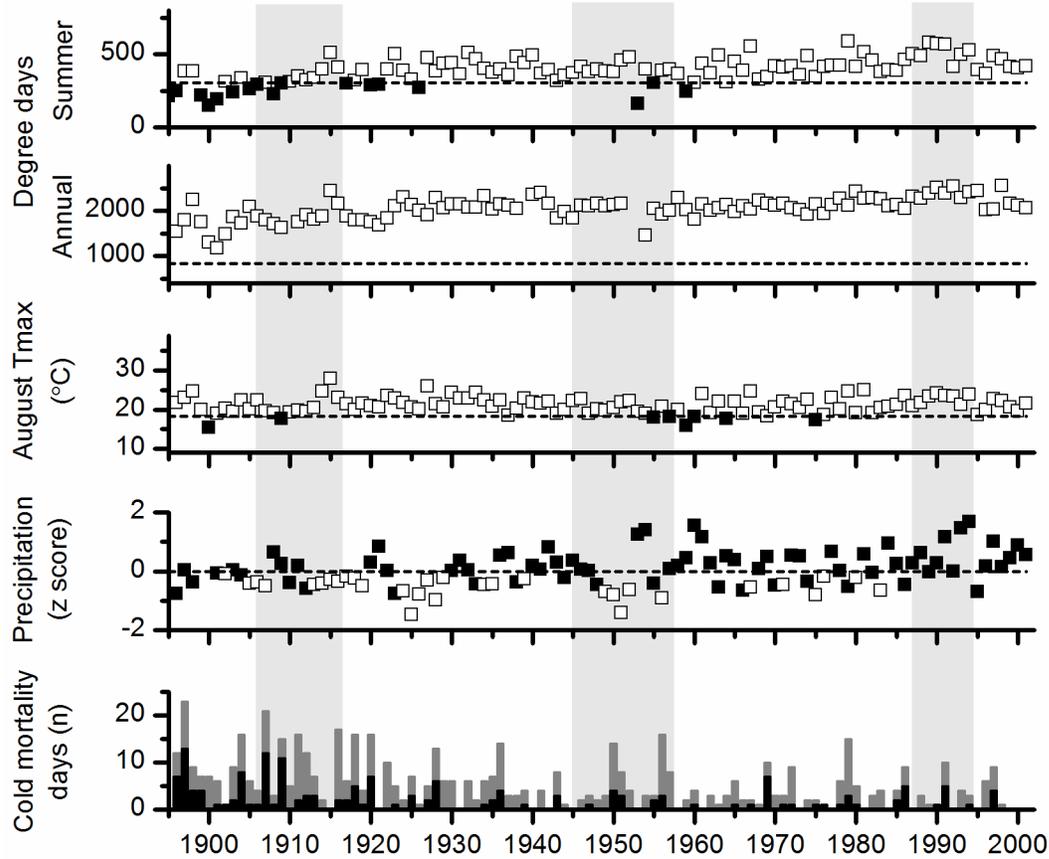


Figure 3.5. Climate suitability parameters for the study area based on established threshold values for each parameter listed in Table 3.2. White boxes indicate favourable climate years for mountain pine beetle and black boxes indicate unfavourable climate years. Cold mortality days (bottom graph) show the number of days below the 50% mortality threshold (dark grey bars) and 100% mortality threshold (black bars). Light grey vertical shading across all plots shows the timing of the reconstructed outbreak periods.

3.5 Discussion

3.5.1 Climate- MPB outbreak-host tree growth relationships

The links I observed between climate, MPB outbreaks, and host tree growth emphasized the importance of long term patterns of climatic variability in the development of large infestations. This is not surprising considering that population buildup over multiple years is a necessary precursor for local incipient-epidemic populations to coalesce into landscape-scale epidemics (Safranyik and Carroll 2006). Winter mean temperature was the only direct climate driver associated with the start of an outbreak, and only for the longest trends (5 years) of warmer than average conditions. Although inter-annual winter temperature variability has been shown to influence local population dynamics and the fine-scale spatiotemporal distributions of MPB outbreaks (Aukema et al. 2008, Fauria and Johnson 2009), the resolution of my MPB data prevents us from examining these detailed population fluctuations. I do show, however, that over centennial time scales, only low-frequency warm winter trends are directly related to the initial MPB population eruption associated with the onset of large outbreaks.

The importance of persistent positive winter temperature anomalies is also evident in the significant association between outbreak timing and the two large-scale climate patterns with known teleconnections to winter temperature in BC. PDO in particular has consistently been cited as an important driver of MPB outbreaks because of its influence on winter temperature over 20-30 year phases (Fauria and Johnson 2009, Thomson 2009). My results extend these findings by showing that the relationship between MPB population eruptions and positive PDO index values holds over multiple phase shifts and four distinct outbreak

periods. The significant associations for all PDO trends tested (1-10 years) indicate there may be a predictive advantage of PDO over direct winter temperature measurements that only relate to outbreak timing for persistent trends (>4 years), whereas even annual PDO conditions appear to be useful for modeling outbreak risk. Specifically, my data showed that outbreaks occur as early as 3 years following a positive PDO winter, with lag time decreasing with successively longer annual positive PDO anomalies.

The negative SOI relationships to outbreak timing are consistent with the known links between El Niño and positive winter temperature anomalies in Canada (Shabbar and Khandekar 1996), which is likely the mechanism driving MPB population eruptions during negative phases of SOI. As with PDO, the consistent association at all running means tested (1-5 years) reflects the lower frequency variability of the SOI relative to annual winter temperatures and the relative predictive advantage of using SOI phases to model outbreak risk. My results showed outbreaks erupting 4 years following a negative SOI, with the probability of an outbreak occurring sooner increasing with successive years of persistent El Niño conditions. Five year negative trends were significantly associated with an outbreak occurring in that year which, relative to the average ENSO cycle of 2-7 years, indicates a high probability of an outbreak occurring during prolonged negative anomalies. Although not explicitly analyzed here, my data suggests the interaction of positive PDO and negative SOI phases represent the highest probability for outbreak development, consistent with the findings of Stahl et al. (2006a) who showed that the most unsuitable winter temperatures for MPB occurred during negative PDO and La Niña or neutral ENSO years.

I did not find any relationship between outbreak timing and the AO or PNA indices, unlike a number of other studies which have linked these patterns to MPB either directly or

indirectly through their effect on winter minimum temperatures. Fauria and Johnson (2009) found a low-frequency relationship between AO and total MPB area affected, which they attribute to the influence of AO on the probability of extreme cold events occurring. They also found widespread correlations between winter minimum temperatures and total MPB area affected, but were unable to establish a direct link between AO and winter minimums. Thomson (2009), however, linked winter minimum temperatures to the AO through an interaction with the PNA. Although I found no direct relationships either between outbreak timing and winter temperature extremes (DJF minimum temperature or days below cold mortality curves), there is little doubt that extreme cold events are important to inter-annual MPB population dynamics (Aukema et al. 2008, Fauria and Johnson 2009) and that the AO and PNA may be involved (Fauria and Johnson 2009, Thompson 2009). However, my results indicate that, over longer time scales, extreme cold events are poor predictors of the MPB population eruptions leading to the onset of outbreaks, probably because extreme events are less predictable and less likely to exhibit regular trends that suppress population buildup in this area.

The relationship between the standardized tree-ring indices and outbreak timing varied depending on the frequency of the signal tested, indicating a more complex association between host stress and outbreak development than I observed for the climate variables. Host stress does appear to be important over short time scales in the year an outbreak develops, consistent with the results of Shrimpton and Thomson (1982) who also observed reduced growth in the year the Chilcotin outbreak began which they later attributed to extreme dry conditions (Thomson and Shrimpton 1984). In contrast Trzcinski and Reid (2009) found no indication of low precipitation at the time of attack for the 1930s outbreak

in the Kootenay Valley, but observed a long term average precipitation deficit over the preceding decade which they propose was responsible for increasing drought-induced host susceptibility. Like Fauria and Johnson (2009), my results show no evidence of a spring drought influence, long- or short-term, indicating that precipitation alone is not a sufficient proxy for host stress in this study area. These contrasting results emphasize the importance of understanding local climate-tree growth relationships when attempting to characterize climatically-induced stress, which may be driven by more than one factor.

My climate-tree growth model showed that host stress is a function of three climate components. Although the strongest correlations are with precipitation and do indicate a contributing role of spring precipitation deficits in inducing host stress, the effects of winter and spring temperature should not be discounted, particularly because these climate parameters are also directly important to MPB population dynamics. The negative relationship between high spring temperatures and tree growth suggest that this factor may benefit MPB populations both directly through the benefits associated with increased brood development rates shown to promote seasonally synchronized emergence (Reid 1962) and indirectly as a driver of host stress. Conversely, the positive relationship between tree growth and winter temperatures suggest that the climatic benefit of warm winters for MPB, namely higher larval survival rates (Safranyik and Carroll 2006), may also increase host defensive capacity (Shrimpton 1973) to the disadvantage of attacking beetles, particularly if temperatures drop below biological tolerances. Although more work is needed to determine which combination of factors is most favorable for outbreak development, my data suggests that the optimal relationship between climate, host and MPB involves a trade-off between the benefits of warm winters for beetle populations and the possible defensive advantages

gained by the host, coupled with warm, dry spring conditions that clearly favor outbreak development from a biological (MPB) and an environmental (host) perspective. Based on the SEA results, none of these factors on their own appear to drive outbreak development, at least over short time scales when host stress is a significant component of the outbreak risk model tested.

When examined over longer time scales (4-10 year growth trends) the reversal of the host tree growth-outbreak relationship I observed supports the hypothesis that sustained tree vigor over multiple years may be as important for outbreak development as is short-term stress-induced susceptibility. There are a number of advantages that prolonged periods of above-average growth in the decade preceding an outbreak may provide in terms of habitat suitability and food quality. Cole (1973) linked higher-than-average growth rates over 5 year periods to increased phloem thickness which has been shown to enhance brood and beetle size as well as developmental and emergence rates (Amman 1972, Amman and Pace 1976, Amman and Cole 1983). Reid and Robb (1999) also found positive effects of long-term growth rate on brood productivity even when phloem thickness was unrelated to vigor, emphasizing the importance of the nutritional quality of the phloem over phloem quantity alone. The advantages associated with larger broods and faster development may be particularly important to MPB in northern environments that are subject to greater climatic pressures by promoting seasonal synchrony and maximizing population growth (Safranyik and Carroll 2006). This may be one mechanism by which low-frequency climate patterns such as PDO and SOI influence the inter-annual population dynamics of MPB (e.g. Aukema et al. 2008, Fauria and Johnson 2009) by causing long-term persistent effects in the host tree that encourage outbreak development.

3.5.2 *Climate suitability*

Annual variability around the threshold values for each of the climate suitability parameters supports the SEA results and provides some additional information about which climate factors are important in the study area. It is not surprising that summer and annual degree day accumulations were unrelated to outbreak timing given that they were generally well above the requirements defined by Carroll et al. (2004). A period of unsuitable summer heat accumulation during the time of the 1900s outbreak suggests that the lower rates of egg gallery construction, egg laying, and egg density associated with lower temperatures during this time (Amman 1972a) did not limit brood production enough to prevent the outbreak from occurring. This climate variable may not be very important when considered on its own, particularly when paired with the suitable conditions across the other heat accumulation parameters that control development rates and synchronize emergence and mass attack. August maximum temperatures, despite some variability around the threshold, do not drop below 18.3°C regularly enough to have much value for predicting when outbreaks will occur. However, the extended period of low August temperatures in the mid-1950s may have had some role in the collapse of the 1940s outbreak, suggesting this variable may be more useful for predicting fine scale inter-annual MPB population dynamics as shown by Aukema et al. (2008) than for predicting long-term outbreak cycles in my study area. Precipitation was highly variable throughout the record, but only one of six distinct dry spells was associated with the start of an outbreak, demonstrating why this variable is unrelated on outbreak timing when considered on its own. A possible explanation for the inconsistent relationships between precipitation and MPB outbreaks found by Thomson and

Shrimpton (1984), Trzcinski and Reid (2009), Fauria and Johnson (2009) and this study is that variance around the mean does not reflect climatic differences between study areas, particularly when precipitation is not the only factor limiting tree growth. For example, temperature is often the dominant signal found in the tree ring record of high elevation sites in the southern interior (Wilson and Luckman 2002) and my mid-elevation site in the northern interior responds to a combination of temperature and precipitation, suggesting that a climate-host stress model developed in the Chilcotin where precipitation is likely the most limiting factor is not applicable across the entire MPB range.

The number of cold mortality days is the only climate parameter that showed a consistent trend in the suitability analysis, with all outbreaks beginning in years with below average or no cold mortality. Despite this relationship, years with little or no cold mortality that do not correspond with outbreaks also occur fairly regularly in the record indicating that these variables are not necessarily good predictors of when the MPB population eruptions will occur. As previously discussed, this does not discount the demonstrated influence that extreme cold events can have on inter-annual population dynamics (e.g. Aukema et al. 2008, Fauria and Johnson 2009). The prevalence of unsuitable days that occur during the reconstructed outbreak periods additionally suggests that duration of cold spells may be more important than the frequency of mortality events on MPB population dynamics. This is not surprising given the various insulating factors associated with snow depth, tree diameter, bark thickness and attack density that can delay significant MPB mortality for several consecutive days of lethal air temperatures until subcortical temperatures drop below larval tolerances (Safranyik and Carroll 2006). Although beyond the scope of this study, calculating the number of consecutive days below the mortality thresholds would be useful

to emphasize the effect of longer cold spells that are potentially the most damaging, particularly in areas with large trees that have greater insulating effects.

3.6. Conclusions

Overall, my results support much of the existing knowledge about climate-MPB outbreak relationships and offer some important new observations gleaned from the use of long-term outbreak data and climate-tree growth models. Persistent positive winter temperature anomalies and the large-scale patterns of climate variability that drive them (PDO and ENSO) appear to be the most important determinants of when outbreaks will occur. The occurrence of extreme cold events and the large-scale patterns associated with them (AO and PNA) show no long-term predictive skill for assessing outbreak return. It is important to note that the advantages of using a long-term MPB outbreak reconstruction to test these relationships over a time scale appropriate for low-frequency oscillations also come with the disadvantage of greatly reduced resolution which prevents us from examining interannual climate-outbreak relationships known to be important to short-term MPB population dynamics over the entire reconstruction period, such as the influence of extreme cold events. Regardless, my results show that long-term outbreak risk assessments will benefit most from incorporating PDO and ENSO predictions into the climate models.

I also showed that the relationship between climate, MPB and host stress is more complicated than existing models recognize. First, the use of a universal climate proxy to represent host stress, such as spring precipitation deficit, does not reflect regional variance in the climate-tree growth response and cannot necessarily be simplified to a single variable.

For my study area it appears that a combination of climatic conditions drives the host-outbreak relationship, emphasizing the importance of understanding the specific drivers of host stress. Furthermore, while host stress is important in the short term, long-term host vigor may be as important for enhancing habitat quality, especially in northern environments where environmental pressures are greater. These findings have implications for improving outbreak risk models through the use of regional climate-tree growth information and for outbreak risk management with respect to understanding the influence of long term forest health on forest disturbance processes.

4. Mountain pine beetle outbreak dynamics and climate interactions in sub-boreal mixed pine forests of north-central British Columbia: a synthesis

4.1 Introduction

The composition, structure and function of forest ecosystems is largely dependent on the forest disturbance processes that shape them, and for disturbance agents capable of causing widespread damage and tree mortality, the social, economic, and ecological consequences of these events can be severe. Many disturbances, however, are natural components of the system that play an important role in the cycle of forest development and regeneration (Logan and Powell 2005), so it is important to balance management objectives with strategies that are consistent with the basic ecology of the forest ecosystem (Romme et al. 2006). This requires a sound understanding of the disturbance processes and their function. Because the interactions driving stand dynamics can extend for centuries, long-term histories are necessary to establish the links between forest development and forest disturbance. This is becoming increasingly important in light of changing climate conditions which have already influenced the timing, frequency, magnitude, severity and duration of disturbances (Dale et al. 2001), greatly accelerating the effects of climate change on forest composition and structure (Overpeck et al. 1990).

The objectives of this study were to develop a long-term record of mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins (Curculionidae: Scolytinae)) outbreaks near the northern limit of the species' range and to examine the interacting factors driving that disturbance regime. In British Columbia (BC) MPB is considered the most destructive biotic disturbance agent of mature pine forests and in recent years has experienced an outbreak that is unprecedented in size and severity relative to any historical outbreaks on

record. Although well-studied in terms of species biology and environmental tolerances, very little information exists about long-term outbreak dynamics at the appropriate ecological timescales. Conceptually, insect outbreaks result from the interactions between three obligate causal factors: a host, a disturbance agent, and a suitable climate for insect population growth (Figure 1.1). Over longer time scales, these interactions collectively describe the outbreak dynamics of the disturbance regime driving forest development. Using a combination of dendrochronological methods to reconstruct stand and outbreak history together with long-term local and large-scale climate data, I developed an integrated model of outbreak dynamics for north-central BC where little is known about the role of MPB in forest stand dynamics or the influence of climate on outbreak development. This study addresses a number of gaps in existing outbreak dynamics research, particularly the need for a greater understanding of MPB in climatically sensitive regions near the northern range limits where the effects of climate change are expected to be most dramatic (Bentz et al. 2010).

In this chapter, I synthesize the information presented in Chapters 2 and 3 about the individual components of outbreak dynamics in this region to discuss the system from a comprehensive ecological perspective that addresses some of the causal links between the outbreak regime, the host forest and the local and large-scale climate drivers. I discuss the relevance of my results with respect to similar research conducted in other areas and consider the overall implications of my results with respect to MPB management in BC, emphasizing the potential impacts of climate change on this disturbance process. Lastly I address some of the limitations of the study and future directions this research could take to improve our understanding of MPB outbreak dynamics and our ability to manage, predict,

and mitigate the ecological and economic effects future epidemics may have in western Canada.

4.2 MPB, host and climate interactions inferred from a multi-century outbreak reconstruction

Between 1800 and 2007 I reconstructed six periods of MPB disturbance occurring in the 1830s, late 1860s-1870s, 1900-1910s, 1940s-1950s, 1980s and the epidemic that was underway at the time of the study (Figure 2.5). The current outbreak was the most severe on record, but the 1900-1910s and the 1940s-1950s events also fit the profile of large epidemics (Amman and Schmitz 1988, Safranyik and Carroll 2006). The 1830s and 1870s events were smaller, and while the 1980s saw high levels of mortality, the infestations remained local until the major population eruption in the 2000s. The reconstructed outbreak cycle of approximately 30 years is fairly consistent with those reported elsewhere ranging between 20 and 53 years (Roe and Amman 1970, Amman and Schmitz 1988, Alfaro et al. 2004, Taylor et al. 2006, Axelson et al. 2009). The timing of my outbreaks is also consistent with MPB outbreak histories from other parts of western North America, especially between 1900 and the present day when synchronous outbreaks occurred in the northern Rocky Mountains of Wyoming and Idaho (Roe and Amman 1970, Amman and Schmitz 1988), Kootenay and Banff National Parks (Taylor et al. 2006), the southern-interior of BC (Axelson et al. 2009) and the Chilcotin Plateau in west-central BC (Alfaro et al. 2004). This suggests that large-scale processes, particularly those driving climate variability, can have a tremendous influence on insect disturbance regimes despite vast regional differences in forest structure

and stand dynamics. The nature of the current MPB outbreak in BC is also only one of several unprecedented bark beetle outbreaks occurring throughout western North America, including the recent spruce beetle outbreaks in Alaska (Berg et al. 2006, Sherriff et al. 2011), and the commonality for all these events that began building in the late 1980s and early 1990s appears to be the increasing temperature trend that continues to present day (Logan and Powell 2005). This probably explains the steady population buildup and tree mortality I observed in my study area beginning in the 1980s (Figure 2.5) that almost certainly contributed to the extremely high mortality continuing in the mid-2000s.

While these insights from paleoecology and current events reveal the disruptive influence that climate change appears to be having on insect disturbance regimes at a tremendously large scale, formulating a response that can lead to effective management requires a more complete understanding of contributing mechanisms driving the disturbance regime. My results for MPB outbreaks in north-central BC suggest that we may need to take a more regional approach that incorporates forest-specific stand dynamics together with climate interactions into management models. Chapter 2 showed that MPB and fire are the two major forest disturbances driving forest structure and composition in my study area, and the relationship between them largely influences when outbreaks occur. It may also be important to recognize the strong presence of the two-year cycle budworm in these stands. Although it does not appear to be a major mortality agent nor directly influence host-availability for MPB, the degree of synchronicity between budworm and MPB outbreaks could indicate an important interaction that has not yet been investigated.

Successional development in these stands is typical for sub-boreal spruce forests. Infrequent, large-scale stand-replacing fires operate over much longer time-scales than MPB,

establishing single-cohort seral lodgepole pine stands that gradually give way to shade-tolerant spruce/fir stands at a rate governed by MPB outbreak frequency and severity. The long fire-free interval in this study area has contributed to the nearly 200 year history of MPB outbreaks dominating this system, beginning around the time the oldest stands reached maturity and become progressively more destructive once landscape scale age-susceptibility was reached, approximately 80 years after the most recent stand-initiation fire event (Raffa and Berryman 1982). Changes in the fire regime, specifically an increased frequency of stand-replacing events, whether through climate warming or management practices, will have a profound effect on the spatial and temporal scales of MPB susceptibility in these forests (Taylor and Carroll 2004). Similarly, because there is no pine regeneration after the initial establishment event (Figure 2.3), changes in the frequency and severity of MPB outbreaks will also influence susceptibility by controlling how long pine remains a component of these stands. Since 1830, my sites experienced between 1 and 4 outbreak events and, with the exception of two sites, all had living pine present in the stand at the time of sampling, indicating a historically low-severity regime. MPB events do not appear to have any influence on regeneration patterns of the other species present in the stand, particularly subalpine fir which, in the absence of fire, will eventually dominate this landscape (Figure 2.4)

Characteristics about host susceptibility and pine mortality rates allowed me to examine the influence that forest structure has on outbreak severity and frequency. Beetle-killed trees in my study area were larger and older (Figure 2.2) than those typically defined for outbreak susceptibility (e.g., Safranyik et al. 1974, 1975, Cole and Amman 1980, Taylor and Carroll 2004), which has dramatic implications for risk modelling and indicates some

important differences in outbreak dynamics between marginal environments and climatically optimal regions. A preference for larger trees suggests that size-related susceptibility in the north may be skewed by greater climatic pressures that inhibit beetle survival and attack success without larger hosts that allow for larger broods, larger beetles, faster life cycles and greater relative emergence rates (Safranyik and Jahren 1970, Amman and Cole 1983, Safranyik and Carroll 2006). Higher age-related susceptibility thresholds also indicate that provincial risk models based on age largely underestimate risk in the north-central interior. Furthermore, the persistence of large diameter pine in most sites throughout multiple outbreaks supports the interpretation of a historically low-severity outbreak regime that, following stand maturation, is most likely limited by climate (Amman and Baker 1972) rather than host availability. This theory directly contrasts with the host-limiting models used to explain outbreak severity and cycles further south (Cole and Amman 1980, Alfaro et al. 2004). Also, the continuous supply of endemic populations observed between outbreak periods (Figure 2.5d), combined with a higher survival rate of large trees during outbreaks, likely enhances the stability of these populations between outbreak phases. This has major implications for climate change because MPB populations in my study area may be able to respond more quickly to increasingly favorable climatic conditions and experience rapid regime shifts similar to those proposed by Bale et al. (2002) for other insect herbivores.

In Chapter 3, I explored specific local and large-scale climate interactions associated with the MPB outbreaks reconstructed in Chapter 2 in order to determine which climate factors were driving outbreak development and frequency. The links I observed between climate, MPB outbreaks, and host tree growth emphasized the importance of long-term patterns of climate variability in the development of large infestations. Persistent positive

winter temperature anomalies were the only significant direct climatic driver, which is not surprising considering that population buildup over multiple years associated with higher winter survival rates would greatly support epidemic development. Both large-scale climate patterns with teleconnections to winter temperatures in BC were important predictors of outbreak development. Outbreaks occurred consistently following multi-year trends of positive PDO index values and negative SOI values or El Niño events, which is consistent with the results of other studies that looked at the relationship between MPB and these indices (Stahl et al. 2006a, Fauria and Johnson 2009). I did not find any significant relationships between my outbreak periods and the other climatic variables known to directly affect MPB populations. This can be explained in part because regional summer heat accumulation was generally well within the limits for successful MPB development and seasonal synchrony (Figure 3.4), and precipitation, although quite variable and including several extended periods of drought, did not seem to cause a strong enough host stress response necessary to initiate an epidemic. The lack of findings for an effect of cold mortality events based on winter minimum temperatures I attribute to the fact that extreme events, while of known importance to inter-annual MPB population dynamics (Aukema et al. 2008, Fauria and Johnson 2009), are not useful predictors of when MPB population eruptions will occur, in part because they are themselves less predictable. This explanation, which I address later in relation to limitations of this study, may also apply to the other variables for which I found no significant effect because the climatic drivers of outbreak development may be very different than the climate relationships that influence MPB population dynamics during a particular outbreak event.

The examination of indirect climatic effects mediated through the host trees provided some useful information with respect to the use of a host-stress variable in climate-suitability models. Host stress does appear to be an important precursor to outbreak development, however, differences in geography and species responses to climatic variability dictate that a universal climatic proxy such as precipitation is not appropriate for modeling host stress between different locations. My climate-tree growth relationships indicated that a combination of climatic variables was driving the host stress response associated with outbreaks. This highlights the importance of understanding climate-host relationships for a given area, and explains much of the inconsistency in the literature as to the effects of precipitation on outbreak development (e.g. Thomson and Shrimpton 1984, Trzcinski and Reid 2009, Fauria and Johnson 2009). I also found that over longer time periods, climatically-induced and prolonged host vigor was significantly related to outbreak development. For marginal environments subject to greater climatic pressures, the advantages associated with sustained vigor in host trees such as increased brood productivity, larger beetles, and faster development and emergence rates (Amman 1972, Amman and Pace 1976, Amman and Cole 1983) may be particularly important to MPB success.

The results of the climate interactions study have some important implications for MPB management in BC, particularly in relation to climate change. In terms of climate suitability modelling, host stress and vigor is important over both short and longer time scales, but the climatic proxy used to represent this variable should be regionally appropriate and may require some climate-tree growth analyses before model development. For outbreak risk models, forest structural assessments should be integrated into climate models to

account for the varied influence that host susceptibility has on outbreak cycles which will likely differ across climatic zones and forest types. Still, the degree of synchrony between outbreaks across western North America indicates that, given available hosts, large-scale climate patterns are the most important driver of broad regional and possibly sub-continental scale outbreak dynamics. Fortunately, these large-scale climate modes such as PDO and ENSO are also becoming increasingly predictable, creating the potential for improving ecologically-relevant climate-related risk predictions (Stenseth et al. 2003). Unfortunately, climate change will likely influence every interaction represented by the outbreak dynamics triangle model (Figure 1.1), either directly through changes in climate suitability for the MPB or indirectly through effects on the host and the host forest stand dynamics. Managing for these changes will require continued research to define these interactions, particularly at species range margins where improved understanding of these dynamics may help to mitigate the effects of range expansion and regime changes.

4.3 Limitations and future directions

As with many ecological studies, long-term data is essential to understanding processes that occur over centuries or sometimes even millennia. In this study I reconstructed over 200 years of forest stand dynamics to develop a MPB outbreak reconstruction that served two purposes: (1) to lengthen the survey records to an appropriate time scale for studying outbreak dynamics and (2) to examine the interacting components of this outbreak regime in a system that has not been well-studied, but as a northern range limit habitat is extremely susceptible to climatic changes and will likely become a focus of future

research as regime and range changes occur. A major limitation to any paleoecological reconstruction is that by relying on proxy data to extend a record of events without direct evidence, in my case MPB-killed trees that could be used to precisely date the timing of mortality, you necessarily introduce some degree of uncertainty to the study. To limit this, my approach in the reconstruction was to combine as many lines of evidence as possible to produce an overlapping record of supporting information that allows for a reasonably undisputable interpretation of outbreak history. I am confident that the methods I used produced as accurate a record as possible and through cautious interpretation of the results I was able to use the reconstruction for its designated purpose.

A major difficulty in the outbreak reconstruction was the strong and persistent presence of the two-year cycle budworm signal in the non-host tree-ring record that seemed to occur in very close succession with the MPB release signal in the same chronologies. Although I was successful in decoupling the signals using methods explained in Chapter 2, this co-occurrence of disturbances affecting different hosts creates questions about possible interactions between agents that have not been addressed yet. While I suspect climatic similarities explain some of this relationship, there are questions about ecological interactions between agents that arise from the host vigor response preceding MPB outbreaks. It is possible that defoliation caused by the two-year cycle budworm in mixed pine, spruce and fir forests provides a nutrient pulse that may contribute to the increase in pine vigor contributing to MPB population growth. This is certainly an interesting question worth pursuing in future research.

In Chapter 3, limitations of the reconstruction that could only provide dates for the initial population eruption associated with the start of an outbreak prevented me from

examining climatic effects associated with inter-annual population dynamics, particularly those that influence outbreak spread and severity during an outbreak. These have been well-studied with the available aerial survey records dating back to 1959 and, as discussed, have confirmed the importance of extreme cold events and in some cases the effect of summer temperature on spatial patterns (e.g. Aukema et al. 2008, Fauria and Johnson 2009). It would be interesting to examine the consistency of this effect over multiple outbreaks spanning a longer time period, particularly with respect to any control these events may have on outbreak duration. To do so would require a much more detailed profile of tree mortality than I had available in my study area because of the decay rates of downed trees. It may be possible in drier climates.

Lastly, a major component of outbreak dynamics I excluded from this study was post-outbreak recovery which is a major concern considering the magnitude of the current outbreak and its effect on the future timber supply. Little is known about natural recovery following MPB outbreaks or what the implications for management are compared to more conventional methods of salvage logging and replanting (Griesbauer and Green 2006), especially over a longer time periods. My study forms the basis for a future study examining natural post-outbreak recovery by providing a time-series of outbreak events from which a chronosequence of regeneration and successional processes based on different outbreak dates could be analyzed. This would be especially interesting because for mixed-species stands that are unlikely to experience recruitment of new pine trees (Figure 2.2), understanding advanced regeneration and the ongoing establishment of shade-tolerant vegetation could be useful for supplementing mid-term timber supplies in the absence of pine.

Literature Cited

- Agrios, G. N. 2005. *Plant Pathology* (5th edition). Elsevier-Academic Press. San Diego, California, USA.
- Alfaro, R. I., R. Campbell, P. Vera, B. Hawkes, and T. L. Shore. 2004. Dendroecological reconstruction of mountain pine beetle outbreaks in the Chilcotin Plateau of British Columbia. Pages 245-256 in T.L. Shore, J. E. Brooks, and J. E. Stone, editors. *Mountain Pine Beetle Symposium: Challenges and Solutions*, Kelowna, British Columbia, October 30-31, 2003. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Information Report BC-X-399.
- Amman, G. D. 1972a. Some factors affecting oviposition behavior of the mountain pine beetle. *Environmental Entomology* 1:691-695.
- Amman, G. D. 1972b. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *Journal of Economic Entomology* 65:138-140.
- Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environmental Entomology* 2:541-547.
- Amman, G. D., and B. H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. *Journal of Forestry* 70:204-209.
- Amman, G. D., and W. E. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part II: Population dynamics. General Technical Report INT-145. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Amman, G. D., and V. E. Pace. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. Research Note INT-209. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.
- Amman, G. D., and R. F. Schmitz. 1988. Mountain pine beetle-lodgepole pine interactions and strategies for reducing tree losses. *Ambio* 17: 62-68.
- Aukema, B. H., A. L. Carroll, Y. Zheng, J. Zhu, K. F. Raffa, R. D. Moore, K. Stahl, and S. W. Taylor. 2008. Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. *Ecography* 31:348-358.
- Axelsson, J. N., R. I. Alfaro, and B. C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. *Forest Ecology and Management* 257: 1874-1882.
- Axelsson, J. N., R. I. Alfaro, and B. C. Hawkes. 2010. Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. *The Forestry Chronicle* 86:87-99.

- Baisan, C H. and T. W. Swetnam. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. *Canadian Journal of Forest Research* 20:1559-1569.
- Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Gartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. 2002. *Global Change Biology* 8:1-16.
- Battisti, A., M. Stastny, S. Netherer, C. Robinet, A. Schopf, A. Roques, and S. Larsson. 2005. Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications* 15:2084-2096.
- BC Ministry of Forests. 1995. 1994 forest, recreation, and range resource analysis. British Columbia Ministry of Forests, Public Affairs Branch, Victoria, BC. 308p.
- BC Ministry of Forests, Lands and Natural Resource Operations. 2011. Facts about B.C.'s mountain pine beetle. http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/facts.htm
- Bentz, B. J., J. Régnière, C. J. Fettif, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience* 60:602-613.
- Berg, E. E., J. D. Henry, C. L. Fastie, A. D. De Volder, and S. M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227: 219–232.
- Berryman, A. A. 1972. Resistance of conifers to invasion by bark beetle-fungal associations. *BioScience* 22:598-602.
- Biondi, F., and K. Waikul. 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences* 30:303-311.
- Blasing, T. J., A. M. Solomon, and D. N. Duvick. 1984. Response functions revisited. *Tree-ring Bulletin* 44:1-15.
- Bloomberg, W. J., and D. J. Morrison. 1989. Relationship of growth reduction in Douglas-fir to infection by *Armillaria* root disease in southeastern British Columbia. *Phytopathology* 79:482–487.
- Bonsal, B. R., X. Zhang, A. Vincent, and W. D. Hogg. 2001. Characteristics of daily and extreme temperatures over Canada. *Journal of Climate* 14:1959-1976.
- Bradshaw, W. E., and C. M. Holzapfel. 2006. Evolutionary response to rapid climate change. *Science*:312:1477-1478.

- Brown, P. M., and T. W. Swetnam. 1994. A cross-dated fire history from coast redwood near Redwood National Park, California. *Canadian Journal of Forest Research* 24:21-31.
- Campbell, E.M., R. I. Alfaro, and B. Hawkes. 2007. Spatial distribution of mountain pine beetle outbreaks in relation to climate and stand characteristics: A dendroecological analysis. *Journal of Integrative Plant Biology* 49:168-178.
- Campbell, R., D.J. Smith, and A. Arsenault. 2006. Multicentruy history of western spruce budworm outbreaks in interior Douglas-fir forests near Kamloops, British Columbia. *Canadian Journal of Forest Research* 36:1758-1769.
- Carroll, A. L., S. W. Taylor, J. Régnière, and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 223-232 *in* T.L Shore, J. E. Brooks, and J. E. Stone, editors. Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, British Columbia, October 30-31, 2003. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Information Report BC-X-399.
- Chan-McLeod A. C. A. 2006. A review and synthesis of the effects of unsalvaged mountain-pine-beetle-attacked stands on wildlife and implications for forest management. *BC Journal of Ecosystems and Management* 7:119-132
- Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, D. J. Parsons, C. H. Peterson, M. G. Turner, and R. G. Woodmansee. 1996. The report of the ecological society of America committee on the scientific basis for ecosystem management. *Ecological Applications* 6:665-691.
- Cole, W. E. 1973. Interaction between mountain pine beetle and dynamics of lodgepole pine stands. Research Note INT-170. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Cole, W. E. 1981. Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. *Researches on Population Ecology* 23:116-144.
- Cole, W. E., and G. D. Amman. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part I: Course of an infestation. General Technical Report INT-89. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Cook E. R. 1985. A time series analysis approach to tree-ring standardization. Dissertation, University of Arizona.
- Cook, E. R., and R. L. Holmes. 1986. User's manual for program ARSTAN. Pages 50-65 *in* R. L. Holmes, R. K. Adams, and H.C. Fritts, editors. Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. Laboratory of Tree Ring Research, The University of Arizona, USA.

- Cook, E. R., and L. A. Kairiukstis. 1992. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Cullingham, C. I., J. E. K. Cooke, S. Dang, C. S. Davis, B. J. Cooke, and D. W. Coltman. 2011. Mountain pine beetle host-range expansion threatens the boreal forest. *Molecular Ecology* 20:2157-2171.
- Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, F. J. Stocks, and B. M. Wotton. *Climate change and forest disturbances*. 2001. *Bioscience* 51:723-734.
- Davi, N. K., G. C. Jacoby, and G. C. Wiles. 2003. Boreal temperature variability inferred from maximum latewood density and tree-ring width data, Wrangell Mountain region, Alaska. *Quaternary Research* 60:252-262.
- Delong, S.C. 1998. Natural disturbance rate and patch size distribution of forests in northern British Columbia: Implications for forest management. *Northwest Science* 72:35-48.
- Diaz, S. C., R. Touchan, and T. W. Swetnam. 2001. A tree-ring reconstruction of past precipitation for Baja California Sur, Mexico. *International Journal of Climatology* 21:1007-1019.
- Douglas, A. E. 1941. Crossdating in dendrochronology. *Journal of Forestry* 39:825-831.
- Environment Canada. 2010. *Canadian Climate Normals (1971-2000)*. Fort St. James, British Columbia. <http://www.climate.weatheroffice.gc.ca/climate_normals/index_e.html>
- Environment Canada 2011. *Adjusted and Homogenized Canadian Climate Data (AHCCD)*. Climate Research Branch, Meteorological Service, Canada. <<http://ec.gc.ca/dccha-ahccd/>>.
- Farnden, C. 1996. *Stand density management diagrams for lodgepole pine, white spruce and interior Douglas-fir*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Information Report BC-X-360. 41p.
- Fauria, M. M., and E. A. Johnson. 2009. Large-scale climatic patterns and area affected by mountain pine beetle in British Columbia, Canada. *Journal of Geophysical Research* 114:G01012.
- Furniss, R. L., and V. M. Carolin. 1977. *Western forest insects*. Miscellaneous Publication 1339. USDA Forest Service.
- Gibson, K., K. Skov, S. Kegley, C. Jorgensen, S. Smith, and J. Witcosky. 2008. *Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges*. Report R1-08-020. USDA Forest Service, Forest Health Protection, Missoula, Montana, USA.

- Girardin, M., J. Tardif, and Y. Bergeron. 2001. Radial growth analysis of *Larix laricina* from the Lake Duparquet area, Quebec, in relation to climate and larch sawfly outbreaks. *Ecoscience* 8:127-138.
- Grissino-Mayer, H. D., W. H. Romme, M. L. Floyd, and D. D. Hanna. 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology* 85:1708-1724.
- Grissino-Mayer, H. D., and T. W. Swetnam. 2000. Century-scale climate forcing of fire regimes in the American Southwest. *The Holocene* 10:213-220.
- Hadley, K. S., and T. T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado front range. *Canadian Journal of Forest Research* 23:479-491.
- He, H. S., D. J. Mladenoff, and T. R. Crow. 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. *Ecological Modelling* 114:213-233.
- Heath, R., and R. Alfaro. 1990. Growth response of a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle. *Journal of the Entomological Society of British Columbia* 87:16-21.
- Hessl, A. E., D. McKenzie, and R. Schellhaas. 2004. Drought and Pacific Decadal Oscillation linked to fire occurrence in the inland Pacific Northwest. *Ecological Applications* 14:425-442.
- Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2002. Annual and decadal climate forcing of historical fire regimes in the interior Pacific Northwest, USA. *The Holocene* 12:597-604.
- Holmes, R. 1983. Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69-78.
- Holmes, R. L., and T. W. Swetnam. 1994. Program EVENT user's manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona USA.
- Hrinkevich, K., and K. Lewis. 2011. Northern range limit mountain pine beetle outbreak dynamics in mixed sub-boreal pine forests of British Columbia. *Ecosphere* 10:116.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *269:676-679*.
- Jacoby, G. C., and R. D'Arrigo. 1989. Reconstructed northern hemisphere annual temperature since 1671 based on high-latitude tree-ring data from North America. *Climatic Change* 14:39-59.

- Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management* 254:16-34.
- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452:987-990.
- Logan, J. A., P. V. Bolstad, B. J. Bentz, and D. L. Perkins. 1995. Assessing the effects of changing climate on mountain pine beetle dynamics. Pages 92-105 in R. W. Tinus, ed. *Proceedings of the Interior west global change workshop, April 25-27, 1995, Fort Collins, Colorado, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-GTR-262.*
- Logan, J. A., and J. A. Powell. 2001. Global warming and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47:160-172.
- Logan, J. A., and J. A. Powell. 2005. Ecological consequences of climate change altered forest insect disturbance regimes. *in* F. H. Wagner, editor. *Climate change in western North America: evidence and environmental effects.* Allen Press.
<<http://www.usu.edu/beetle/documents/Logan-Powell2005.pdf>>
- Logan, J. A., J. Régnière, and J. A. Powell. 2003. Assessing the impacts of global climate change on forest pests. *Frontiers in Ecology and the Environment* 1:130-137.
- Loehle, C., and D. LeBlanc. 1996. Model-based assessments of climate change effects on forests: a critical review. *Ecological Modelling* 90:1-31.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069-1079.
- Mattson, W. J. 1996. Escalating anthropogenic stresses on forest ecosystems: forcing benign plant-insect interactions into new interaction trajectories. Pages 338-342 *in* E. Korpilahti, H. Mikkela, and T. Salonen, editors. *Caring for the forest: research in a changing world.* Congress Report Vol. 2. IUFRO World Congress Organizing Committee. Finland.
- McCambridge, F.W. 1971. Temperature limits of flight of the mountain pine beetle, *Dendroctonus ponderosae*. *Annals of the Entomological Society of America* 64:534-535.
- McGregor, M. D. and D. M. Cole 1985. Integrating management strategies for the mountain pine beetle with multiple-resource management of lodgepole pine forests. *General Technical Report INT-174.* USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

- Meidinger, D. and J. Pojar (Eds.). 1991. Ecosystems of British Columbia. Special Report Series No. 6. British Columbia Ministry of Forests, Research Branch, Victoria, BC, Canada.
- Mooney, C. Z., and R. D. Duval. 1993. Bootstrapping: A nonparametric approach to statistical inference. Sage Publications, Newbury Park, California, USA.
- Moore, R. D., I. G. McKendry, and K. Stahl. 2005. Mountain pine beetle outbreaks in western Canada: coupled influences of climate variability and stand development. Final Report for Climate Change Action Fund Project A676, Natural Resources Canada, Ottawa, ON.
- Nola, P., M. Morales, R. Motta, and R. Villalba. 2006. The role of larch budmoth (*Zeiraphera diniana* Gn.) on forest succession in a larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) stand in the Susa Valley (Piedmont, Italy). *Trees* 20:371-382.
- Oliver, C. D., and B. C. Larson. 1996. *Forest Stand Dynamics*. John Wiley and Sons, Inc. New York, USA.
- Overpeck, J. T., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343:51-53.
- Parker, T. J., K. M. Clancy, and R. L. Mathiasen. 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agricultural and Forest Entomology* 8:167-189.
- Parkins, J. R., and N. A. McKendrick. 2007. Assessing community vulnerability: a study of the mountain pine beetle outbreak in British Columbia, Canada. *Global Environmental Change* 17:460-471.
- Pohl, K. A., K. S. Hadley, and K. B. Arabas. 2006. Decoupling tree-ring signatures of climate variation, fire, and insect outbreaks in central Oregon. *Tree-Ring Research* 62:37-50.
- Pureswaran, D.S. and J. H. Borden. 2003. Test of semiochemical mediated host specificity in four species of tree killing bark beetles (Coleoptera: Scolytidae). *Environmental Entomology* 32:963-969.
- Raffa, K. F., and A. A. Berryman. 1982. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. *Environmental Entomology* 11:486-492.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*. 58:501-517.

- Redding, T., R. Winkler, D. Spittlehouse, R. D. Morre, A. Wei, and P. Teti. 2008. Mountain pine beetle and watershed hydrology: a synthesis focused on the Okanagan basin. One Watershed – One Water Conference Proceedings. Kelowna, October 21-23, 2008.
- Redmond, K. T., and R. W. Koch. 1991. Surface climate and streamflow variability in the western United States and their relationship to large-scale circulation indices. *Water Resources Research* 27:2381-2399.
- Reid, R. W. 1958. Internal changes in the female mountain pine beetle, *Dendroctonus monticolae* Hopk., associated with egg laying and flight,. *The Canadian Entomologist* 90:464-468.
- Reid, R. W. 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia I. Life cycle, brood development, and flight periods. *The Canadian Entomologist* 94:531-538.
- Reid, R. W. 1963. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. *The Canadian Entomologist* 95:225-238.
- Reid, M. L., and T. Robb. 1999. Death of vigorous trees benefits bark beetles. *Oecologia* 120:555-562.
- Rogers, P. 1996. Disturbance ecology and forest management: a review of the literature. General Technical Report INT-GTR-336. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Romme, W. H., J. Clement, J. Hicke, D. Kulakowski, L. H. MacDonald, T. L. Schoennagel, and T. T. Veblen. 2006. Recent forest insect outbreaks and fire risk in Colorado forests: A brief synthesis of relevant research. Colorado Forest Restoration Institute, Fort Collins, Colorado, USA
- Rose, M. R., and R. Harmsen. 1981. Ecological outbreak dynamics and the cusp catastrophe. *Acta Biotheoretica* 30:229-253.
- Royama, T. 1992. Analytical population dynamics. Chapman and Hall, New York, New York, USA.
- Rubino, D. L., and B. C. McCarthy. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21:97-115.
- Safranyik, L., and A. L. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3-66 *in* L. Safranyik and B. Wilson, editors. The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada.

- Safranyik, L., and R. Jahn. 1970. Emergence patterns of the mountain pine beetle from lodgepole pine. Canadian Forest Service, Bi-monthly Research Notes 26:11-19.
- Safranyik, L., D. A. Linton, R. Silversides, and L. H. McMullen. 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. Journal of Applied Entomology 113:441-450.
- Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Forestry Technical Report No. 1. Environment Canada, Canadian Forest Service, Pacific Forest Research Centre, Victoria, BC.
- Safranyik, L., D. M. Shrimpton, H. S. Whitney, and D. M. Baumgartner. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. Pages 406-428 in D. M. Baumgartner, editor. Management of lodgepole pine ecosystems. Washington State University Cooperative Extension Service, Pullman, WA.
- Shabbar, A., and B. Bonsal. 2004. Associations between low frequency variability modes and winter temperature extremes in Canada. Atmosphere-Ocean 42:127-140.
- Shabbar, A., B. Bonsal, and M. Khandekar. 1997. Canadian precipitation patterns associated with the Southern Oscillation. Journal of Climate 10:3016-3027.
- Shabbar, A., and M. Khandekar. 1996. The impact of El Niño-Southern Oscillation on the temperature field over Canada. Atmosphere-Ocean:34-401-416.
- Sherriff, R. L., E. E. Berg, and A. E. Miller. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. Ecology 92:1459-1470.
- Shore, T. L., and L. Safranyik. 1992. Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Information Report BC-X-336. Forestry Canada, Pacific and Yukon Region.
- Shrimpton, D. M. 1973. Age- and size-related response of lodgepole pine to inoculation with *Euromium clavigerum*. Canadian Journal of Botany 51:1155-1160.
- Shrimpton, D. M., and A. J. Thomson. 1982. Growth characteristics of lodgepole pine associated with the start of mountain pine beetle outbreaks. Canadian Journal of Forest Research 13:137-144.
- Speer, J. H. 2010. Fundamentals of tree-ring research. The University of Arizona Press, Tucson, Arizona, USA.
- Speer, J. H., T. W. Swetnam, B. E. Wickman, and A. Youngblood. 2001. Changes in Pandora Moth Outbreak Dynamics during the Past 622 Years. Ecology 82:679-697.

- Stahl, K., R. D. Moore, and I. G. McKendry. 2006a. Climatology of winter cold spells in relation to mountain pine beetle mortality in British Columbia, Canada. *Climate Research* 32:13-23.
- Stahl, K., R. D. Moore, and I. G. McKendry. 2006b. The role of synoptic-scale circulation in the linkage between large-scale ocean-atmosphere indices and winter surface climate in British Columbia, Canada. *International Journal of Climatology* 26:541-560.
- Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K. Chan, N. G. Yoccoz, and B. Ådlandsvik. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London Biological Sciences* 270:2087-2096.
- Stevens, R.B. 1960. *Plant Pathology, an Advanced Treatise*, Vol. 3. J.G. Horsfall and A.E. Dimond, editors. Academic Press, New York, USA.
- Stephens, S. L., C. N. Skinner, and S. J. Gill. Dendrochronology-based fire history of Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. 2003. *Canadian Journal of Forest Research* 33:1090-1101.
- Steventon, J.D. 2001. Historic disturbance regimes of the Morice and Lakes Timber Supply Areas. Northern Interior Forest Region, B.C. Ministry of Forests, Smithers, B.C. Draft Research Working Paper.
- Stokes, M. A., and T. L. Smiley. 1968. *An introduction to tree-ring dating*. University of Arizona Press, Tucson, Arizona, USA.
- Stuart, J. D., J. K. Agee, and R. I. Gara. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. *Canadian Journal of Forest Research* 19:1096-1104.
- Swetnam, T. W. 1993. Fire history and climate change in giant sequoia groves. *Science* 262:885-889.
- Swetnam, T. W., and A. M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63:399-424.
- Taylor, S. W, and A. L. Carroll. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. Pages 41-51 *in* T.L Shore, J. E. Brooks, and J. E. Stone, editors. *Mountain Pine Beetle Symposium: Challenges and Solutions*, Kelowna, British Columbia, October 30-31, 2003. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Information Report BC-X-399.
- Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. Pages 67-94 *in* L. Safranyik and B. Wilson, editors. *The mountain pine beetle: a synthesis of biology*,

- management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada.
- Thomson, A. J. 2009. Climate indices and mountain pine beetle-killing temperatures. *The Forestry Chronicle* 85:105-109.
- Thomson, A. J., and D. M. Shrimpton. 1984. Weather associated with the start of mountain pine beetle outbreaks. *Canadian Journal of Forest Research* 14:255-258.
- Trouet, V., and A. H. Taylor. 2009. Multi-century variability in the Pacific North American circulation pattern reconstructed from tree rings. *Climate Dynamics* 35:953-963.
- Trzcinski, M. K., and M. L. Reid. 2009. Intrinsic and extrinsic determinants of mountain pine beetle population growth. *Agricultural and Forest Entomology* 11:185-196.
- Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833-2849.
- Unger, L. 1993. Mountain pine beetle. Forest Pest Leaflet 76. Forestry Canada, Pacific Forestry Centre, Victoria, BC. 7p.
- US Department of Agriculture. 1997. Forest insect and disease conditions in the United States 1996. Washington DC: U.S. Department of Agriculture, Forest Service, Forest Health Protection. 87 p.
- Veblen, T. T., K. S. Hadley, E. M. Nel, T. Kitzberger, M. Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* 82:125-135
- Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1991*a*. Methods of detecting past spruce beetle outbreaks in Rocky Mountain subalpine forests. *Canadian Journal of Forest Research* 21:242-254.
- Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1991*b*. The response of subalpine forests to spruce beetle outbreaks in Colorado. *Ecology* 72:213-231.
- Welsh, C., K. Lewis, and A. Woods. 2009. The outbreak history of *Dothistroma* needle blight: an emerging forest disease in northwestern British Columbia, Canada. *Canadian Journal of Forest Research* 39:2505-2519.
- Westfall, J., and T. Ebata. 2007. Summary of forest health conditions in British Columbia. Pest Management Report No. 15. British Columbia Ministry of Forests and Range, Victoria, BC.
- White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3-13 *in* S. T. A. Pickett, and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, USA.

- Wilson, R. J. S., and B. H. Luckman. 2002. Tree-ring reconstruction of maximum and minimum temperatures and the diurnal temperature range in British Columbia, Canada. *Dendrochronologia* 20:257-268.
- Wong, C., H. Sandmann, and B. Dorner. 2004. Historical variability of natural disturbances in British Columbia: A literature review. FORREX Series 12. FORREX-Forest Research Extension Partnership, Kamloops, British Columbia, Canada.
- Wood, C. S., and L. Unger. 1996. Mountain pine beetle: A history of outbreaks in pine forests in British Columbia, 1910 to 1995. Forest Health Network. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Canada.
- Wygant, N. D. 1940. Effects of low temperature on the Black Hills Beetle (*Dendroctonus Ponderosae* Hopk.). Doctoral Thesis. Syracuse University.
- Yamaguchi, D. K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21:414-416.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology* 14:107-129.
- Zhang, Q. B., and R. I. Alfaro. 2002. Periodicity of two-year cycle spruce budworm outbreaks in central British Columbia: A dendro-ecological analysis. *Forest Science* 48:722-731.
- Zhang, Q. B., and R. I. Alfaro. 2003. Spatial synchrony of the two-year cycle budworm outbreaks in central British Columbia, Canada. *Oikos* 102:146-154.
- Zhang, Q., R. I. Alfaro, and R. J. Hebda. 1999. Dendroecological studies of tree growth, climate and spruce beetle outbreaks in Central British Columbia, Canada. *Forest Ecology and Management* 121:215-225.
- Zhou, Y., R. W. Higgins, and H. K. Kim. 2001. Relationships between El Niño-Southern Oscillation and the Arctic Oscillation: A climate-weather link. NCEP/Climate Prediction Center. Available at http://www.cpc.ncep.noaa.gov/research_papers/ncep_cpc_atlas/8/.