

2017

White spruce (*Picea glauca*) traits affecting the success of spruce beetles (*Dendroctonus rufipennis*) in the southwest Yukon

Goulding, Megan

Goulding, M. (2017). White spruce (*Picea glauca*) traits affecting the success of spruce beetles (*Dendroctonus rufipennis*) in the southwest Yukon (Master's thesis, University of Calgary, Calgary, Canada). Retrieved from <https://prism.ucalgary.ca>. doi:10.11575/PRISM/28703
<http://hdl.handle.net/11023/3730>

Downloaded from PRISM Repository, University of Calgary

UNIVERSITY OF CALGARY

White spruce (*Picea glauca*) traits affecting the success of spruce beetles (*Dendroctonus rufipennis*) in the southwest Yukon

by

Megan Goulding

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF SCIENCE

GRADUATE PROGRAM IN BIOLOGICAL SCIENCES

CALGARY, ALBERTA

APRIL, 2017

© Megan Goulding 2017

Abstract

A major outbreak of spruce beetle (*Dendroctonus rufipennis*) occurred in the southwest Yukon between 1990 and 2007. I determined how white spruce (*Picea glauca*) allocation to growth, defence and reproduction affected spruce beetle population growth, and how climate mediated these interactions. Spruce beetle population growth was greatest in years when spruce grew more slowly and had fewer cones, with no detectable effect of mean summer or winter temperature. For individual spruce trees, the probability of being attacked by spruce beetles increased with decreasing relative growth rates, increasing tree diameter, and increasing number of resin ducts produced in the previous five years; cone production did not affect attack probability. Once attacked, the probability of tree death increased with both decreasing relative growth rate and number of induced resin ducts produced in the attack year. These results show that tree growth and defence but not reproduction determined spruce beetle susceptibility.

Acknowledgements

First and foremost I would like to thank Dr. Mary Reid for her continued support, guidance and encouragement throughout this process. Thank-you also to Dr. Jalene LaMontagne for providing the original white spruce data set, and for her consultation on the development of this project. I am immensely grateful to have been able to complete my fieldwork in the southwest Yukon, and thank the Arctic Institute of North America and Kluane Lake Research Station for providing welcoming accommodations. Thank-you also to the Champagne and Aishihik First Nations for allowing this research to be conducted on their traditional lands, and to my field and laboratory assistants (Hilary Gazie, Michael Gavin, and Jesse Macri) for their invaluable help with data collection and processing.

Thank-you to the wonderful graduate students in the Department of Biological Sciences that I am so thankful to have met and experienced this journey with, and to all of my fellow Reid-Cartar lab mates, past and present. Special thanks to Riley Waytes, Emma Carroll, Steph Mogensen, Haydeé Peralta-Vázquez, Sarah Johnson and Jenn Retzlaff for the lunch-hour skating, tea-outings, words of encouragement, and for helping me successfully overcome the many unexpected hurdles of grad school. To Jordan: thank-you for your patience, and constant emotional support. Finally, to my parents: thank-you for the unwavering support, encouragement, and love. I would never have made it this far without such a solid support network, and I am eternally grateful.

This research was funded by a Canada Graduate Scholarship awarded by the National Sciences and Engineering Research Council (NSERC), a Northern Scientific Training Program grant from the Canadian Polar Commission, a W. Garfield Weston Fellowship grant awarded by Wildlife Conservation Society Canada, and a NSERC Discovery Grant awarded to M. Reid.

Table of Contents

Abstract.....	ii
Acknowledgements.....	iii
Table of Contents.....	iv
List of Tables.....	vi
List of Figures and Illustrations.....	vii
List of Symbols, Abbreviations and Nomenclature.....	ix
Epigraph.....	x
CHAPTER ONE: GENERAL INTRODUCTION.....	1
1.1 Plant-resource allocation and trade-offs.....	1
1.1.1 Growth and defence.....	1
1.1.2 Masting: where does reproduction fit in?.....	3
1.2 Thesis overview.....	6
1.3 Bark beetle outbreaks.....	6
1.3.1 Bark beetle biology.....	6
1.3.2 Effect of climate.....	8
1.3.3 Conifer defenses.....	9
1.3.3.1 Measuring defense.....	10
1.4 Spruce beetle outbreak in the SW Yukon.....	12
1.4.1 Outbreak of spruce beetles: 1990-2007.....	12
1.4.2 Spruce beetle ecology in the Yukon.....	12
1.4.3 White spruce ecology.....	14
1.5 Thesis objectives.....	16
1.5.1 Chapter 2: Spruce beetle population growth.....	16
1.5.2 Chapter 3: Consequences of spruce allocation on spruce beetle attack and survival.....	16
.....	16
CHAPTER TWO: POPULATION-LEVEL FACTORS INFLUENCING SPRUCE BEETLE POPULATION GROWTH IN THE SW YUKON DURING A LARGE-SCALE OUTBREAK.....	18
2.1 Introduction.....	18
2.2 Methods.....	23
2.2.1 Study area.....	23
2.2.2 Spruce beetle population data.....	24
2.2.3 Cone count data.....	24
2.2.4 Annual growth of white spruce.....	25
2.2.5 Temperature data.....	25
2.2.6 Statistical analyses.....	26
2.3 Results.....	27
2.3.1 Temperature, growth, and cones.....	27
2.3.2 Spruce beetle outbreak.....	27
2.4 Discussion.....	37
2.4.1 General trends.....	37
2.4.2 Effect of climate.....	37
2.4.3 Allocation to defense.....	41

2.4.4 Allocation to storage.....	43
2.4.5 Resource currencies.....	44
2.4.6 Conclusions	45
CHAPTER THREE: EFFECTS OF RESOURCE ALLOCATION IN INDIVIDUAL SPRUCE TREES ON SPRUCE BEETLE ATTACK AND TREE MORTALITY IN SOUTHWESTERN YUKON, CANADA.....	47
3.1 Introduction.....	47
3.2 Methods	52
3.2.1 Study area	52
3.2.2 Spruce beetle attack.....	53
3.2.3 Growth and defence.....	55
3.2.4 Statistical Analysis	57
3.2.4.1 Relationships between tree traits	57
3.2.4.2 Attack and survival modeling.....	58
3.2.4.3 Yearly-level cone production analysis.....	58
3.3 Results.....	63
3.3.1 Patterns of beetle activity	63
3.3.2 Relationships between tree traits	63
3.3.3 Tree attack and mortality.....	64
3.3.4 Effect of resource depletion.....	65
3.4 Discussion.....	74
3.4.1 Likelihood of spruce beetle attack.....	74
3.4.2 Multi-tiered role of carbon-based defenses in conifers	76
3.4.3 Likelihood of spruce tree mortality	77
3.4.4 The role of reproduction: masting in plants and the role of storage.....	79
3.4.5 Alignment with the Growth-Differentiation-Balance Hypothesis	81
3.4.6 Conclusions	83
CHAPTER FOUR: GENERAL CONCLUSIONS.....	85
REFERENCES	88

List of Tables

Table 2.1: Full standard least squares model for the population growth rate of spruce beetle (<i>Dendroctonus rufipennis</i>) in white spruce (<i>Picea glauca</i>) in Kluane, Yukon. $R^2=0.45$, $N=18$ years	35
Table 2.2: Standard least squares model for the population growth rate of spruce beetle (<i>Dendroctonus rufipennis</i>) in white spruce (<i>Picea glauca</i>) in Kluane, Yukon. $R^2=0.45$, $N=18$ years	35
Table 2.3: Standard least squares model, including the effect of the previous year's cone crop, for rate of spruce beetle (<i>Dendroctonus rufipennis</i>) population growth in white spruce (<i>Picea glauca</i>) located in Kluane, Yukon. $R^2=0.14$, $N=18$ years.....	36
Table 3.1: Nominal logistic regression for likelihood of white spruce trees being (1) attacked by spruce beetles and (2) killed by spruce beetles	72
Table 3.2: Nominal logistic regression for likelihood of white spruce trees being (1) spruce beetle attacked, and (2) killed by spruce beetles, examining the effect of cones that were produced during the year of beetle attack	73
Table 3.3: Nominal logistic regression for likelihood of white spruce trees being (1) attacked by spruce beetles and (2) killed by spruce beetles, examining the effect of cones that were produced in the year prior to beetle attack	74
Table 3.4: Nominal logistic regressions for likelihood of white spruce trees being attacked by the spruce beetle (<i>Dendroctonus rufipennis</i>), examining the effect of cone production in the year prior to attack for only those trees that were attacked in 2003	74

List of Figures and Illustrations

Figure 1.1: Conceptual diagram indicating the sequence of thresholds required to obtain landscape-level bark beetle outbreaks, obtained from Raffa et al. 2008	17
Figure 2.1: Mean (A) summer temperature, (B) winter temperature, (C) white spruce growth rate, (D) white spruce cone production and (E) spruce beetle population growth observed across the study area between 1994 and 2011	29
Figure 2.2: (A) Yearly mean growth rates between 1990 and 2012 for all 293 white spruce trees used in the current study. (B) Mean May-August temperatures obtained from the Burwash Landing weather station between 1990 and 2012.....	30
Figure 2.3: Relationship between mean summer temperature (°C) and mean yearly white spruce growth rate (ln mm).....	31
Figure 2.4: (A) Relationship between the current year's cone crop in white spruce (ln N+1) and yearly mean growth rate (ln mm). (B) Relationship between the previous year's cone crop (ln N+1) and the current year's mean growth rate (ln mm)	32
Figure 2.5: Effect leverage plots showing the relationship between spruce beetle population growth and (A) mean summer temperature, (B) mean winter temperature, (C) mean yearly growth rate, and (D) mean cone count.....	33
Figure 2.6: Effect leverage plots showing the relationship between spruce beetle population growth and (A) mean growth (ln mm) and (B) cone crop (ln N+1)	34
Figure 3.1: Map of the study area showing white spruce trees and their relationships to the spruce beetle outbreak (660380E 6761091N, UTM Zone 7). Map shows the location of the study site as a red star	60
Figure 3.2: (A) Photo taken of Sulphur grid from the Alaska Highway, (B) photo of a grid stake used in determining location within the study area, (C) photo of previous labeling used to identify individual trees.....	61
Figure 3.3: Cross-section of white spruce (<i>Picea glauca</i>) tree core.....	62
Figure 3.4: Relationships between predictor variables. (A) Relationship between individual white spruce (<i>Picea glauca</i>) resin duct production and mean growth rate over a 5-year period prior to spruce beetle (<i>Dendroctonus rufipennis</i>) attack, (B) relationship between individual white spruce resin duct and cone production, (C) relationship between individual white spruce growth rate and cone production	67
Figure 3.5: Relationship between individual white spruce (<i>Picea glauca</i>) tree diameter and other tree measurements. (A) Relationship between mean growth rate over a 5-year period prior to spruce beetle attack and diameter, (B) relationship between yearly cone count and diameter, (C) relationship between resin duct counts produced in 5-year interval prior to spruce beetle attack and diameter	68

Figure 3.6: Relationship between white spruce (*Picea glauca*) tree diameter, growth rate, resin duct production, cone production, and the predicted probability of being attacked by the spruce beetle (from logistic regression, Table 3.1). Spline lambda=3, N=271. Mean (+/- SE) for each category provided in panel B 69

Figure 3.7: Interaction between diameter and duct production in white spruce (*Picea glauca*) when examining the probability of tree mortality..... 70

Figure 3.8: Relationship between individual white spruce (*Picea glauca*) tree diameter, growth rate, resin duct production, cone production, and the predicted probability of mortality following attack by spruce beetles (from logistic regression, Table 3.1). Spline lambda=3, N=136 71

List of Symbols, Abbreviations and Nomenclature

Symbol	Definition
GDBH	Growth-differentiation balance hypothesis
DBH	Diameter at breast height
C/N	Carbon-nutrient balance
RB	Resource budget
PCM	Protein competition model
UTM	Universal transverse Mercator
SU	Sulphur grid
KL	Kloo grid
NSC	Non-structural carbohydrate
N	Nitrogen
P	Phosphorus
MPB	Mountain pine beetle
CMI	Climate moisture index
pGA	Partial green attack
GA	Green attack
RA	Red attack
NGD	New grey dead
OD	Old dead
RMA	Reduced major axis
OLS	Ordinary least squares

Epigraph

*In the end we will conserve only what we love;
we will love only what we understand;
and we will understand only what we have been taught.*

- Baba Dioum

Chapter One: **General Introduction**

1.1 Plant-resource allocation and trade-offs

Plant survival relies on the ability to avoid, or at least partially deter, herbivory.

As such, plants have evolved a range of important defensive mechanisms. In many cases, plant defense involves the production of chemical toxins, or the development of unpalatable tissues such as lignin, cellulose, tannins and silicates (Schardl and Feng 2010). Terpenes are one class of organic compounds produced by plants for defense. Terpenes are hydrocarbons that are derived from five-carbon isoprene units (C_5H_8), and when additional functional groups are present they are referred to as terpenoids (Lerdau et al. 1994, Schardl and Feng 2010). Conifer species in particular rely heavily on a number of resin-producing terpenoid compounds in their defensive strategies (Lewinsohn et al. 1991).

1.1.1 Growth and defence

The amount of carbon allocated to defense is expected to depend on total carbon uptake, as well as the amount of carbon that is allocated to other factors such as growth and reproduction (Herms and Mattson 1992). The idea of plant allocation to defense and the trade-offs involved with this allocation is not new, and a considerable amount of attention has been given to plant responses to herbivory over the last 30-40 years (Karban and Baldwin 1997). A number of hypotheses that provide the rationale for predictions of how much carbon is allocated to defense have been proposed since the initial interest and description of this phenomenon (Green and Ryan 1972, McKey 1974, Haukioja and Hakala 1975, Bryant et al. 1983, Coley et al. 1985, Herms and Mattson 1992). In general, the hypotheses that have been proposed can be subdivided into two broad categories: supply-side hypotheses and demand-side hypotheses (Lerdau et al. 1994). Supply-side hypotheses such as the carbon-nutrient (C/N) hypothesis and the

growth/differentiation balance hypothesis (GDBH) posit that defenses are largely influenced by the availability or supply of resources, and that the plants themselves are not able to control this availability. Demand-side hypotheses differ from these and are based on the premise that concentrations of available resources and secondary metabolites are dictated by the plants' need for them (Lerdau et al. 1994, Karban and Baldwin 1997).

One of the proposed supply-side hypotheses that has received considerable attention is the growth-differentiation balance hypothesis (Herms and Mattson 1992). Primary metabolism (the growth of new tissue) is viewed separately from differentiation processes such as the production of specialized tissue for defense, and it is predicted that there will be a negative correlation between these two types of metabolism. According to the GDBH, resources should be allocated to growth first rather than secondary metabolism and differentiation when resource availability is high. Even when resource availability is high, there is a finite level of resources, and there is therefore a predicted trade-off that occurs between the allocation towards growth and differentiation. The trade-offs between growth and secondary metabolism/differentiation will have ecological costs that vary depending on the environment's level of resources (Herms and Mattson 1992, Lerdau et al. 1994).

The growth-differentiation balance hypothesis predicts that at lower levels of resource availability growth processes will be slowed by shortages of nutrients or water, whereas net photosynthesis will not be as affected by these conditions. This will result in the accumulation of carbon that cannot be dedicated to growth, and therefore at low resource levels the trade-off between growth and defense may be masked (Herms and Mattson 1992). This would result in a positive relationship between allocation to growth and defense, not due to an allocation decision. At moderate to high resource availability however, an observed trade-off between allocation to

defense and growth is predicted (Herms and Mattson 1992). The overall premise of the GDBH is that plants need to ensure adequate growth in order to remain competitive, while still remaining sufficiently defended to prevent the loss of already acquired resources through injury or death.

Although defenses and their associated carbon/nutrient trade-off with growth have been well studied in some respects, much remains unknown and the support for the growth-differentiation balance hypothesis is limited (Stamp 2004, Karban 2011). Negative correlations between growth and defense have been found (Blanche et al. 1992, Glynn et al. 2007), but in many cases, positive relationships between measures of growth and defense have been observed (Nagy et al. 2000, Kane and Kolb 2010, Clark et al. 2012, Gaylord et al. 2013, Ferrenberg et al. 2014, Hood et al. 2015). The trade-off that must be present is not directly observed in these cases, potentially as a result of environmental conditions and the total amount of resources available to an individual. A neutral or positive relationship observed between growth and defense would indicate that conditions favourable for growth are also conducive for defense, and when an individual has a large amount of total resources available they will be able to invest more towards both functions.

1.1.2 Masting: where does reproduction fit in?

‘Mast-fruiting’ or ‘masting’ refers to synchronized episodically-large reproduction among individuals of a species (Kelly and Sork 2002, Pearse et al. 2016). In masting plant species, seed production can be high in some years and low in others, however mast years, with increased reproductive output, are synchronized among individuals. This synchronization is widespread, with some conifer species synchronized in their production of seeds among sites that are as much as 2,500 km apart (Koenig and Knops 2005).

Synchronized, substantial reproductive events have generally been thought to deplete carbon and nutrient reserves, likely resulting in an imposed period of replenishment before subsequent mast events can occur. Direct evidence of this resource depletion is lacking, however, with few studies that have examined the question directly (Sala et al. 2012). In a recent study examining the predicted negative relationship between the current and following year's seed production, out of the five masting species examined only one (*Picea abies*) displayed the predicted trend (Wesołowski et al. 2015). The production of large-scale reproductive output did not necessarily result in an imposed period of replenishment for the majority of tree species examined, indicating that there is likely not a high level of energy trade-off between growth and reproduction (Wesołowski et al. 2015). Alternative explanations as to why it is relatively uncommon to observe heavy reproductive events in subsequent years do not necessarily require there to be a depletion of resources, however, and depend more on the mechanism that is thought to mediate masting events.

The mechanisms by which masting species synchronize their reproductive efforts are a source of ongoing debate, with a large number of hypotheses for masting behaviour put forth at both the ultimate and proximate levels. Ultimate-level hypotheses for masting focus on the evolutionary benefits of the behaviour, and proximate-level hypotheses focus on the mechanisms that produce masting (Pearse et al. 2016). As ultimate explanations, it has been proposed that predator satiation, pollen coupling (pollination efficiency), and/or environmental cues could favour synchronization, but the evidence available for these three mechanisms shows mixed support (Koenig and Knops 2005). At the proximate-level, once again a number of potential hypotheses have been suggested. These hypotheses vary in whether or not what they propose is

adaptive, and some confusion arises due to the interaction of proximate and ultimate factors, with both necessary for an understanding of masting.

Two major mechanistic hypotheses for masting are based around resources: the resource-matching hypothesis and resource budget models (Pearse et al. 2016). The resource-matching hypothesis is considered non-adaptive, predicting a constant fraction of resources being devoted to reproduction, leading to a positive relationship between growth and reproduction, and therefore variation in yearly seed crops depending wholly on yearly resource accumulation (Pearse et al. 2016). There is little evidence for resource matching, with negative correlations between growth and reproduction more commonly observed (Monks and Kelly 2006, Barringer et al. 2013). There is also often greater variation in reproductive output than there is in the environment, which implies that resource matching is unlikely to be responsible (Koenig and Knops 2000). Resource budget (RB) models are also based upon resource availability, suggesting that individual plants will produce a high reproductive crop only after resources have accumulated and surpassed a certain threshold, therefore partially relying on the use of stored nutrients for masting. This explanation requires an ultimate-level component (such as pollen coupling) to explain synchrony, as one of its fundamental assumptions is that the size of a full crop is set at an unsustainably high level (Pearse et al. 2016). Resource-budget models have only been empirically tested in a few species, with some recent support (Sala et al. 2012, Rapp et al. 2013, Funk et al. 2016, Pesendorfer et al. 2016).

Growth, defense, and reproduction may not all be limited by the same resource. Conifer defenses, such as the terpenes and terpenoids discussed above, are primarily carbon-based. Non-structural carbohydrate (NSC) depletion has been documented following mast years for a number of species (Marquis et al. 1997, Miyazaki et al. 2002, Crone et al. 2009), however nutrients such

as nitrogen (N) and phosphorus (P) may be more appropriate to consider when examining the costs of reproduction. These are often more limiting in the environment, and reproductive structures are often nutrient enriched (Reekie and Bazzaz 1987b). In addition to NSC, nitrogen (Han et al. 2008, Sala et al. 2011, Ichie and Nakagawa 2013), and phosphorus (Sala et al. 2011, Ichie and Nakagawa 2013) have been found to be depleted following masting. If reproduction is limited by the amount of carbon available, then I would predict there to be a trade-off between growth and defense.

1.2 Thesis overview

In this thesis, I will apply the above ideas of carbon allocation to white spruce (*Picea glauca* [Moench]) in the context of the spruce beetle (*Dendroctonus rufipennis* [Kirby]), a key herbivore. The overarching goal of this study is to examine the relationships between host tree allocation of carbon towards growth, defense, and reproduction, and to determine how this allocation affects tree survival against bark beetle attack at both the population and individual-level.

1.3 Bark beetle outbreaks

1.3.1 Bark beetle biology

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are a highly diverse subfamily of weevils (Raffa et al. 2015). Although there are more than 6,000 known species of bark beetle, most share the common characteristic of a life spent largely hidden beneath the bark of their host tree (Wood 1982). The typical life cycle of a bark beetle is composed of a number of distinct stages: a brief period of adult dispersal, attack of a host tree, oviposition and offspring development within the phloem layer, re-emergence of adults in some species, and finally emergence of new adults (Rudinsky 1962). Bark beetles occur in regions all across the globe,

and play key roles in the structure of natural plant communities (Raffa et al. 2015). Although they can be viewed and do function as integral components of ecosystem function, they are also capable of causing widespread economic loss and are often considered to be major environmental threats (Raffa et al. 2008). In western North America in particular they are considered to be one of the most destructive forest pests, with some species capable of mass attacking otherwise healthy trees to overcome the host tree's resistance and successfully colonize and reproduce (Bright 1976, Wood 1982).

Bark beetle populations are most commonly found in their endemic population stage, when population density is naturally constrained to a relatively low level (Raffa et al. 2008). Under conditions that are conducive to higher than normal population densities, however, certain eruptive species are able to increase in population density well beyond their typical endemic levels. To achieve a landscape-scale eruption, a number of thresholds must be surpassed, which are regulated through a complex interplay of both internal and external controls and releasers (reviewed in Raffa et al. 2008, Figure 1.1). Surpassing the endemic-eruptive threshold, the new population stage that is reached is often referred to as the outbreaking or eruptive stage of population dynamics, and this type of 'eruptive window' or 'outbreak' is common for a number of bark beetle species. Although fewer than 1% of bark beetle species undergo large-scale outbreaks (Raffa et al. 2008, Bentz et al. 2010), much of the research that has been completed to date on eruptive species such as the spruce beetle and mountain pine beetle (*Dendroctonus ponderosae*) has taken place during the eruptive phase. This bias occurs primarily as a result of research logistics, given that it is much easier to detect and study the beetles when they are abundant, as well as due to an increased environmental and political interest that arises as the result of the often massive tree death incurred during an outbreak.

Due to the interest in outbreaking populations of beetles and the research that has been completed on how populations can surpass the endemic threshold and enter the eruptive phase, a number of the environmental conditions favourable for outbreaks have been elucidated. Forest structure is one factor that can greatly influence the population dynamics of bark beetles and indeed insects in general, with contiguous areas that are largely homogeneous in both species composition and age providing an opportunity for easier travel between hosts and a higher likelihood of successful colonization over a region. Mature stands in particular, with many large trees that are suitable hosts, are more amenable to bark beetle outbreaks than areas with mixed species composition and/or age (Werner and Holsten 1985, Raffa et al. 2015).

Other disturbances and stressors present in an area can additionally serve to create suitable outbreak conditions, such as with the occurrence of windthrow and logging (Dyer and Taylor 1971, Okland and Berryman 2004, Marini et al. 2013) or in other situations that result in a decrease in the number of natural enemies present (Raffa et al. 2015). In general, bark beetle dynamics are thought to be largely dominated by bottom-up forces such as the availability and suitability of host trees, rather than top-down forces such as predation (Reeve 1997).

1.3.2 Effect of climate

The effects of temperature and climate change are generally accepted as significant causes for at least some of the recent and current bark beetle outbreaks (Ayres and Lombardero 2000, Logan et al. 2003, Logan and Powell 2009, Bentz et al. 2010, Klapwijk et al. 2012, Marini et al. 2012). Climate change is thought to be priming many regions for unprecedented levels of insect outbreaks, creating amenable conditions in a two-fold manner. For conifer hosts such as spruce (*Picea* spp.) and pine (*Pinus* spp.), warm, dry conditions are leading to host trees that are already weakened by water stress prior to bark beetle arrival (Mattson and Haack 1987, Boonstra

et al. 2008). As bark beetles have been shown to thrive in warmer conditions where there are increased brood-development rates (Hansen et al. 2001, Werner et al. 2006), and lower rates of overwinter mortality (Miller and Werner 1987), an increase in temperature could result in greater tree mortality as a result of both the beetle and tree side of the interaction (Berg et al. 2006, Safranyik and Carroll 2006, Aukema et al. 2008, Powell and Bentz 2009, Priesler et al. 2012, Regniere et al. 2012, Raffa et al. 2015).

Because there are a number of biotic and abiotic factors believed to be at least in part responsible for insect outbreaks, this process is complicated even further when considering the interactive effects between them. A large, well-connected and mature forest in an area undergoing an increase in mean temperatures, for example, could potentially be thought of as a ‘perfect storm’ of conditions conducive for outbreaks.

1.3.3 Conifer defenses

Along with the threat of tree-killing bark beetles, such as the spruce beetle, to coniferous ecosystems, conifers themselves have complex defensive systems that incoming beetles must overcome before successful colonization is achieved. In general, conifers primarily defend themselves against injury with carbon-based defenses such as terpenes that are concentrated in viscous resin within the outer tree bole (Franceschi et al. 2005, Seybold et al. 2006). Resin serves as both a mechanical and chemical defense, as invading beetles can be physically obstructed from entry into the host tree and entombed within the resin, or killed by the toxicity of the terpenes and other terpenoid compounds comprised within (Keeling and Bohlmann 2006, Seybold et al. 2006, Raffa 2014).

The overall defensive strategy is multi-tiered and involves both constitutive and inducible defenses. Constitutive defenses, such as preformed resin ducts, resin blisters and resin cells, are

those present in advance of a threat to provide an immediate barrier against an initial attack by a herbivore (Franceschi et al. 2005). Inducible defenses, on the other hand, are plastic responses mounted in response to actual invaders, acting as a second line of defense against attackers (Franceschi et al. 2005). This type of multi-layered defense system is thought to be ubiquitous across conifer species. However, the level of investment towards both constitutive and induced defense varies across genera and species. Pine trees have demonstrated a greater level of dependence on resin that is already present in ducts pre-formed as a result of their high level of constitutive defense (Lewinsohn et al. 1991). Spruce trees, on the other hand, tend to invest less in constitutive defenses and rely much more heavily upon a stronger induced response to invaders, leading to the production of higher levels of traumatic resin ducts (Lewinsohn et al. 1991). Functional traumatic resin ducts are created relatively rapidly, requiring on average 2-4 weeks in Norway spruce (*Picea abies*) following induction (Nagy et al. 2000).

1.3.3.1 Measuring defense

To measure the level of defense in an individual tree, be it largely constitutive, inducible, or a mixture of both, a number of different metrics are used. Given that it is the monoterpenes found within the exuded resin itself that are the primary defensive material, resin flow itself is often used as the primary measure for defense when studying live trees (Netherer et al. 2015). The resin ducts are also an appropriate method of measuring the tree's level of investment towards defense, as these are the structures responsible for initial production and storage of monoterpenes, and provide an indication of an individual's resin reservoir capacity. Metrics examining resin ducts may in fact serve as a better representative of a tree's overall defensive situation than examining resin flow itself would, as resin flow varies significantly with different site characteristics such as temperature, season, and site quality, as well as with genetics, tree

age, and wounding (Ayres and Lombardero 2000, Knebel et al. 2008, Novick et al. 2012, Hood and Sala 2015, Hood et al. 2015, Moreira et al. 2015). Resin duct metrics are more strongly associated with tree mortality than direct measurements of resin flow in some conifers, such as mature pinon pine (*Pinus edulis*) (Gaylord et al. 2013).

There have also been several studies that demonstrated positive correlations between resin flow and resin ducts, indicating the suitability of either metric of defense (Ayres and Lombardero 2000, Rodríguez-García et al. 2014, Westbrook et al. 2015). When using resin ducts as a proxy for the amount of resin produced, analyses can be completed with either duct count data or some measure of the duct itself (i.e. duct width, total duct area, duct density, etc.). In pine trees, positive correlations have been found between resin flow and resin duct metrics in a number of cases (Rosner and Hannrup 2004, Westbrook et al. 2015). In at least one study on Norway spruce (*Picea abies*), resin flow was highly correlated with both the total number of resin canals as well as the total duct area, making either choice of measurement appropriate in this system (Netherer et al. 2015). Alternatively, in some species of pine (*Pinus ponderosae* and *Pinus sylvestris*), resin duct production (number of resin ducts), duct density and relative duct area do not predict resin flow, with the best predictors of resin flow being resin duct size and total duct area over a 5-year period (Kyto et al. 1999, Hood and Sala 2015). At this time, the relationships between resin flow, the number of resin ducts and their traits are still unclear, making the specific metric to best represent an individual tree's defensive potential unknown (Hood and Sala 2015).

1.4 Spruce beetle outbreak in the SW Yukon

1.4.1 Outbreak of spruce beetles: 1990-2007

Approximately 400,000 ha of forest across the southwest Yukon, including the Kluane region examined in my study, was severely impacted by an unprecedented outbreak of spruce beetle that took place in the area beginning in the early 1990s (Garbutt et al. 2006, YukonGovernment 2010). The outbreak in this region has been reported as the largest, most severe, and longest lasting outbreak of the spruce beetle in Canada (YukonGovernment 2013), with more than 50% of mature white spruce being killed in many areas (Garbutt et al. 2006). This outbreak is widely believed to be in part due to a warming climate, with shorter beetle generation times and reduced rates of overwinter mortality, in addition to an increase in weakened host trees as a result of drought-stress (Berg et al. 2006, Bentz et al. 2010). Located in the Canadian north, this area is one that has undergone significant changes in temperature over the last 60 years, and one in which substantial changes to temperature and precipitation are projected for the remainder of the 21st Century (Prowse et al. 2009).

1.4.2 Spruce beetle ecology in the Yukon

The spruce beetle is found widely throughout Canada and the United States (Bright 1976). This particular species is a major, destructive forest pest, and it is well known for a number of major outbreaks in areas such as the Yukon, Alaska, and British Columbia. Fully developed adult spruce beetles are between 4.4 and 7.0 mm long, with dark brown body colouration and reddish-brown elytra (Wood 1982). As with other *Dendroctonus* species, they are capable of attacking live trees en masse, and outbreaks often result in widespread host tree mortality and changes in overall stand structure.

For spruce beetles found at higher latitudes such as those of the SW Yukon, their life cycle typically takes 2 years to complete and involves overwintering in both larval and adult stages. The development time can vary between one and three years, however, depending on where in its range the population is located. One-year cycles develop in areas that experience an average phloem temperature of at least 16.5°C during the summer months, whereas the two-year life cycle observed at higher latitudes has been generally characterized by average phloem temperatures of 10.6°C (Werner and Holsten 1985). Switches from a normally semivoltine (2-year) to a newly univoltine (1-year) life cycle is therefore predicted to be observed with increased summer temperatures, and has already been documented for spruce beetle populations in Alaska, Utah, and Colorado (Hansen et al. 2001, Werner et al. 2006, Bentz et al. 2010).

Over-winter mortality, caused by exposure to cold temperatures, has long been thought of as a key temperature-related factor contributing to population dynamics of bark-beetle populations, despite a lack of data for most species (Bentz et al. 2010). Spruce beetles in particular accumulate glycerol as a cryoprotectant in autumn, and are able to dramatically decrease their supercooling points over the winter months to allow for the survival of overwintering larvae and adults (Miller and Werner 1987). Despite this protectant, however, especially cold winters (minimum temperatures below -31°C) result in lethal freezing of beetles overwintering near or above snowline (Miller and Werner 1987). In spruce beetles (*Dendroctonus engelmanni* [Hopkins]), cold winter temperatures have resulted in 75% and 88% over-winter mortality in Colorado and Arizona, respectively (Massey and Wygant 1954, Frye et al. 1974). With increasing minimum temperatures associated with climate change and milder than average winters, a decrease in cold-temperature-induced overwintering mortality is predicted.

1.4.3 White spruce ecology

White spruce, the primary host of the spruce beetle, has a transcontinental range across North America, with a wide distribution that includes growth at sea level and upwards to over 1500m. Maturity occurs after 30 years on average, but for some individuals age at maturity is much reduced (i.e. 14 years) (Nienstaedt and Zasada 1990).

Based on both constitutive and induced responses, spruce has a defensive strategy that aims to prevent, or minimize, harm from its many potentially damaging agents (Ives and Wong 1988, Nienstaedt and Zasada 1990, Christiansen et al. 1999). Multiple species of bark beetle attack white spruce, although most species other than *D. rufipennis* will attack already weakened, dying trees (Nienstaedt and Zasada 1990). Spruce beetle outbreaks on healthy trees are often associated with areas more susceptible to outbreak due to prolonged periods of warm summer temperature, or regions where there are interspersed large supplies of otherwise weakened or dead trees (Ives and Wong 1988, Berg et al. 2006).

Cone development has conventionally been thought to depend largely on climatic conditions in the current (t) and previous year (t-1) (Juday et al. 2003, Koenig and Knops 2005). White spruce reproductive buds are differentiated in the year before flowering and seed dispersal (t-1), and bud development continues for 2-2.5 months before buds become dormant in early October (Eis et al. 1965, Nienstaedt and Zasada 1990). The period of peak pollination, and critical stage for seed production, occurs in the following summer (t), along with seed development. As reproductive buds are differentiated at the end of shoot elongation in the year prior to flowering (t-1), warm, dry temperatures observed during this ‘critical’ time period were thought to be at least partially responsible for increased cone production (Nienstaedt and Zasada 1990, Juday et al. 2003). This, along with four other key criteria or ‘gateways’ were identified by

Juday et al. (2003), forming a model for the requirements needed to achieve significant cone production. A subsequent study tested this model, examining the climatic determinants of white spruce cone crops in the southwest Yukon. From the 26 years of cone-crop data that were analyzed, it was determined that the proposed key factors in years t and $t-1$ explained surprisingly little of the variation observed in cone production (Krebs et al. 2012). From further exploratory modeling it was determined that conditions in $t-2$ were the most significant predictors of cone crop production, specifically the temperature in late summer of $t-1$ and $t-2$, along with rainfall in spring of $t-2$ (Krebs et al. 2012).

More recently, a new predictor of cone crop determination for a variety of masting plant species was suggested: the change in mean summer temperature (ΔT) between one (T_{n-1}) and two (T_{n-2}) years prior to a mast year (Kelly et al. 2013). This study found ΔT to be the most significant predictor of masting in all 26 datasets that were examined, and provides an explanation for rarely observing back-to-back mast years, without needing to invoke resource depletion (Kelly et al. 2013). Krebs et al. (2017) re-examined the climatic determinants of white spruce cone counts in the southwest Yukon area, and ΔT was found to be the most significant predictor across all 5 Yukon sites, explaining on average 65% of the variation between years. Rainfall was no longer observed to be significant, with no evidence of any association between rainfall and cone crop variation (Krebs et al. 2017). According to Kelly et al. (2013), the ΔT model for masting has important implications for the predicted response of masting tree species under climate change. Given that it is the difference between previous summer temperatures that is responsible for determining mast years, increasing temperature under climate change would no longer be predicted to affect masting frequency, as would have been expected under the single or 2-year temperature model (either T_{n-1} , T_{n-2} , or the 2T model including both as predictors) (Kelly

et al. 2013). This explanation can only be employed when considering ΔT as a cue for masting, however, and not if ΔT functions as a proximate driver of masting with mechanistic links between ΔT and formation of cone crops (Pearse et al. 2014). If ΔT is a proxy for some mechanistic factor that will directly affect production of reproductive output (seeds), then climate change will still be predicted to have a significant effect.

1.5 Thesis objectives

1.5.1 Chapter 2: Spruce beetle population growth

The overarching goal of my study was to examine the relationships between host-tree allocation of resources and survival against bark beetle attack in the Yukon. In Chapter 2 of this thesis, I examine how yearly white spruce allocation to growth and reproduction at the population level affected the subsequent success of spruce beetle in the region, and whether or not these relationships were mediated by climate.

1.5.2 Chapter 3: Consequences of spruce allocation on spruce beetle attack and survival

In Chapter 3, I determine how carbon allocation towards growth, defense, and reproduction, at the individual-tree level affected the overall likelihood of an individual tree being attacked, and subsequently killed. Although the general relationship between growth and defense has been well studied in many systems in the past, I examine growth and defense allocation retrospectively in the context of spruce tree susceptibility, during a large-scale outbreak. Additionally, I examine the cost of reproduction on growth and defense for the current study system, an aspect that to my knowledge has not previously been reported on.

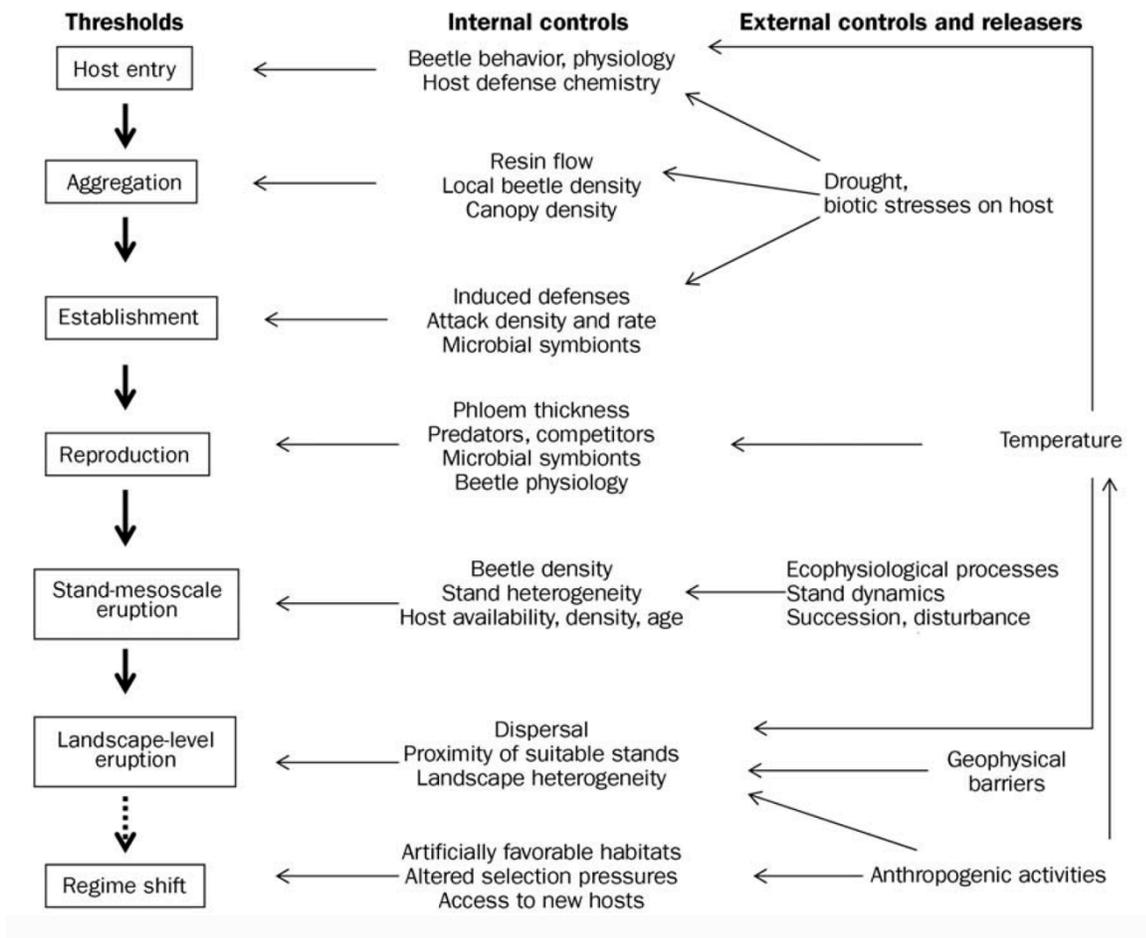


Figure 1.1. Conceptual diagram indicating the sequence of thresholds required to obtain landscape-level bark beetle outbreaks, obtained from Raffa et al. 2008. Internal controls, external controls and releasers influencing the probability of beetles surpassing a particular threshold are indicated.

Chapter Two: **Population-level factors influencing spruce beetle population growth in the SW Yukon during a large-scale outbreak**

2.1 Introduction

Interactions between insects and plants are thought to encompass 50% of all ecological relationships (Strong et al. 1984, Raffa et al. 2008). Natural constraints keep most insect species from undergoing large-scale population outbreaks (Raffa et al. 2015), but examining eruptive species in particular can provide valuable insights into fundamental ecological processes (Raffa et al. 2008). Native bark beetles (Coleoptera: Curculionidae: Scolytidae) are a group of insects that are common in the forests of western North America, and are key drivers of change within these systems (Bentz et al. 2010), especially following outbreaks of the more aggressive, tree-killing, species.

Less than 1% of bark beetle species undergo large-scale outbreaks, and the majority of species capable of attacking and colonizing live hosts are largely concentrated in the genera *Dendroctonus*, *Ips*, and *Scolytus* (Raffa et al. 2008, Bentz et al. 2010). These beetles are capable of causing landscape-level mortality using mass attacks to overwhelm host tree defenses, and their intermittent outbreaks are under complex control. Beetle population size is determined in part by forest structure (Werner and Holsten 1985, Raffa et al. 2015) and disturbances and stressors such as windthrow (Schmid 1981), logging (Dyer and Taylor 1971, Okland and Berryman 2004, Marini et al. 2013), avalanches (Hebertson and Jenkins 2007), and fire (Schmid and Frye 1977, Werner and Holsten 1985, Berg et al. 2006).

Climate also has important effects on bark-beetle systems and population densities (Ayres and Lombardero 2000, Logan et al. 2003, Berg et al. 2006, Logan and Powell 2009, Klapwijk et al. 2012, Marini et al. 2012). Climate has both direct and indirect effects on bark

beetles. Temperature-dependent physiological processes such as synchronous adult dispersal and life-cycle timing are critical to the success of many aggressive bark beetle species in successfully colonizing live tree hosts (Bentz et al. 2010). As such, the direct effects of climate on beetle population dynamics include both the maintenance, or adjustment, of developmental timing, in addition to the facilitation of cold tolerance. Bark beetle species thrive in warmer conditions, with increased brood development rates (Hansen et al. 2001, Werner et al. 2006), and lower rates of overwinter mortality (Miller and Werner 1987, Bentz et al. 2010).

Indirectly, climate can affect bark beetles through changes that are incurred in host tree physiology. Warm, dry conditions result in host trees that are already weakened by water stress, resulting in an increased susceptibility to bark beetle attack (Mattson and Haack 1987, Boonstra et al. 2008). Drought-stress can also significantly affect host defenses, potentially weakening them in the short-term, further increasing tree susceptibility to beetle attack (McDowell et al. 2011, Hart et al. 2014).

The environmental conditions that are encountered by the majority of trees in a population will play a significant role in the initiation and development of insect outbreaks (Raffa et al. 2008, Raffa et al. 2015). On a year-to-year basis, changes in the total level of resources that get allocated towards individuals' growth, defence, reproduction, and other miscellaneous energy expenditures, will affect the overall susceptibility of a particular population to incoming bark beetle attack. Given that there is a finite level of resources available to an individual, the amount that is allocated towards defense is predicted to depend on both the total amount available as well as the amount that is allocated to other factors such as growth and reproduction (Herms and Mattson 1992). The absolute amount of defence that is produced will

therefore depend not only on how carbon is allocated, but also on the total amount of carbon available (van Noordwijk and de Jong 1986).

The total amount of carbon that is accessible to a plant will vary with climate. Plants often respond to drought-stress by closing their stomata to prevent unnecessary water loss and prevent hydraulic failure (Fettig et al. 2013). Stomatal closure also results in a plant's inability to take up carbon dioxide required for photosynthesis, resulting in reduced productivity (Fettig et al. 2013), and less carbon available for either primary or secondary metabolism. Under normal conditions, plant respiration would not exceed photosynthesis, and so this form of carbon limitation would not be present.

Many conifer species respond to insect attackers with a rapid increase in the number of defenses that are mobilized to fight off incoming attackers (Christiansen et al. 1987). This defensive response will determine how effectively incoming attackers can be stopped before significant damage is incurred. One hypothesis regarding carbon allocation to defense that has received considerable attention is the growth-differentiation balance hypothesis (GDBH) (Herms and Mattson 1992). This hypothesis predicts that at lower levels of resource availability, growth will be slowed by shortages of nutrients or water, whereas net photosynthesis will not be as affected by these conditions. This will result in the accumulation of carbon that cannot be dedicated to growth, and therefore at low resource levels the trade-off between growth and defense may be masked (Herms and Mattson 1992). This would also result in a positive relationship between allocation to growth and defense, not due to an allocation decision. At moderate to high resource availability, however, an observed trade-off between allocation to defense and growth is predicted (Herms and Mattson 1992).

The GDBH has received some support (Mihaliak and Lincoln 1985, Blanche et al. 1992, Wilkens et al. 1996, Glynn et al. 2003, Stamp 2004, Stamp et al. 2004, Glynn et al. 2007). However, the majority of studies report positive relationships between measures of growth and defense (Bannan 1936, Kane and Kolb 2010, Gaylord et al. 2013, Ferrenberg et al. 2014, Hood et al. 2015). These positive relationships may be explained by considering the total amount of resources available to an individual (van Noordwijk and de Jong 1986). At the population level, these allocation patterns are likely to be equally important in determining where outbreaks are most likely to occur, although some studies suggest that tree defenses are ineffective once beetle population density has increased sufficiently (Boone et al. 2011).

One often ignored but significant factor that should be considered when examining stand susceptibility to bark beetle attack is the cost of reproduction (Obeso 2002). Masting species in particular can provide valuable insights into the costs of reproduction in nature. Masting refers to synchronous, episodically large investment towards reproduction, and masting species exhibit certain years where seed production is extremely high, known as mast years (Koenig and Knops 2005). As ‘mast-fruiting’ involves the synchronized reproduction of individuals of a species, a mast year will be observed at the population level with highly increased reproductive output across the majority of individuals. To garner the resources required for such a strong reproductive effort, a negative correlation between masting and both growth and defense in years where investment towards reproduction is high can be predicted.

Here I examine the contribution of tree growth and reproduction to an outbreak of spruce beetle (*Dendroctonus rufipennis*) in the SW Yukon. A large-scale outbreak took place in the area beginning in the early 1990s and continuing until approximately 2007 (Yukon Government 2013). During that time, mature white spruce, *Picea glauca* [Moench], were killed across more

than 380,000 ha. This region of the boreal forest is dominated by white spruce, the only conifer present in the region, and as such this outbreak had significant ramifications both ecologically and economically (Garbutt et al. 2006). Spruce beetle in this region typically experience a 2-year (semivoltine) life cycle, with individuals overwintering in both larval and adult stages before emerging to search for new hosts. Relatively warm conditions can accelerate development to a single year (univoltine) life cycle, however, which may have contributed to the recent outbreak of spruce beetles in nearby Alaskan populations (Berg et al. 2006).

White spruce is a masting species (LaMontagne and Boutin 2007, Krebs et al. 2012). In the Kluane region of the Yukon, the size of annual cone crops have been measured for the purposes of examining the climatic determinants of white spruce cone crop in the area (Krebs et al. 2012). Because average cone counts are available throughout the duration of the beetle outbreak, this study system provides an opportunity to examine the cost of reproduction and masting on overall allocation patterns, and the effect that these costs have on overall susceptibility to beetle outbreak for an area.

The purpose of my study was to examine how spruce-beetle population-growth was affected by yearly variation in overall white spruce investment towards growth, reproduction, and in turn defense, and whether or not these relationships were mediated by climate. If direct effects of climate are important determinants of spruce beetle population growth, I predicted that higher summer or winter temperatures, or both, would positively affect beetle populations.

When examining spruce-beetle population-growth with respect to spruce growth and reproduction, two potential relationships may be observed. Following the logic of the growth-differentiation balance hypothesis (Herms and Mattson 1992), if there is an observed trade-off between growth, reproduction and defense, then I predicted that beetle success would be

positively correlated with tree growth and reproduction. This would indicate that by investing in both growth and reproduction, less investment was allocated towards defense. Alternatively, if at an absolute level trees were still able to invest heavily in defense due to their access to an increased amount of resources, I predicted a neutral or negative association between spruce-beetle population-growth and spruce growth and reproduction. Under this scenario, I predicted that years where investment towards reproduction is high would have slower spruce beetle population growth, due to a higher amount of defenses present.

2.2 Methods

2.2.1 Study area

This study was conducted in the Kluane region of the southwest Yukon. Due to its location in the rain shadow of the St. Elias Mountains, the area experiences a semiarid and more continental climate than might be expected based solely on its proximity to the Pacific Ocean (Krebs and Boonstra 2001). The area receives on average less than 30cm of annual precipitation, with approximately 40-50% of yearly totals falling as snow in the winter months (Krebs and Boonstra 2001). The vegetation of the area is typical of the subalpine boreal forest, dominated primarily by white spruce, and interspersed with both balsam poplar (*Populus balsamifera*) and aspen (*Populus tremuloides*) as well as shrub-covered areas that are primarily composed of willow (*Salix* spp.) (Rowe 1972, Krebs and Boonstra 2001).

Approximately 400,000 ha of forest across the southwest Yukon, including the Kluane region, was severely impacted by the unprecedented outbreak of spruce beetle that took place in the area beginning in the early 1990s (Garbutt et al. 2006, Yukon Government 2010). The outbreak in this region has been reported as the largest, most severe, and longest lasting outbreak

of the spruce beetle in Canada (Yukon Government 2013), with more than 50% of mature white spruce being killed in many areas (Garbutt et al. 2006).

2.2.2 Spruce beetle population data

Spruce beetle infestation data for the southwestern Yukon region were obtained from Chart 1 of the Yukon Government's forest health report based on aerial surveys conducted across the entire region (2013). Between 1994 and 2011, inclusive, yearly area of spruce mortality caused by spruce beetles was reported and organized by severity class. Red trees that were counted and reported in one year (t) indicate trees that were killed by the spruce beetle in the previous year ($t-1$) (Yukon Government 2013). In my dataset, I adjusted this so that mortality estimates reflected mortality within the given year (trees that were killed in year t). Total area affected was extracted using GraphClick version 3.0.3 (Arizona Software Inc.) software. The area of spruce beetle killed trees was assumed to reflect the population size of spruce beetles (Trzcinski and Reid 2008).

2.2.3 Cone count data

I obtained annual white spruce cone counts for the Kluane region of Yukon from Figure 2 of Krebs et al. (2012) for the years between 1994 and 2011 inclusive. Cone data were obtained from the southwestern Yukon Territory near Kluane Lake, within the Shakwak Trench system ($61^{\circ}01'N$, $138^{\circ}24'W$) (Krebs et al. 2012). I obtained total annual cone counts from the published figure using GraphClick version 3.0.3 (Arizona Software Inc.) software. Spruce cones were counted while they were still green, and before red squirrels (*Tamiasciurus hudsonius*) began to harvest them in late August (Krebs et al. 2012).

2.2.4 Annual growth of white spruce

I determined annual growth increments of white spruce using tree cores that I collected from the field (60°58'N, 138°20'W) during July 2015, from 293 trees approximately equally divided among trees that were never attacked by the spruce beetle, were attacked and survived, or were attacked and were killed (Chapter 3). The sampled trees were located within the same study sites that were used by Krebs et al. (2001), and overlap spatially with the area of the southwest Yukon Territory near Kluane Lake for which cone count data were obtained (Krebs et al. 2012). Cores were processed using standard dendrochronological techniques (Stokes and Smiley 1968). Individual cores were cross-dated using skeleton plotting, and all cores obtained from live trees were additionally date referenced using the most recent year of annual growth (2015). Trees selected for sampling varied in age at core height (ca. 1.4m high), ranging from 20 to 191 years old (mean \pm SD: 54.69 \pm 1.05 years). Mean annual growth rate was 1.60 \pm 0.87mm per year, which was relatively fast compared to previous estimates for the region (Boonstra et al. 2008).

2.2.5 Temperature data

I obtained meteorological data for Burwash Landing (61°22'N, 139°03'W) from Charles Krebs (University of British Columbia) who in turned obtained the data from Ed Berg (US Fish and Wildlife Service, Kenai National Wildlife Refuge, Soldotna, Alaska). Yukon Territory Government (YTG) data was used by Berg when available, and missing values were supplemented with data obtained from Brian Luckman (Western University, London, ON).

I used the mean temperature for May through August to determine the effect of summer temperature on spruce beetle population growth. May-August mean temperature has been previously found to be significantly associated with spruce beetle attack and success (Berg

2006), and encompasses the period of the spruce beetle life cycle where warmer air temperatures can lead to a switch from a locally normal 2-year development period to a 1-year cycle (Werner and Holsten 1985). Additionally, mean summer temperature positively affects white spruce growth rate (Boonstra et al. 2008), with the majority of yearly wood deposition for the Kluane region occurring in May through August (Berg and Henry 2003). To determine the effect of winter temperature on spruce beetle success, I used the mean temperature for the preceding November through March. Winter temperature was chosen as a predictor variable due to its known association with overwintering spruce beetle mortality rates (Miller and Werner 1987).

2.2.6 Statistical analyses

To examine population growth (or decrease) of spruce beetles, change in beetle pressure from year $t-1$ to t was calculated as $(\ln(n_t/n_{t-1}))$, where n is the area of spruce trees killed by spruce beetles, following established methodology (Trzcinski and Reid 2009). The predictor variables were May-August (summer) mean temperature ($\ln(^{\circ}\text{C})$), November-March (winter) mean temperature ($\ln(^{\circ}\text{C} + 20)$), mean tree growth rate ($\ln(\text{mm})$), and mean cone production ($\ln(\text{cone count} + 1)$), using standard least squares modeling. Model assumptions were verified by examining residuals after model fitting. The value added to winter temperature (20) was used as a translation constant prior to \ln -transformation in order to deal with the negative values obtained for mean winter temperatures. Because neither temperature variable was found to have a significant effect on spruce beetle population growth, a second model was constructed by removing the least significant variable, winter temperature. Finally, I ran a third model to examine how spruce beetle population growth in a given year was affected by cone crop production in the previous year because there could be a lagged effect between investment towards reproduction and subsequent investment towards defense.

All statistical analyses were completed using JMP Version 13 software (SAS Institute Inc., Cary, NC).

2.3 Results

2.3.1 Temperature, growth, and cones

The mean summer temperature from 1994-2011 was $10.25 \pm 0.93^{\circ}\text{C}$ (Figure 2.1A). Interestingly, both the lowest (8.25°C) and highest (12.15°C) mean summer temperatures observed in the last 50 years were included in the 18-year period of interest between 1994 and 2011 (data not shown). Mean winter temperature during this time was $-15.4 \pm 2.84^{\circ}\text{C}$ (Figure 2.1B). Mean summer temperature was not correlated with mean winter temperature for the area in a given year ($r = -0.1481$). Summer temperature was not significantly associated with annual white spruce growth rate ($r = -0.007$, $df = 1,16$, $F = 0.001$, $p = 0.977$) (Figure 2.3).

No significant trade-off between mean annual growth increment and cone production in a given year was observed ($r = -0.2769$, $df = 1,16$, $F = 1.33$, $p = 0.2659$) (Figure 2.4A). Similarly, mean growth rate in the current year did not depend on cone production in the previous year ($r = 0.030$, $df = 1,16$, $F = 0.014$, $p = 0.908$) (Figure 2.4B).

2.3.2 Spruce beetle outbreak

Neither mean summer or winter temperature significantly affected the annual population growth of spruce beetles (Figure 2.5A,B, Table 2.1). Population growth appeared to decline with increasing spruce growth rate, although this relationship was not significant in the full model (Figure 2.5C, Table 2.1). Cone production was the only significant predictor in this model, with spruce beetle population growth declining with increased cone production (Figure 2.5D, Table 2.1).

I then removed the least significant predictor variable (winter temperature) and ran a second model including only growth, cones, and summer temperature. Here, there was no significant effect of mean summer temperature on spruce beetle population growth rate, however the annual population growth of spruce beetles declined as the annual growth and cone production of white spruce increased (Figure 2.6, Table 2.2).

To determine whether there was a lagged effect of cone production on the spruce beetle population growth trend observed in a given year, I replaced cone counts in the current year with those from the previous year. This model explained the least amount of variance in population growth ($R^2 = 0.14$, with no significant effects observed for any of the included predictors (Table 2.3).

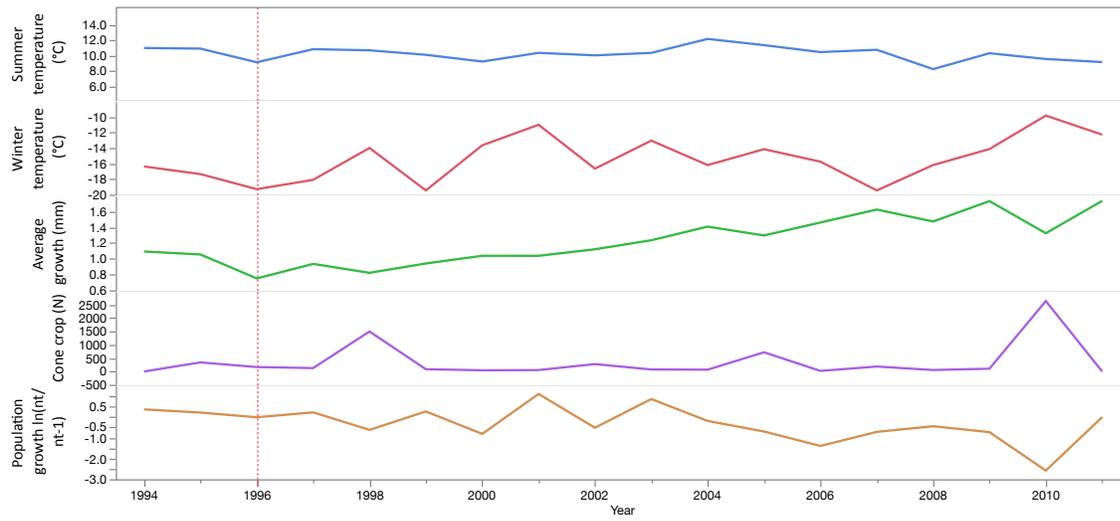


Figure 2.1. Mean (A) summer temperature, (B) winter temperature, (C) white-spruce growth rate, (D) white-spruce cone production, and (E) spruce-beetle population-growth observed across the study area between 1994 and 2011. Red dashed line corresponds to 1996, used in the present study as a marker year for cross dating of tree cores.

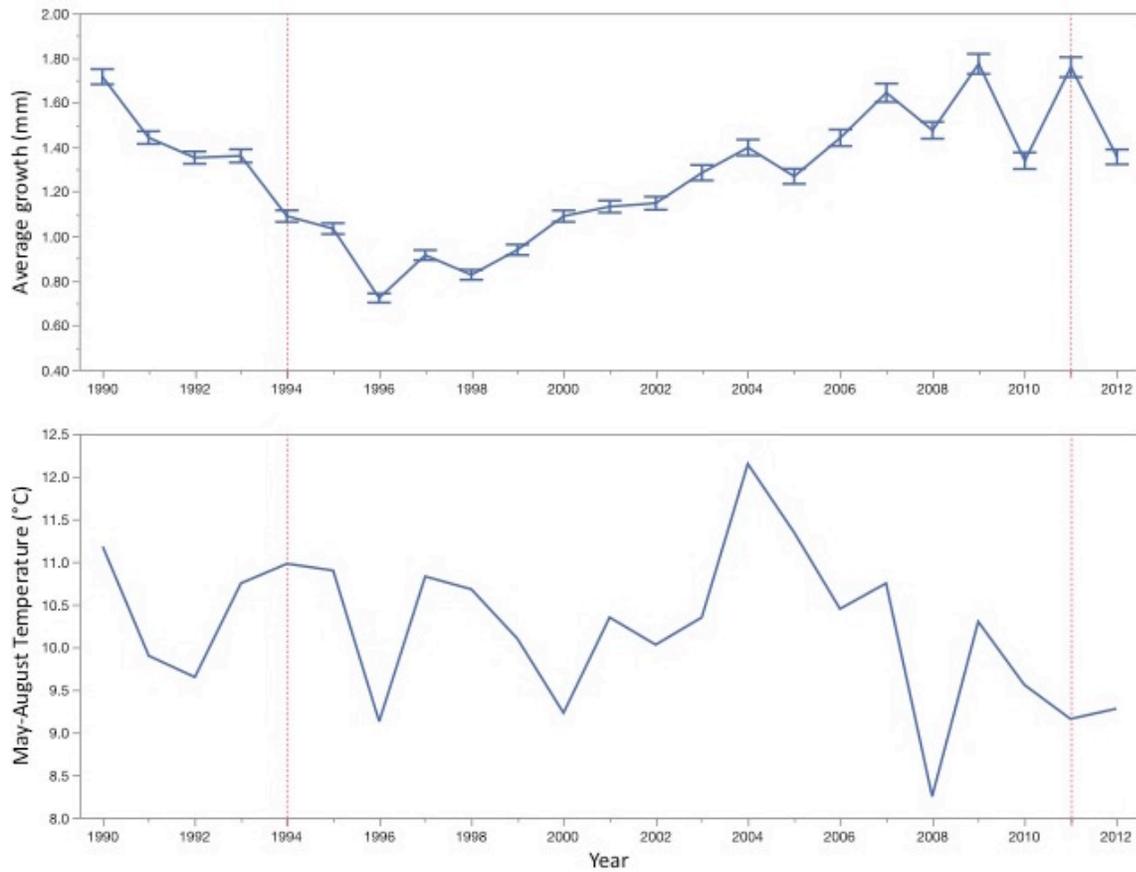


Figure 2.2: (A) Yearly mean growth rates between 1990 and 2012 for all 293 white spruce trees used in the current study. Error bars represent +/-SEM. Year with the lowest growth rate shown as 1996 and was used as a marker year for skeleton plotting and cross dating tree cores. (B) Mean May-August temperatures (°C) obtained from the Burwash Landing weather station (61°22'N, 139°03'W) between 1990 and 2012. Section enclosed by red dotted lines represents the years included in spruce beetle outbreak analyses.

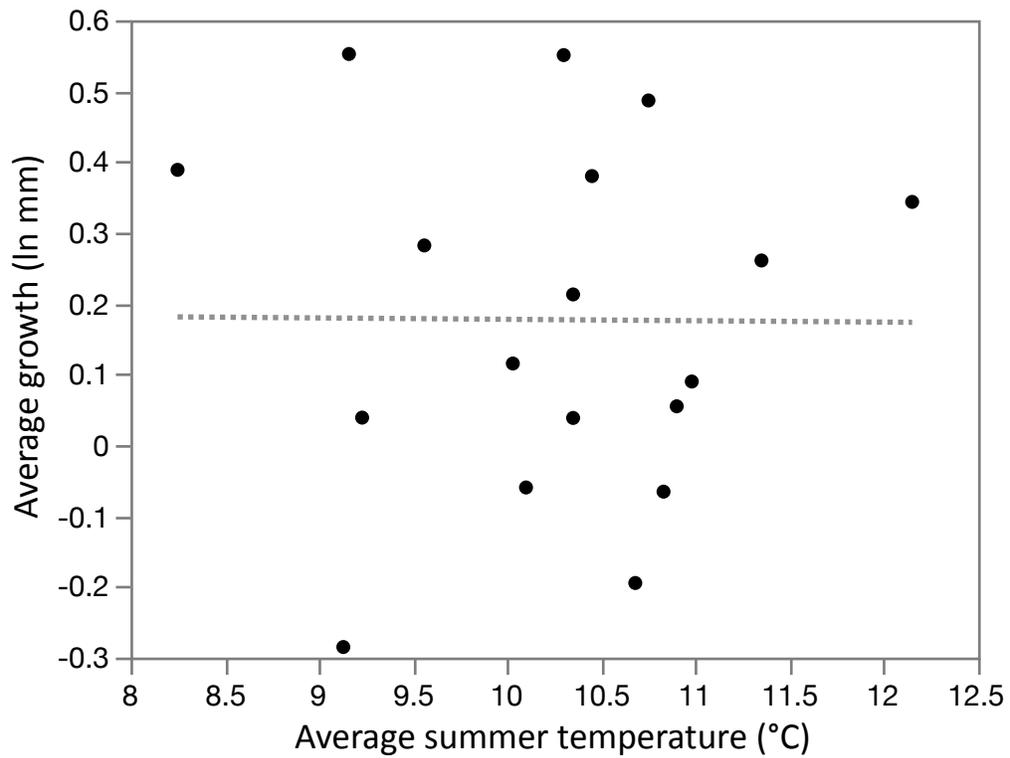


Figure 2.3. Relationship between mean summer temperature (°C) and mean yearly white spruce growth rate (ln mm) for all years of spruce beetle outbreak examined (1994-2011) in Kluane, YK. Dashed line of fit represents a non-significant effect.

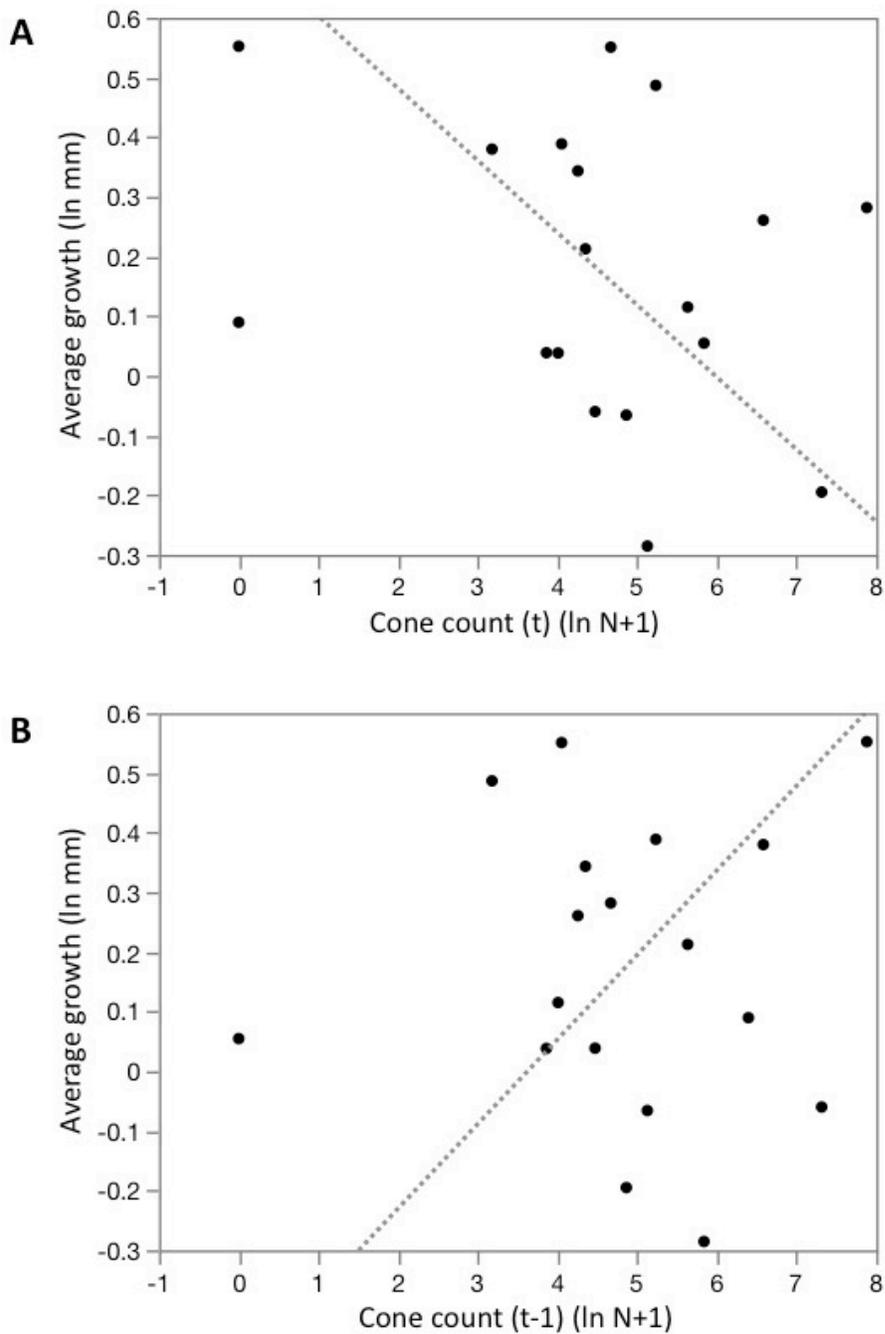


Figure 2.4. (A) Relationship between the current year's cone crop in white spruce ($\ln N+1$) and yearly mean growth rate ($\ln \text{mm}$). Dashed grey line is orthogonal fit line, correlation= - 0.277, $N= 18$ years. (B) Relationship between the previous year's cone crop ($\ln N+1$) and the current year's mean growth rate ($\ln \text{mm}$). Dashed grey line is orthogonal fit line, correlation= 0.030, $N= 18$ years. Dashed lines represent non-significant effects.

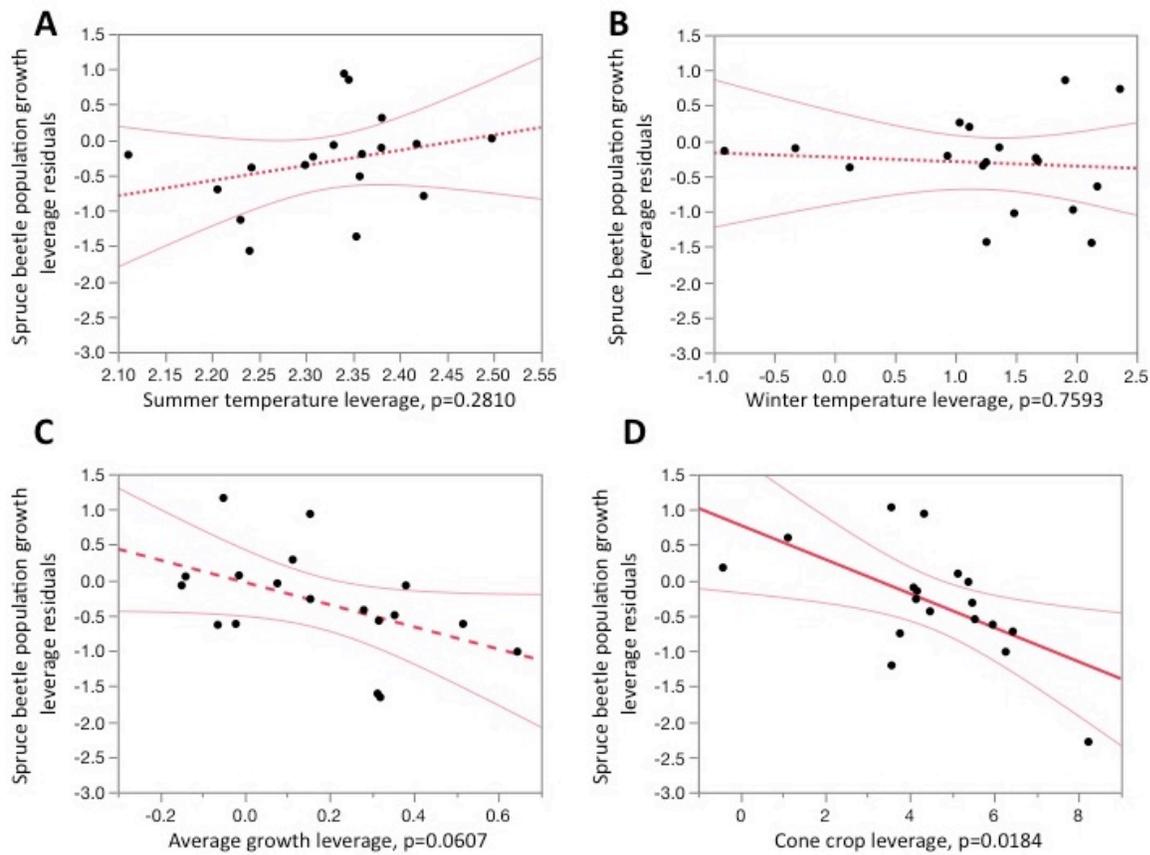


Figure 2.5. Effect leverage plots showing the relationship between spruce beetle population growth ($\log(N_t/N_{t-1})$) and (A) mean summer temperature ($^{\circ}\text{C}$) (B) mean winter temperature ($^{\circ}\text{C}$), (C) mean yearly growth rate ($\ln \text{mm}$), and (D) mean cone count ($\ln(\text{cones} + 1)$) when accounting for other predictors in the model provided in Table 2.1 ($N=18$). Middle line represents line of fit, with a solid line indicating a significant effect, and thin outer red lines represent 95% confidence intervals.

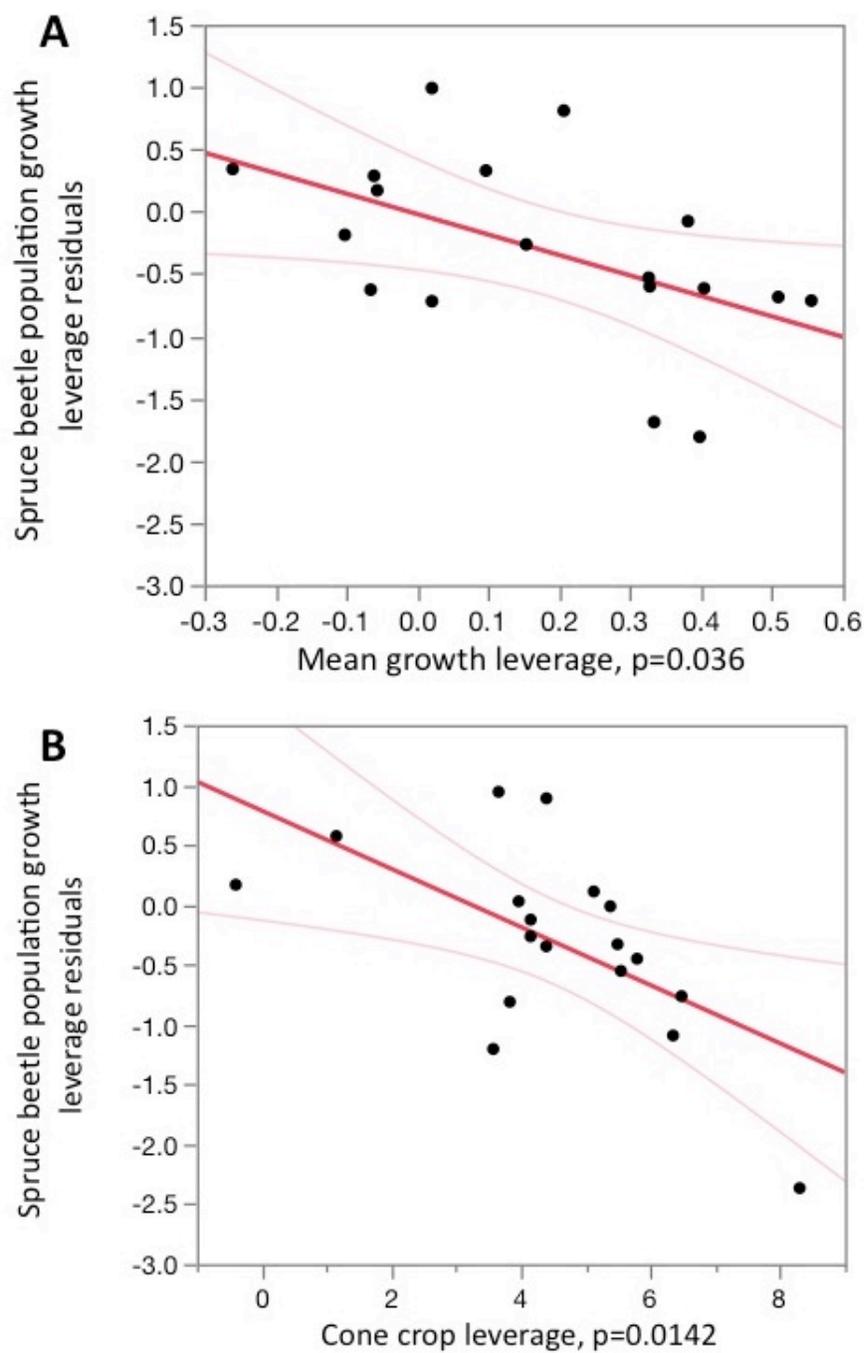


Figure 2.6. Effect leverage plots showing the relationship between spruce beetle population growth and (A) mean growth (\ln mm) and (B) cone crop ($\ln N + 1$), when accounting for other predictors in the model provided in Table 2.2 ($N=18$). Thick red line represents line of fit, and thin red lines represent 95% confidence intervals.

Table 2.1: Standard least squares model for the population growth rate of spruce beetle (*Dendroctonus rufipennis*) ($\ln(N_t/N_{t-1})$) in white spruce (*Picea glauca*) in Kluane, Yukon. $R^2 = 0.45$, $N = 18$ years. Bolded text indicates significant effects ($p < 0.05$).

Predictor variable	Response variable				
	Rate of Attack Increase				
	Estimate	SE	<i>df</i>	<i>F</i>	<i>p</i>
Annual growth (ln mm)	-1.576	0.77	1,13	4.22	0.0607
Annual cone count (ln N+1)	-0.241	0.09	1,13	7.25	0.0184
May-Aug temperature (ln°C)	2.15	1.91	1,13	1.27	0.281
Nov-Mar temperature (ln°C)	-0.063	0.2	1,13	0.1	0.7593

Table 2.2: Standard least squares model for the population growth rate of spruce beetle (*Dendroctonus rufipennis*) ($\ln(N_t/N_{t-1})$) in white spruce (*Picea glauca*) in Kluane, Yukon. $R^2 = 0.45$, $N = 18$ years. Bolded text indicates significant effects ($p < 0.05$).

Predictor variable	Response variable				
	Rate of Attack Increase				
	Estimate	SE	<i>df</i>	<i>F</i>	<i>p</i>
Annual growth (ln mm)	-1.644	0.71	1,13	5.35	0.0364
Average cone count (ln N+1)	-0.243	0.09	1,13	7.83	0.0142
May-Aug temperature (ln°C)	2.174	1.85	1,13	1.38	0.2589

Table 2.3: Standard least squares model, including the effect of the previous year's cone crop, for rate of spruce beetle (*Dendroctonus rufipennis*) population growth ($\ln(N_t/N_{t-1})$) in white spruce (*Picea glauca*) located in Kluane, Yukon. $R^2 = 0.14$, $N = 18$ years.

Predictor variable	Response variable				
	Rate of Attack Increase				
	Estimate	SE	<i>df</i>	<i>F</i>	<i>p</i>
Annual growth (ln mm)	-1.02	0.92	1,13	1.24	0.286
Previous year cone count (ln N+1)	0.049	0.13	1,13	0.14	0.712
May-Aug temperature (ln°C)	1.771	2.48	1,13	0.51	0.489
Nov-Mar temperature (ln°C)	-0.078	0.25	1,13	0.1	0.759

2.4 Discussion

2.4.1 General trends

Population-level investment by spruce trees towards both growth and reproduction significantly predicted the rate of spruce beetle population growth between years when examined alongside mean summer temperature. Contrary to my prediction, however, the rate of spruce beetle population growth was higher in years that had slower growth rates and fewer cones produced. In other words, years where there was a significantly higher overall investment in both growth and reproduction at the population level had a slower rate of spruce beetle outbreak progression. This finding does not support the initial hypothesis regarding resource allocation patterns, which was that there would be an observed trade-off between growth and reproduction. May-August temperature, predicted to result in an increase in beetle attack rate with increasing temperature, also had no detectable effect. When examining the effect of winter (November-March) temperature, with warmer winters predicted to result in lower over-winter mortality and increased beetle attack rate, this too was found to have no detectable effect. Finally, when spruce beetle population growth was examined with respect to the production of cones in the previous year, no significant effect was observed.

2.4.2 Effect of climate

Summer temperature had no detectable effect on spruce beetle population growth. It is unlikely that this lack of effect was due to unusually low variation in summer temperature because within the study period the minimum and maximum summer temperatures were as great as observed in the previous 50 years (data not shown). May-August temperature was chosen as the climatic variable of interest for a number of reasons. This period encompasses the key life cycle stage of spruce beetle development when temperatures have been shown to dictate whether

broods will develop at a normal (2-year cycle) or enhanced (yearly) rate (Werner and Holsten 1985, Barber et al. 2000, Berg et al. 2006). Given that the majority of yearly wood deposition in Kluane also occurs within this time frame, mean summer temperature has an additionally important effect on the system (Berg and Henry 2003). Because warmer summer temperatures are generally thought to be priming areas for bark beetle outbreak in two major ways, it is important to consider both mechanisms separately.

On the bark beetle side of the climate interaction, I predicted that increases in summer temperatures would increase beetle success. Shorter spruce beetle development time, and an increase in beetle presence and performance, was predicted to subsequently result in an increased infestation pressure and a higher level of tree mortality (Werner & Holsten 1985). It may be that the summer temperatures observed in my study, although relatively variable, were not sufficient to cause switches from a 2-year to a 1-year life cycle. A normal two-year life cycle in Alaska is characterized by an average phloem temperature of 10.6°C during the summer months while one-year cycles typically develop in trees that experience a phloem temperature of at least 16.5°C (Werner and Holsten 1985). With a maximum mean exterior temperature of 12.15°C observed in my study, no change in voltinism would be expected. Although the demonstrated threshold of 16.5°C has been corroborated and is generally accepted to be required for transitioning between life cycles, the duration this temperature must be maintained before seeing a change is still unknown (Berg 2006).

I predicted that increases in winter temperature would result in a lower rate of spruce beetle overwinter mortality, also resulting in an increase in beetle population density and subsequently an increased infestation pressure. Although mean winter temperature was not found to be a significant predictor of spruce beetle population growth in the current study, this could be

because the mean winter temperature experienced at the study site was not low enough to cause significant overwintering mortality. This would result in a higher-level of dependency on summer temperature in the determination of spruce beetle population density for the region. Because spruce beetles accumulate glycerol and other cryoprotectants prior to the onset of winter, they are able to drastically lower their supercooling points allowing survival of overwintering larvae and adults (Miller and Werner 1987). In the past, temperatures below -31°C were found to result in the lethal freezing of beetles that were overwintering at or above the snowline (Miller and Werner 1987), suggesting that beetles in cold climates where little snowfall is observed are most susceptible. In Kluane, nearly 50% of the total yearly precipitation falls as snow in the winter months (Krebs and Boonstra 2001), and the mean winter temperatures observed throughout the current 18-year study period ranged from -9 to just above -20°C . These patterns could explain why, in the current study, winter temperature was not a significant predictor for spruce beetle population growth.

I expected that summer temperatures would also affect spruce beetles indirectly through their effects on host tree traits. It has previously been demonstrated that an increase in summer temperatures, within the range observed in my study, results in an increase in the growth of white spruce in the southwestern Yukon (Boonstra et al. 2008, Krebs et al. 2017). This pattern could be associated with decreased defences, if the trade-off between growth and defence was a dominant process, or an increase in defence if it reflects an increase in total resources and an increase in defence in absolute terms. However, in contrast to the previous studies, I observed no relationship between mean summer temperature (May-August) and overall yearly growth rate (Figure 2.3). Different climate variables can be examined in the future to determine which, if any, are found to correlate with average growth rate, but it would be useful to have site-specific

weather data to see if predictions and observations could be improved with more accurate on-site temperature information. If higher growth rates are indeed correlated to increased summer temperatures, it is also possible that rather than a trade-off between growth and defense, having these vary together could also be predicted. Trees that have greater access to total resources may be able to invest heavily in both growth and defense, making the predicted trade-off between them less evident. This would suggest that years with high growth rates may also be predicted to have high investment in defense, leading to lower rates of expected spruce beetle population growth in those years.

Although weather and climate are generally considered to be important drivers of insect outbreaks (Bentz et al. 2010, Raffa et al. 2008), the specific variables that could be explored are seemingly limitless. Given that only May-August and November-March temperature was examined here, future studies should consider including additional variables that have been shown to be significant such as rainfall, and the effect of lag on these relationships (Chavardes et al. 2013). An alternative to consider is that drought stress itself, proposed as the mechanism for weakening host trees and increasing their susceptibility to spruce beetle attack, may not be well indicated solely with increasing temperatures or decreased rainfall. Many drought indices involve both a temperature and precipitation component: a commonly used one was developed by normalizing mean May-August temperatures and total October-September precipitation, and subtracting the two to provide a relative drought term (Berg and Henry 2003). Alternatively, to examine the regional relationship between forest distribution and moisture gradients the Climate Moisture Index (CMI) could be used, examining mean annual precipitation and mean annual potential evapotranspiration (Hogg 1994, Hogg and Schwarz 1997). I did not analyze rainfall in

my analyses in order to limit the number of climate variables that were included, given the limited time series.

Obtaining $^{13}\text{C}/^{12}\text{C}$ stable isotope ratios from tree rings is also an alternative method of more easily studying the effect of drought stress on white spruce, and in turn could be used to indirectly provide information on how spruce beetle infestation is affected by drought-stressed trees (Barber et al. 2000, Dawson et al. 2002). This method of analysis was outside of the scope of the present study, but could be included in future analyses in order to more confidently assess the level of drought-stress experienced by an individual tree, or the average level of drought-stress experienced across an area.

2.4.3 Allocation to defense

In my study, growth and reproduction were not negatively correlated at the population level (Figure 2.4A). Spruce beetle population growth was significantly slower in years in which spruce had more cones, and higher average growth rates (Figure 2.6, Table 2.2). Similar patterns have been observed in the past with respect to growth rate in spruce (Hard 1985, 1987), however, the pattern observed with reproduction is novel to the best of my knowledge.

Given the assumed negative relationship between spruce-tree mortality and defense, these findings would suggest that that in certain years, under the right conditions, allocation towards growth, reproduction, and defense may increase together. One possibility to consider, as mentioned above, is that in those years where high growth rates, cone output and increased investment towards defense were observed, the total level of carbon available to individual spruce was enough so that the trade-offs occurring between these allocation choices could not be observed.

Examining spruce beetle population growth and attempting to draw conclusions about the overall defensive level of the population of white spruce may be problematic. At high population densities of beetles such as those that occur during an outbreak, the beetles' likelihood of a successful attack is increased whether or not the host tree is well defended. It is therefore possible that they are more likely to attack trees with greater defenses during outbreaks due to the ease in locating these hosts, in addition to the lowered risk of attack failure (Raffa et al. 2015). There is empirical evidence to support the idea of plastic behavioural strategies exhibited by bark beetles following either endemic or outbreak regimes (Elkin and Reid 2010, Kausrud et al. 2011, Kausrud et al. 2012). Tree mortality may not be directly linked to defensive capability once outbreak conditions are met (Boone et al. 2011), and if this relationship does not hold then its use in the present study as a representation of defense can be called into question. If the spruce beetle population dynamics were varying independently of tree traits in the southwest Yukon during the outbreak in question, the predicted relationships used in the current study would no longer be expected.

Spruce defense is based heavily on an induced response at the time of the attack rather than on a constitutive level of defenses present (Lewinsohn et al. 1991). Because this means that most of the time individuals will not be investing heavily in defense, this may allow spruce to skirt the trade-off with growth and cones even if the carbon required for defense is obtained from the current year's photosynthate. Carbon that is taken in can be allocated to growth and cones most of the summer, and switched to defense when needed. Stored resources may be required to support plant survival and tissue regeneration following insect attack, and because of this are sometimes considered part of the integrated defense system (Wyka et al. 2016). However, few studies have examined the relationship between plant storage and defense (de Jong and van der

Meijden 2000). If the carbon needed to produce an induced defense is obtained from stored reserves, a negative relationship with growth (which relies primarily on current photoassimilates) would not necessarily be expected.

2.4.4 Allocation to storage

Given that there was no trade-off observed between average yearly growth rate and the average number of cones produced in the population, it is possible that in the case of white spruce, previously stored reserves are used more heavily than the current years photoassimilates. Although growth, reproduction, and defense are all major plant functions that require a high investment of resources, incoming photoassimilates can also be diverted towards storage. Non-structural carbohydrates (NSC) are involved in both the primary and secondary metabolism of tissues, and storage reserves are formed via their metabolically-regulated compartmentalization (Chapin et al. 1990, Hartmann and Trumbore 2016). Reserves are usually stored in isolation from other metabolic pathways to reduce reserve degradation, and storage is primarily found in vacuoles and plastids for that reason (Chapin et al. 1990). While being formed initially, these reserves would directly compete with resources required for growth and defense, resulting in an additional area of resource allocation not considered in the present study. Virtually all plants invest in some degree of savings and the extent to which individuals are able to draw from those reserves when required will vary (Chapin et al. 1990). There is some evidence to suggest that stores are not always available to individuals (reviewed in Chapin et al. 1990). Even still, despite a century of research into NSC reserves, our understanding of resource redistribution to and from storage within plants is severely limited, and it is difficult to accurately include allocation to storage in current models (Dietze et al. 2014, Fatichi et al. 2014, Hartmann and Trumbore 2016). The allocation of resources towards storage is central to both individual plant function as well as

stand-level carbon cycling (Hartmann and Trumbore 2016), and it is therefore reasonable to suspect it plays a significant role in how resources are allocated in the present system.

The evidence surrounding the degree to which plants rely on storage reserves for functions such as growth and reproduction is mixed, with some studies suggesting that in mast-cropping conifers such as white spruce, marked declines in growth and storage reserves are seen following reproduction (Koenig and Knops 2000). The direct evidence for this reserve depletion is lacking however. In ponderosa pine (*Pinus ponderosa*), no correlation could be established between wood deposition of individual trees and their reproductive vigour (Daubenmire 1960), indicating that individuals could potentially be relying on storage reserves to assist with reproduction. Similarly, in fragrant snowbell (*Styrax obassia*), the overall cost of reproduction was reliant predominantly on storage reserves in reproductive shoots (Miyazaki et al. 2002).

Some studies show that seed production in a given year is entirely reliant upon the current year's photoassimilates (Hoch et al. 2013), showing that the width of annual growth rings were only depressed in the years where high cone production was observed (Eis et al. 1965). This indicates that carbohydrates involved in cone development were likely supplied by the current year's photosynthesis rather than stored reserves, and would suggest that if these same trends could be extended to white spruce, the predicted trade-offs between growth, reproduction, and defense used here would be expected. Trends between allocation to growth and reproduction may not be observable at the population level, and individual-tree analyses may be required to elucidate the relationship between growth and cones in a given year.

2.4.5 Resource currencies

It has been suggested that the difficulty in applying the concept of resource allocation to reproduction and in observing the trade-offs between reproduction and other functions such as

growth and defense is attributable to two main causes (Reekie and Bazzaz 1987b). Firstly, it is difficult to identify the limiting resource in an area (whether it be carbon, nitrogen, phosphorus, etc.), and secondly it is unlikely that the same resources will be limiting growth in different environments, making comparisons between the reproductive effort of plants in different environments additionally complicated (Reekie and Bazzaz 1987b).

Carbon has been suggested as a valid currency for evaluating resource-allocation patterns, as was done in this study, due to its overall importance to plants and tendency to integrate the allocation patterns of other resources (Reekie and Bazzaz 1987b). Having said that, simple estimates of reproductive effort based only on biomass allocation to flower and/or fruiting structures have been suggested to poorly reflect total carbon allocation to reproduction (Reekie and Bazzaz 1987b). This signifies that a larger piece of the allocation pattern may be missing in the current study due to its reliance on the number of produced cones as a measure of reproductive allocation. Compared to carbon, nitrogen or phosphorus has also been suggested to be more appropriate when examining investment towards cone production, as they are often limited in environments, and plant reproductive structures are usually more nutrient-enriched than other biomass (Reekie and Bazzaz 1987a, b, Hemborg and Karlsson 1998, Sala et al. 2012). Future studies should investigate allocation of these key nutrients in addition to simply the allocation of carbon.

2.4.6 Conclusions

I set out to determine how yearly variation in stand-level investment towards growth, reproduction, and defense in white spruce affected the success of spruce beetles in Kluane, Yukon. Spruce beetle population growth was greater in years with slower tree growth and fewer cones produced. These patterns are inconsistent with the hypothesis that tree allocation to growth

and reproduction compromises investment in defences in absolute terms. Similarly, there was no negative correlation between growth and reproduction at the population scale. Years with slower growth and fewer cones may also correspond to years with fewer tree defenses being formed; direct measurements of defence are required to test this hypothesis. Summer temperature had no effect on the overall rate of spruce beetle outbreak progression in the region, and neither did winter temperature, indicating that either climate was not an important process explaining population growth in this outbreak, or other potential climate variables should be investigated. It remains to be seen whether the preliminary relationships seen here can be expected in other spruce beetle-host systems, and I suggest that allocation be examined at the individual tree level to provide a deeper understanding of how these choices affect survival.

Chapter Three: **Effects of resource allocation in individual spruce trees on spruce beetle attack and tree mortality in southwestern Yukon, Canada**

3.1 Introduction

The concept of partitioning limited resources that are allocated towards various life history traits such as growth, defense and reproduction is fundamental across a number of broad disciplines in ecology. Given that the amount of time, energy, and/or specific resources available to an individual is limited, an increase in allocation towards one function (such as growth) must necessarily result in a decrease in the level of resource that is available to other functions (such as defense and reproduction). This is known as the ‘Principle of Allocation’ (Levins 1968), and its theory has been applied to studies ranging from the explanation of clutch size in birds, theoretical studies of life history evolution, to physiological and biochemical studies of diversification in plant defenses (Cody 1966, Levins 1968, Bazzaz et al. 1987, Lloyd 1988, Obeso 2002). The compromises that are made between allocation investments are referred to as ‘trade-offs’, and can be thought of as costs that are incurred by varying degrees of investment towards different life history traits (Reznick 1985). Trade-offs may not be observed, however, due to differences in total resources available. Positive correlations can be seen when trade-offs are expected if certain individuals are simply able to allocate more in absolute terms because they have access to more resources (van Noordwijk and de Jong 1986).

Growth is a fundamental process to all organisms, and in plants it is tightly linked to resource acquisition. The processes associated with plant growth are resource demanding and have precise requirements for a number of factors such as light, photoassimilates, water, nutrient and mineral levels, and temperature (Herms and Mattson 1992). When conditions for growth are met, an individual is expected to invest in growth to develop and remain competitive. The level

of investment towards growth, however, will in turn affect the level of plant resources available for other functions, such as defense.

A number of hypotheses regarding carbon allocation to defense have been proposed since the initial interest and early description of this phenomenon (Green and Ryan 1972, McKey 1974, Haukioja and Hakala 1975, Bryant et al. 1983, Coley et al. 1985, Herms and Mattson 1992). One hypothesis that has gained considerable attention is the growth-differentiation-balance hypothesis (GDBH), which proposes that plants are faced with a dilemma with respect to their allocation to growth and defense, given that at the mechanistic level the processes of growth (primary metabolism) and defense (secondary metabolism) are separate and competing (Herms and Mattson 1992). Other hypotheses such as the carbon-nutrient balance theory (C/N) and protein competition model (PCM) are also related primarily to resource availability and associated allocation trade-offs (Bryant et al. 1983, Coley et al. 1985, Jones and Hartley 1999). Many species of plants require similar resources for growth, defense, and reproduction, but vary in how they use these resources (Bazzaz et al. 1987, Chapin et al. 1990). Resources such as carbon (C), nitrogen (N), and phosphorus (P), are obtained from the environment and used by the plant. Often these resources are involved in manufacturing various plant structures, such as those required for defense against herbivores (Bazzaz 1997). Different processes are not equally needy with respect to these nutrients, however. Defenses are often primarily carbon-based, while growth is more dependent on water, light, and nutrients. According to the GDBH, this explains why under very stressful conditions plants may grow slowly and have excess carbon available for defense due to the limitation of other nutrients on growth (Herms and Mattson 1992).

Plant defensive strategies are often multi-tiered and involve both a constitutive and induced component (Karban and Baldwin 1997). Constitutive defenses are produced and

available well in advance of an actual threat, and therefore provide a base level of defense that is immediately available upon attack. Inducible defenses, on the other hand, are only formed in response to actual invaders and can be quite pronounced. This has important implications for observing the predicted trade-off between growth and defense, as plants with a reliance on induced defense will have only a low level of investment towards constitutive defense formation in most years.

Plants with episodic and large investment in reproduction can provide insights into trade-offs with growth and defense. ‘Mast-fruiting’ or ‘masting’ are both terms that refer to the synchronized, intermittently high level of reproduction among individuals of a species (Kelly and Sork 2002, Pearse et al. 2016). Ultimate-level hypotheses for masting have to invoke some economy of scale, and a number of hypotheses such as predator satiation and pollination efficiency have been suggested (Koenig and Knops 2005). Evidence for trade-offs observed between reproduction and growth is varied, however many studies have demonstrated a marked decline in growth following reproduction, and growth rings that were significantly depressed in mast years (Eis et al. 1965, Koenig and Knops 2000, Hoch et al. 2013, Krebs et al. 2017). Direct evidence for a trade-off between reproduction and defense is lacking however, with few (if any) studies that have examined this question directly.

In conifers, growth, defense, and reproduction are relatively easy to measure. Growth can be measured directly from annual growth rings, and defenses can also be examined retrospectively within those rings. The defensive system is primarily composed of carbon-based defenses such as terpenes and terpenoids, with a high concentration of viscous resin that can also serve as a physical defense (Franceschi et al. 2005, Seybold et al. 2006). Inducible defenses include necrotic wound lesioning and the formation of a large number of induced resin ducts and

increased resin flow (Bannan 1936, Christiansen et al. 1987, Christiansen et al. 1999). Resin ducts are visible in growth rings, with many ducts observed in years where an induced defensive response was triggered.

The level of investment that is put towards both constitutive and induced defense varies across genera and species, with spruce trees (*Picea* spp.) most likely to invest more heavily in induced defensive responses than other genera, for example pine (*Pinus* spp.), that rely more heavily on a strong constitutive level of defense (Lewinsohn et al. 1991). As such, when incoming herbivores and/or insect invaders are attacking spruce trees, it is reasonable to expect a significantly higher level of an individual tree's resources being allocated towards defense than might otherwise be expected. Given that the energy and resources required for a strong induced response have to be available and mobilized, the trade-offs with growth and reproduction are expected to be much more apparent in these years.

Spruce are also masting tree species (LaMontagne and Boutin 2007). Trade-offs between investment towards defense, reproduction, and vegetative growth should be most apparent during these years. This genus provides an excellent opportunity to examine the effects of masting-caused alterations of carbon availability on plant defense, as well as the effects of high investment towards an inducible, carbon-based, defense response following the introduction or ongoing presence of an attacker in the system.

Bark beetles (Curculionidae: Scolytinae) are considered to be one of the most destructive forest pests, and are of increasing concern globally (Bentz et al. 2010). They attack host trees that are often weakened by other factors such as disease and drought (Bright 1976, Lindgren and Raffa 2013), with some species capable of mass attacking otherwise healthy trees to overcome the host tree's defenses and successfully colonize and reproduce (de Jong and Saarenmaa 1985).

One particularly destructive species of bark beetle, the spruce beetle (*Dendroctonus rufipennis*), occurs across Canada and is well known for a major outbreak that occurred in the southwest Yukon region. Mainly attacking white spruce (*Picea glauca* [Moench]), these beetles severely impacted the white spruce populations along and within Kluane National Park, killing trees over 380,000 ha by 2007 and upwards of 400,000 ha in total by the outbreak's end (Yukon Government 2010, 2013).

My research aimed to test the hypothesis that if carbon allocation towards defense is a limiting factor in tree survival, then tree survival status will also depend on both annual tree growth and reproductive output. Although inducible defenses and the associated carbon/nutrient trade-offs have been well studied in some respects, much remains unknown and the support for the growth-differentiation balance hypothesis is limited (Karban 2011). The study system described above is ideal not only for examining the relationship between growth and defense in conifers, where inducible defenses such as traumatic xylem resin ducts are easy to detect, but also for investigating masting-caused alterations to carbon allocation in spruce. In this chapter, I examine the relationships between host-tree allocation of resources and survival against bark-beetle attack in the Yukon at the individual tree level.

Trade-offs between growth, reproduction, and defense are predicted to be apparent depending on whether or not total carbon availability surpasses and overrides the trade-off that must be present, and spruce beetle success is predicted to depend on the level of tree investment towards these functions. If there is an observed negative relationship between growth and defense, or growth and the number of cones produced, this would serve as evidence for the trade-off that must be present. It is possible, however, that a positive relationship could be observed, indicating that faster growing trees are also able to invest more towards defence. Positive

correlations between growth and resin ducts have been observed frequently (Bannan 1936, Kane and Kolb 2010, Gaylord et al. 2013, Ferrenberg et al. 2014, Hood et al. 2015). This positive relationship could be due to larger or faster growing trees having improved access to resources, resulting in an ability to invest more towards defense and/or reproduction in absolute terms. Trees with improved access to more resources could be observed to be faster growing with more defenses and a higher reproductive output, as conditions that are favourable for growth may also be favourable for secondary metabolism of tissues. I examine, how these allocation patterns relate to the overall likelihood of an individual tree being (1) attacked and (2) killed by spruce beetles, in addition to the effect that tree diameter has on these likelihoods.

3.2 Methods

3.2.1 Study area

The 60-hectare study area was chosen in part based on its extensive previous use in red squirrel (*Tamiasciurus hudsonicus*) research and monitoring, and is located approximately midway between the Kluane Lake Research Station (on the south shore of Kluane Lake), and the village of Haines Junction, Yukon (660380 E 6761091 N, UTM Zone 7N; Figure 3.1). The overall study area was initially chosen due to its location within a much larger area of known spruce beetle outbreak across the southwest Yukon (Garbutt et al. 2006, Yukon Government 2010). Other than a much smaller outbreak in the area from 1934 to 1942, no previous major outbreaks are thought to have occurred in the region, making the large, destructive outbreak that began in the early 1990s and ended in 2007 unprecedented (Berg and Henry 2003). The Kluane region has been particularly well studied, with the current study area having been used previously as a control site for the large-scale Kluane Ecosystem Dynamics Project (Krebs and Boonstra 2001).

The study area is bisected into two 30-hectare plots on either side of the roadway that runs parallel with the Alaska Highway; these plots were named Sulphur (SU) and Kloo (KL) by previous researchers (Figure 3.2A). Both sites have an established ground-based grid system for demarcating location within the sites. Grid stakes were located every 30m and indicate the distance traveled along the transects, in addition to the stakes' location within the larger grid (Figure 3.2B). Sites share many of the same geographic features and likely experience many of the same conditions due to their proximity to one another. The dominant tree species in the area, and only conifer present in the region, is white spruce. Other tree species such as trembling aspen (*Populus tremuloides*), and deciduous shrubs such as willow (*Salix* spp.) were also observed. However, both sites were primarily composed of open-canopy white spruce (Krebs and Boonstra 2001). Sulphur, in particular, is composed of 34.37% open spruce, 18.87% closed spruce, 21.00% willow shrub, 2.16% poplar- aspen, 22.96% grass-open, and 0.64% water (Krebs and Boonstra 2001). This detailed breakdown of vegetation type was not available for Kloo, however both sites appeared to be similar in the vegetation that was observed. Additionally, there is no recorded fire history in either site for >100 years (Krebs and Boonstra 2001).

3.2.2 Spruce beetle attack

My study used pre-existing data on spruce beetle attacks and cone crops collected by Jalene LaMontagne (De Paul University, Chicago, IL). The dataset provided information on 1360 individually labeled (Figure 3.2C) and grid-located white spruce trees that were examined yearly from 2001-2005 with respect to bark beetle status. This was done to monitor infestation status through time and mortality rates of white spruce. Peak spruce mortality during the outbreak occurred in 2003, approximately 10 years after initial beetle presence in the area was

detected (Hawkes et al. 2014). In addition to the beetle monitoring data, individual cone crops were quantified for a subset of these trees in either 2002 or 2003.

Each year between 2002 and 2005, trees were classified as either “OK- not attacked”, “pGA- partial green attack”, “GA- green attack”, “RA- red attack”, “NGD- new gray dead”, “GD- gray dead”, or “OD- old dead” based on the extent of damage observed and number of beetle entrance holes, sap flows, and needles present on the tree/fallen on the ground (LaMontagne 2007). The percentage of trees classified as either pGA or GA varied between years, with 9.4% of trees in 2002, 16.7% in 2003, 10.7% in 2004 and 56.7% in 2005. Prior to commencing fieldwork, I classified each tree as belonging to one of three categories: trees that were attacked by the spruce beetle and subsequently died, trees that were attacked by the spruce beetle and subsequently survived, and trees that were unattacked by the spruce beetle throughout the monitoring period. When classifying individual trees, caution was taken to limit the number of trees placed in the wrong category. For trees to have been classified as attacked and killed, the observation NGD, GD, or OD had to be present in the final year of monitoring data available. For an attacked tree to be classified as a survivor, the initial attack would have had to be listed as GA in one year, or pGA in multiple years, followed by the classification ‘OK’. Individuals that were pGA in one year and were listed as ‘OK’ in subsequent years were not initially considered for inclusion in the study, due to the possibility of error in the original partial attack observation. This meant that I designated only trees that were listed as either pGA in multiple years, or GA in at least one year as ‘attacked’. Finally, for trees to be considered unattacked, all of the observations throughout the monitoring period must have been listed as ‘OK’. Of the original 1360 trees monitored, I classified 149 as attacked and killed, 125 as attacked and survived, and

409 as unattacked. The remaining 677 trees, including those attacked in 2005, were unable to be classified prior to visiting the field and therefore I excluded them from use in the current study.

From each category, I selected 100 trees randomly for sampling, with the realized sample size expected to be smaller due to loss of trees or issues with processing in the intervening years. Anticipating the potential difficulty in locating the selected trees, I created an additional list of trees belonging to each category for reference as needed in the field.

3.2.3 Growth and defence

I determined tree growth and defence by collecting tree cores from the selected trees in July 2015. Individual trees were located using the grid reference system described above, and verified according to previous labeling (Figure 3.3C). When specific trees chosen prior to fieldwork could not be accurately identified after an extensive search of the area, they were replaced with one of the extra trees belonging to the appropriate category. Upon locating the tree of interest, I measured the tree's diameter at breast height (DBH, cm), and counted the number of neighbouring white spruce trees (alive and dead) within 3 m.

I took tree cores at approximately breast height when possible (1.4m), using increment borers of various bit lengths (9" or 12") depending on tree diameter. In some cases, location of large branches or the proximity to neighbouring trees necessitated sampling at slightly different heights. For small to medium-sized trees, I retrieved one single core going from bark through pith and back to bark, to provide two separate measurements for each year of growth and a representative sample of the tree's growth pattern. For larger trees where the increment borer could not travel from bark through to bark, I retrieved two separate cores. If cores were observed to have obvious initial problems (crumbling, scarring, etc.) this process was repeated until a suitable core was obtained. Once removed from the tree, these cores were placed directly from

the borer's extraction tray into a plastic straw that had been pre-cut along one side. Both ends were then sealed using masking tape, which was then labeled with the assigned Tree ID for transport.

Tree cores that were obtained each day were transferred out of the temporary straws and into drying trays at the Kluane Lake Research Station, where they were once again temporarily labeled and left for 24 h to air-dry. On the following evening, if the cores in each drying tray appeared to be dry, they were mounted onto individual cardboard strips using Elmer's "Glue-All" multi-purpose glue. Each core was glued to its own individual cut piece of cardboard, and the cardboard was labeled to indicate the Tree ID. I sanded tree cores by hand, using progressively finer grit sandpapers (60, 100, 400 and 600 grit), until such a time as clearly visible rings were observed and individual cells could be observed under a microscope.

Regardless of spruce beetle activity and the attack category of each tree, cores were all handled, prepared, and processed using the same standard dendrochronological techniques (Stokes and Smiley 1968). I measured ring widths using a sliding stage Velmex measuring system (Velmex Inc., Bloomfield, New York, USA), stereomicroscope, and Measure J2X software (VoorTech Consulting, Holderness, New Hampshire, USA). In addition to total ring width, earlywood and latewood measurements were also taken using the latewood boundary distinguished by cell colour and tracheid size, with latewood cells being smaller and darker in appearance (Figure 3.3). Within each annual growth ring, I also counted the total number of resin ducts present (Figure 3.3). I created skeleton plots and identified marker years to ensure accurate crossdating of tree rings across cores. For all tree cores obtained from an individual tree (usually two, sometimes three), I obtained correlation coefficients for all growth measurements, and I included only samples that had $r > 0.7$ in the analyses. Yearly ring widths and resin duct counts

were averaged across all cores collected for each tree to provide an average yearly growth rate (mm) and average yearly resin duct counts (number of resin ducts per 5mm transect (core) width).

Additionally, for each attacked tree I calculated the mean growth rate for the 5-year period leading up to bark beetle attack, and tallied the total number of resin ducts produced in that timeframe. These averages were obtained by initially calculating a yearly growth rate over the specified time period and then multiplying by 5-years. This was done to account for instances where data were not available for all of the years included in the 5-year period due to broken cores or indistinguishable rings. A 5-year increment was chosen for inclusion in analyses rather than the 10-year increment that I also calculated, as the 5-year growth increment has been shown to have best predicted trees attacked and killed by spruce beetles in the past (Hard et al. 1983, Hard 1985, Doak 2004, Berg et al. 2006). For unattacked (control) trees, I obtained 5-year averages using 2003 as the simulated attack year, due to the majority of bark beetle attacks across the study area occurring in that year.

3.2.4 Statistical Analysis

3.2.4.1 Relationships between tree traits

Relationships between tree traits (diameter, growth rate, resin duct and cone production) were examined with simple correlations, and through standard least square models including diameter as a covariate to determine if any relationships exist beyond those determined by size. Relationships were plotted using the reduced major axis (RMA) method for defining a line of best fit rather than the ordinary least squares (OLS) in order to account for error in both x- and y-variables, and because the biological relationships between the variables examined were not expected to be asymmetrical (traits could be examined on either the x- or y-axes) (Smith 2009).

3.2.4.2 Attack and survival modeling

Generalized linear models with a binomial distribution and logit link function were used to analyze attack (attacked vs. unattacked) status as a function of growth (mean 5-year growth rate, mm), defense (mean 5-year resin duct count), reproduction (number of cones produced in either the year of spruce beetle attack, or one-year prior), year, diameter, and site (KL vs. SU). Predictor variables were relatively consistent between models, and growth and defense measures, cone counts and diameter variables were all ln-transformed prior to analyses.

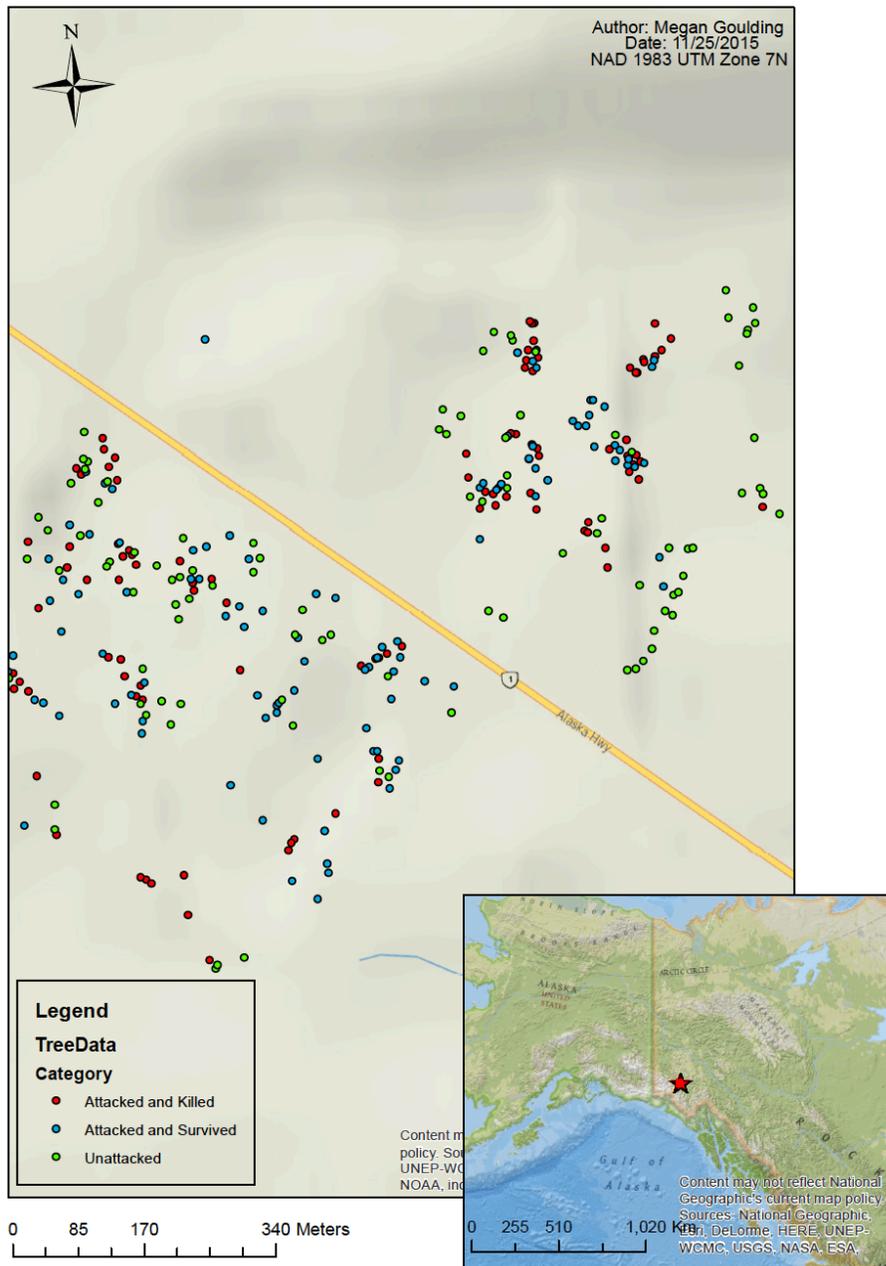
Survival status (lived vs. died) was used as a second categorical variable for analyses, with the independent variables once again consisting of a measure of growth, defense, cones, diameter, and site. For survival models, mean growth rate during the attack year (mm in t , where t is the year of spruce beetle attack) and the number of resin ducts produced in the attack year (resin duct count in t) were used as predictor variables rather than the 5-year increments due to their hypothesized higher importance to tree survival. Current year ducts were examined because of the strong induced defensive response of white spruce. Biologically relevant interaction terms between diameter and predictor variables were included in the modeling process, with non-significant terms removed from the final models.

3.2.4.3 Yearly-level cone production analysis

To assess the importance of the relationship between cone production and attack, separate generalized nominal logistic regressions were run to re-examine both attack and survival status of individual trees when cone year was either (i) equal to attack year (cone year = t), or (ii) one year prior to attack (cone year = $t - 1$). A one-year lag was chosen to determine whether cone production in one year more strongly affects the resources available to an individual the following year than those that are produced concurrently. Cones produced in $t - 1$

might affect tree vulnerability in t due to the potential for reserve depletion. Once again for these analyses, attack status and survival status were used as the categorical response variables, with independent predictor variables being site and ln-transformed measures of growth rate, investment in defense, cone production, and diameter.

All statistical analyses were conducted using JMP Version 13 software (SAS Institute Inc., Cary, NC).



Data Source: Researcher's own data collected

Figure 3.1: Map of the study area showing white spruce trees and their relationships to the spruce beetle outbreak (660380E 6761091N, UTM Zone 7). Map created using ArcMap version 10.3 (ESRI, Redlands, CA). Each point represents one individual tree sampled, with red dots indicating trees that were attacked and killed, blue dots being trees that were attacked and survived, and green dots being unattacked trees. Kloo site is located to the northeast of the Alaska Highway, and Sulphur site is located to the southwest. **Inset map shows the location of the study site as a red star.**

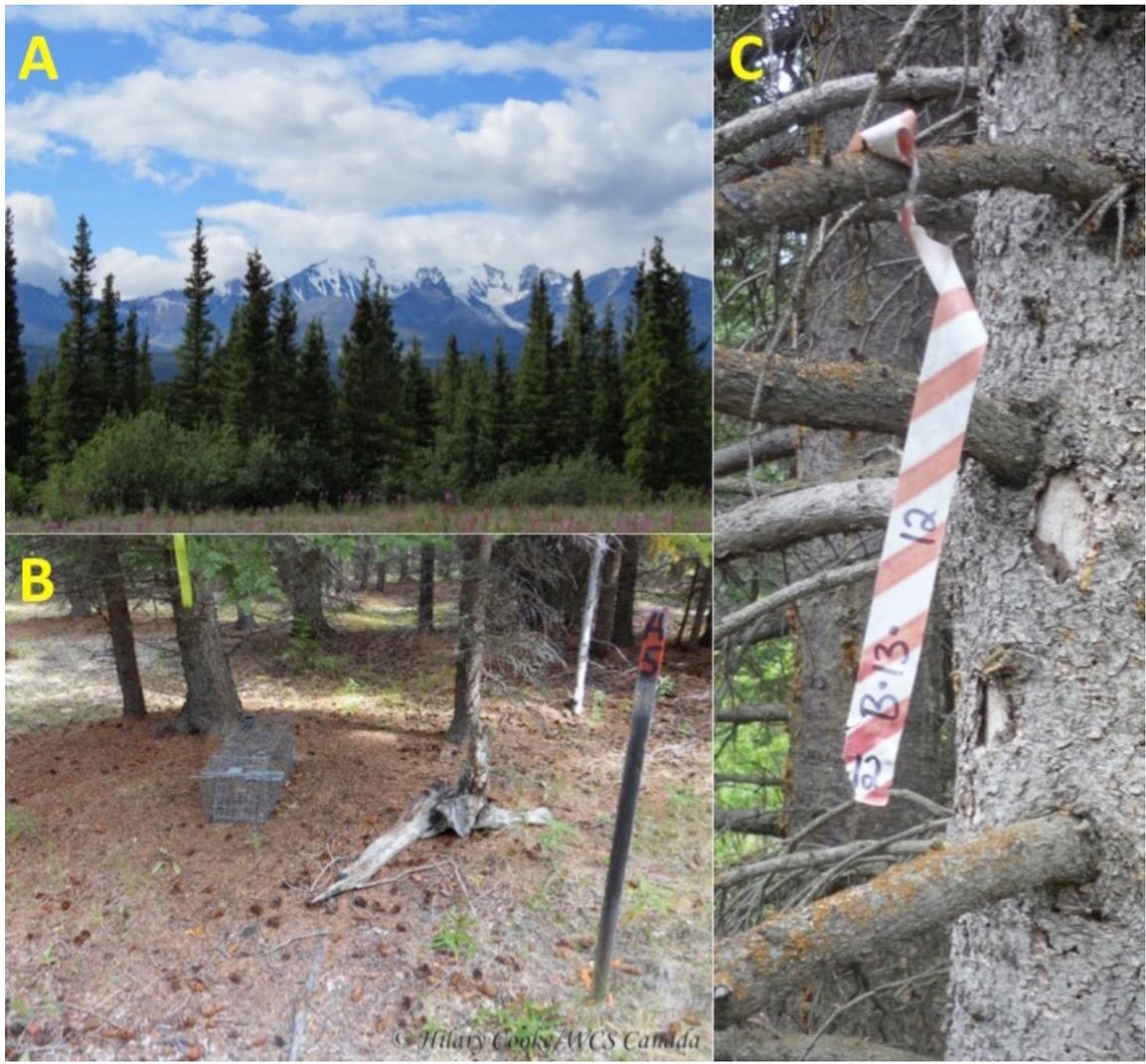


Figure 3.2: (A) Photo taken of Sulphur grid from the Alaska Highway. (B) Photo of a grid stake used in determining location within the study area. (C) Photo of previous labeling used to identify individual trees.



Figure 3.3: Cross-section of white spruce (*Picea glauca*) tree core. The core is positioned with the bark located to the left of the image, followed by a period of latewood (indicated by dark, smaller tracheids) and earlywood sections of the annual growth rings. This individual is showing a strong induced defense response in the 5th previous year shown, with the presence of numerous traumatic resin ducts.

3.3 Results

3.3.1 *Patterns of beetle activity*

Of the 300 trees selected for coring, a total of 293 were included in analyses, with the loss of several individuals due to issues with accurately identifying individual trees, damaged cores caused by problems with the wood and/or increment borer, mislabelling, or an inability to reconcile cross-dating issues. Of those 293 total trees, 196 individuals were attacked by spruce beetles between the years 2002 and 2005, and 97 individuals were unattacked throughout that period. The majority of spruce trees attacked by the spruce beetle in the study area during the monitoring period were found to have been initially attacked in 2002 and 2003, with 23.0% (N=45) and 60.7% (N=119) of total attacks respectively. After 2003, a sharp decline in the number of trees being attacked was observed in the trees chosen for use, with fewer individuals attacked across both sites in 2004 (13.8%, N=27), and only 2.6% of total beetle attacks observed in 2005 (N=5). Trees in both sites had both similar mean diameters and ages from core height (mean \pm SD: KL= 20.54 \pm 6.88 cm and 49.95 \pm 11.31 years, SU= 20.59 \pm 6.81 cm and 58.47 \pm 21.14 years). No significant correlation between age and diameter was observed ($r=0.2156$).

3.3.2 *Relationships between tree traits*

When examining the characteristics of all trees sampled, regardless of attack classification, a number of relationships were observed between individual tree traits (Figure 3.4). Larger diameter trees grew faster (Figure 3.5A, $r=0.4077$, $p<0.0001$), produced more ducts (Figure 3.5C, $r=0.2239$, $p<0.0001$), and had more cones (Figure 3.5B, $r=0.4407$, $p<0.0001$) relative to diameter. When accounting for diameter, faster growing trees produced fewer resin ducts in the 5-years prior to attack (Figure 3.4A, $r= -0.10$, $p=0.0467$) but not fewer cones (Figure 3.4C $r=0.2010$, $p=0.8438$). No significant relationship between cone and resin duct production

was observed when diameter was accounted for (Figure 3.4C, $r=0.0625$, $p=0.7728$). Of all trees, 61.09% had no ducts in the five year increment examined, with 49.24% of attacked trees having no ducts in the five years prior to attack by spruce beetles. Resin duct production over the 5-year period prior to attack had no significant effect on traumatic resin duct production in the attack year ($r=0.0428$, $p=0.5615$). In the year they were attacked, 37.54% of trees produced no cones.

3.3.3 Tree attack and mortality

White spruce trees were more likely to be attacked by spruce beetles when they were larger, grew more slowly, and had more ducts (Figure 3.6, Table 3.1). The number of cones that a tree produced in either the year before or the year of spruce beetle attack had no effect on the probability of being attacked (Figure 3.6, Table 3.1). Probability of attack did not differ among years or sites (Table 3.1).

Annual growth rate was the strongest predictor of the likelihood of white spruce tree mortality following attack (Table 3.1), with faster growing trees less likely to die (Figure 3.8). The number of resin ducts produced in the attack year was also a significant predictor variable, with a significant interaction between attack year resin ducts and tree diameter (Figure 3.7). Diameter was significant only when trees produced resin ducts, and was not significant on its own in the final model (Figure 3.8, Table 3.1). White spruce trees most likely to die following an attack by the spruce beetle were slower growing trees, relative to diameter, that produced fewer resin ducts (Figure 3.8). Similar to the results of the attack status model, the number of cones that an individual produced in a given year had no effect on the overall probability of an individual tree's mortality following spruce beetle attack (Table 3.1). The year that an individual was attacked also had no effect on probability of mortality, while trees attacked in KL grid were more likely to die following an attack than those in SU grid.

Comparing the results predicting attack with those predicting death, slower growing trees, once again relative to diameter, were more likely to be attacked and more likely to die. However, while tree size was a strong predictor of attack, it did not predict mortality well. Tree defences had opposing effects on tree vulnerability: trees with more resin ducts were more likely to be attacked but also more likely to survive the attack than trees with fewer ducts. Cone production had no effect on either attack status or tree mortality.

3.3.4 Effect of resource depletion

The following analyses set out to examine whether the significance of predictor variables for spruce beetle attack and survival change depending on whether the cone data during either the year of attack were used (cone year = t), or when a lag was present between the two (cone year = $t-1$). Rather than examining all trees and including cone year as a separate predictor, these analyses were run separately using only the subset of trees with cone data belonging to each of the above categories. No effect of the number of cones produced in the previous year on either attack status or tree mortality was observed in any of these analyses. For the attack status models, no changes were observed in the trends for other predictor variables; in all cases, attack likelihood was highest for large diameter, slow-growing trees with a higher number of constitutive resin ducts.

When examining tree mortality, the significant effect of the number of induced resin ducts seen in the original model is no longer observed when only examining a subset of the data (Tables 3.2, 3.3). The p-values obtained for this predictor variable lose significance as sample size decreases, indicating that the loss of significance may be a sample size issue for a weak effect.

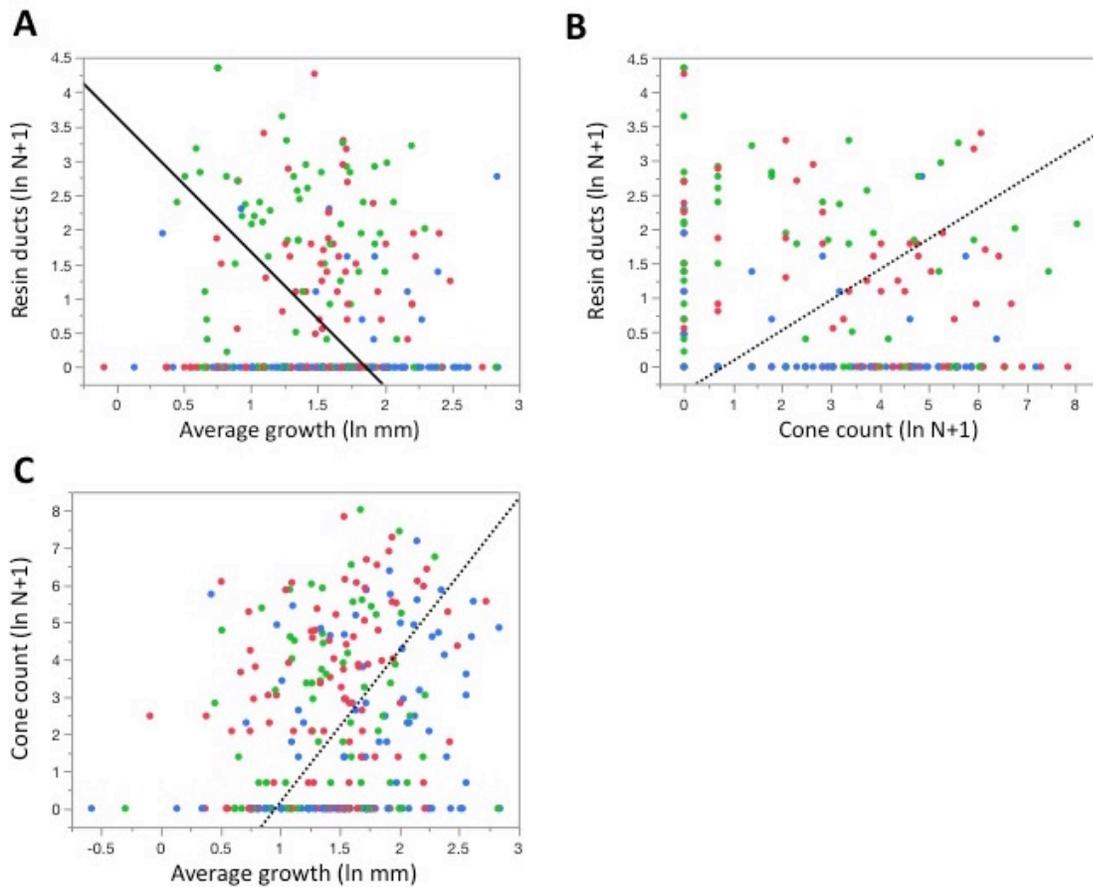


Figure 3.4. Relationships between predictor variables (A) Relationship between individual white spruce (*Picea glauca*) resin duct production and mean growth rate over a 5-year period prior to spruce beetle (*Dendroctonus rufipennis*) attack. Black line is orthogonal fit line, $r = -0.10$ ($N=297$). (B) Relationship between individual white spruce resin duct and cone production. Black line is orthogonal fit line, $r = 0.0625$ ($N=297$). (C) Relationship between individual white spruce growth rate and cone production. Black line is orthogonal fit line, $r = 0.2010$ ($N=297$). Dotted lines indicate non-significant effects.

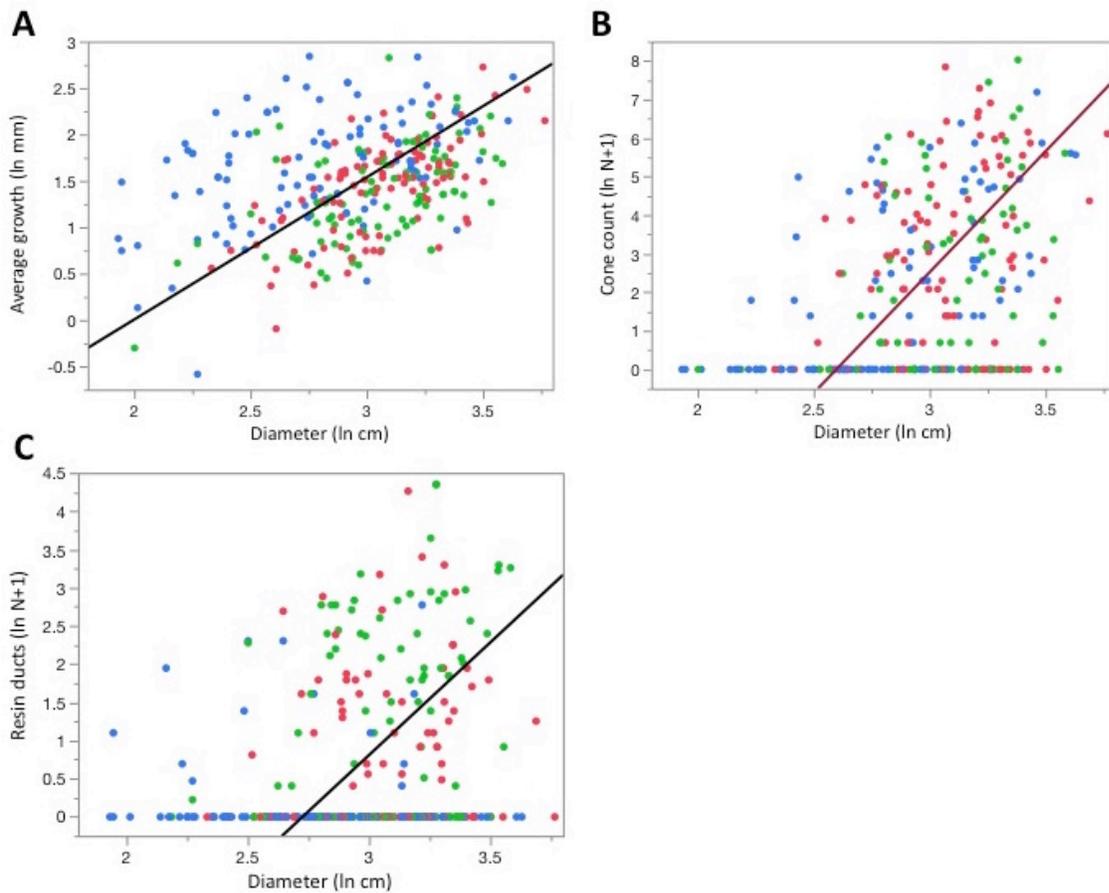


Figure 3.5: Relationship between individual white spruce (*Picea glauca*) tree diameter (ln cm) and other tree measurements. Each point represents one tree, with red dots representing trees that were attacked and killed by the spruce beetle (N=102), green dots representing trees that were attacked and survived (N=99), and blue dots representing trees that were unattacked (N=96). Solid lines represent significant effects. **(A) Relationship between mean growth rate over a 5-year period prior to spruce beetle attack and diameter (ln cm)** Black line is orthogonal fit line, $r=0.408$ (N=297). **(B) Relationship between yearly cone count and diameter.** Black line is orthogonal fit line, $r=0.441$ (N=273). **(C) Relationship between resin duct counts produced in 5-year interval prior to spruce beetle attack and diameter.** Black line is orthogonal fit line, $r=0.224$ (N=297).

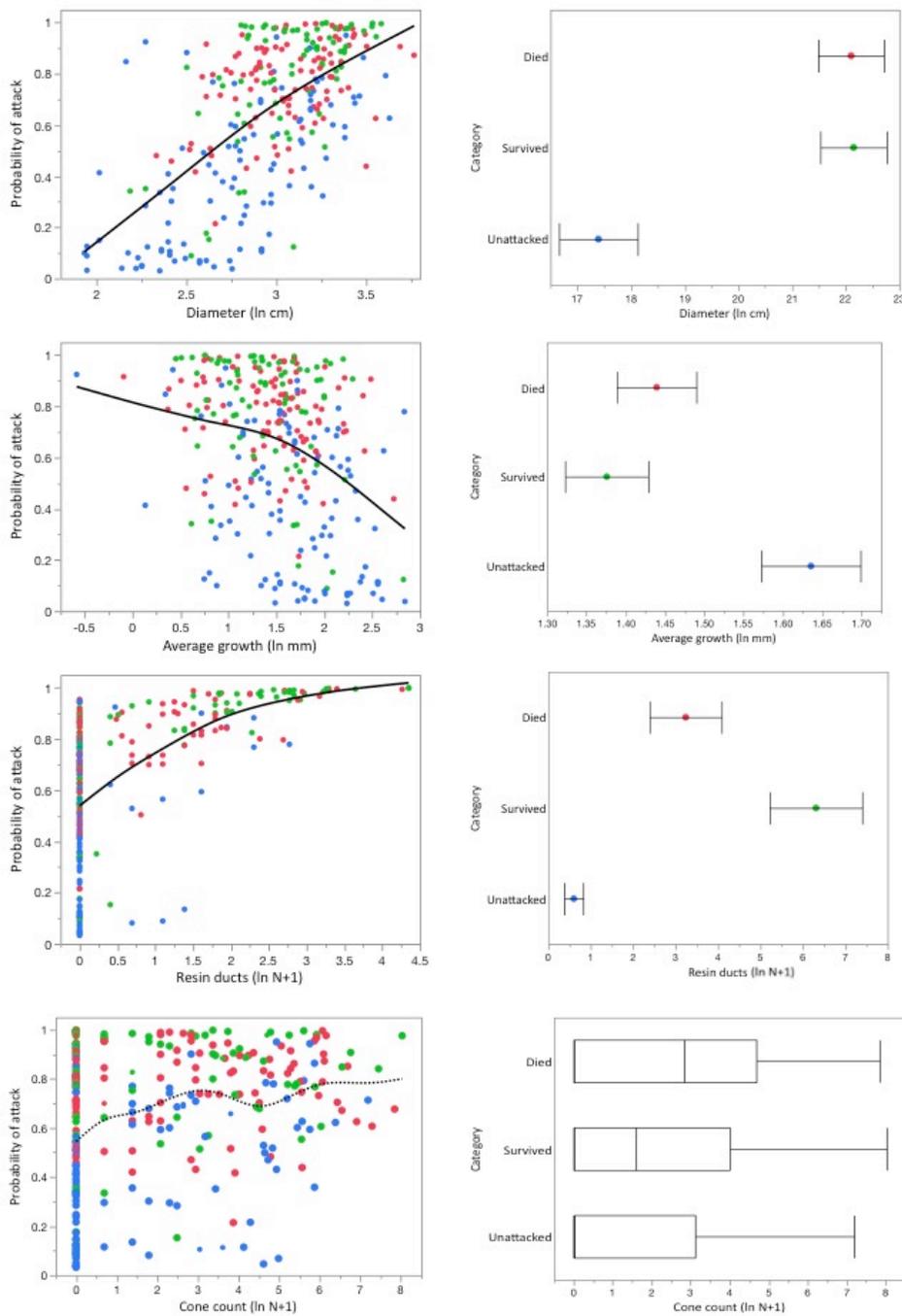


Figure 3.6: Relationship between white spruce (*Picea glauca*) tree diameter, growth rate, resin duct production, cone production and the predicted probability of being attacked by the spruce beetle (from logistic regression, see Table 3.1). Smooth fit lines, Lambda = 3, N=271. Means (+/- SE) for each category provided in panel B. Formatting conventions as per previous figures.

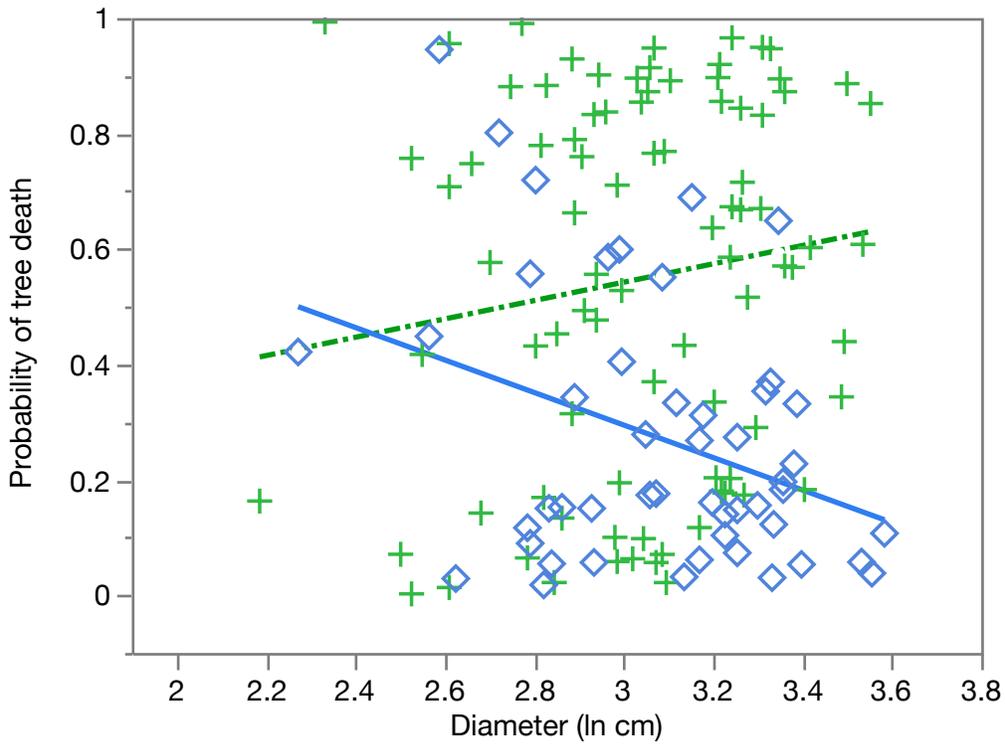


Figure 3.7. Interaction between tree diameter and duct production in white spruce (*Picea glauca*) when examining the probability of tree mortality. Green crosses indicate trees that produced no resin ducts in the year of spruce beetle attack, and blue diamonds represent trees that did produce resin ducts.

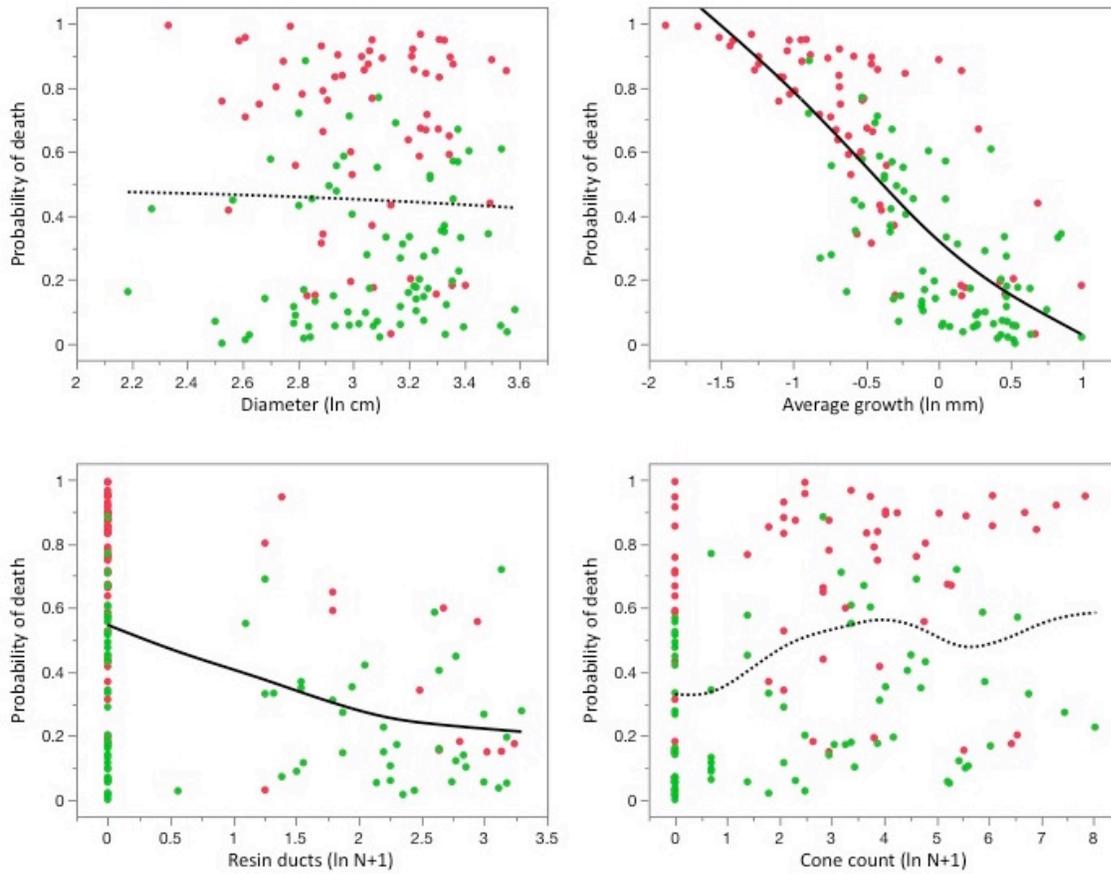


Figure 3.8: Relationship between individual white spruce (*Picea glauca*) tree diameter, growth rate, resin duct production, cone production and the predicted probability of mortality following attack by spruce beetles (from logistic regression, see Table 3.1). Duct production and growth were measured in the year of attack. Spline lambda = 3, N=136. Formatting and conventions as per previous figures.

Table 3.1: Nominal logistic regressions for likelihood of white spruce trees being (1) attacked by spruce beetles, and (2) killed by spruce beetles. Bolded text indicates a significant effect ($p < 0.05$) with italics used to distinguish negative effects. Predictor variables indicated with a * were different between regression models. For the attack status model, growth and resin duct parameters were examined over an increment of 5 years prior to beetle attack. For the mortality status model, growth and resin duct parameters were examined during the year of beetle attack only.

Predictor variable	Response variable			
	Attack Status		Mortality Status	
	χ^2	<i>p</i>	χ^2	<i>p</i>
Diameter (ln cm)	32.45	< 0.0001	3.3	0.0693
*Growth Increment (ln mm)	28.67	< 0.0001	25.6	< 0.0001
*Resin Ducts (ln N +1)	16.59	< 0.0001	5.1	0.0239
Cone Count (ln N +1)	0.04	0.8414	1.09	0.2956
[Diameter x Resin Ducts]	-	-	4.04	0.0445
Site	0.03	0.8573	4.4	0.036
Year	0.05	0.8211	0.03	0.867
<i>df</i>	6		7	
<i>R</i> ²	0.301		0.324	
<i>N</i>	271		136	

Table 3.2: Nominal logistic regressions for likelihood of white spruce trees being (1) spruce beetle attacked, and (2) killed by spruce beetles, examining the effect of cones that were produced during the year of beetle attack. Bold and italics as per Table 3.1.

Predictor variable	Response variable			
	Attack Status		Mortality Status	
	χ^2	<i>p</i>	χ^2	<i>p</i>
Diameter (ln cm)	27.72	<0.0001	1.81	0.1787
*Growth Increment (ln mm)	29.27	<0.0001	14.68	<0.0001
*Resin Ducts (ln N +1)	8.43	0.0037	3.31	0.0689
Cone Count (ln N +1)	1.28	0.2587	1.25	0.2634
[Diameter x Resin Ducts]	5.03	0.0249	-	-
Site	1.9	0.1685	1.59	0.2076
Year	4.17	0.0413	0	0.9922
<i>df</i>	7		6	
<i>R</i> ²	0.417		0.2549	
<i>N</i>	213		96	

Table 3.3: Nominal logistic regressions for likelihood of white spruce trees being (1) spruce beetle attacked, and (2) killed by spruce beetles, examining the effect of cones that were produced in the year prior to beetle attack. Bold and italics as per Table 3.1.

Predictor variable	Response variable			
	Attack Status		Mortality Status	
	χ^2	p	χ^2	p
Diameter (ln cm)	15.03	< 0.0001	1.71	0.1906
*Growth Increment (ln mm)	9.97	<i>0.0016</i>	5.8	0.016
*Resin Ducts (ln N +1)	19.63	< 0.0001	1.7	0.1923
Cone Count (ln N +1)	1.56	0.2123	0	0.9944
Site	2.69	0.1011	0.23	0.6325
Year	3.94	0.0471	-	-
df	6		5	
R ²	0.2867		0.4681	
N	140		32	

Table 3.4: Nominal logistic regressions for likelihood of white spruce trees being attacked by the spruce beetle (*Dendroctonus rufipennis*), examining the effect of cone production in the year prior to attack for only those trees that were attacked in 2003. Bold and italics as per Table 3.1.

Predictor variable	Response variable	
	Attack Status	
	χ^2	p
Diameter (ln cm)	12.21	0.0005
*Growth Increment (ln mm)	10.55	<i>0.0012</i>
*Resin Ducts (ln N +1)	12.36	0.0004
Cone Count (ln N +1)	2.88	0.0896
Site	3.78	0.0518
df	5	
R ²	0.3774	
N	74	

3.4 Discussion

3.4.1 Likelihood of spruce beetle attack

Spruce beetles attacked larger-diameter trees with slower growth rates and a higher level of investment in defense (resin duct production) in the 5-years preceding beetle attack. The first result, that white spruce trees attacked by the spruce beetle were significantly larger in diameter than those that were unattacked, agrees with what has been previously reported (Watson 1928, Balch 1942, Hard et al. 1983, Hard 1985, Reynolds and Holsten 1996, Doak 2004, DeRose and Long 2012). In fact, bark beetle preference for large diameter trees is generally well accepted and often thought to be primarily a result of the positive relationship observed between diameter and overall phloem thickness (Hawksworth et al. 1983, Alkan-Akinci and Ersen-Bak 2016). As the phloem layer is where beetle larvae develop and feed, thicker phloem is considered to be of higher quality for bark beetle brood development, and as such has often been proposed as one explanation for beetle preference for large diameter trees (Raffa et al. 2015). This explanation has often been employed, however empirical tests of the relationship between phloem thickness and tree diameter are inconsistent (Berryman 1976, Reid and Robb 1999).

Growth rate and its interaction with diameter is important to consider when examining the impact that diameter has on the probability of being attacked, because growth often decreases with increasing diameter. However, diameter was found to be a significant predictor variable even when accounting for growth rate. Despite the positive correlation between growth rate and diameter (Figure 3.5A), growth rate on its own was also significant when examining attack likelihood, with slower-growing trees most susceptible to attack. This result corroborates what others have found (Watson 1928, Hard et al. 1983, Hard 1985, Doak 2004), although the reason for spruce beetle preference of slow-growing trees is unknown. This preference has recently been

observed in other closely related bark beetle species such as the mountain pine beetle (*Dendroctonus ponderosae*) (Reid lab, unpublished data), however it is contrary to previous research carried out on pine engraver bark beetles (*Ips pini*) in which recent tree growth rate had a strong, positive effect on pine engraver beetle reproduction (Reid and Robb 1999). These effects were shown to be unrelated to phloem thickness, as may otherwise have been assumed, however a key difference is that pine engravers were in freshly dead trees with no induced defenses and no choice of trees (Reid and Robb 1999). Given that faster growing trees resulted in more successful reproduction for pine engravers, a preference for attacking more vigorous individuals could have been predicted but was not observed in my study.

A proposed explanation for why slower growing trees are more susceptible to spruce beetles is that due to their slow growth rates, moisture uptake is too low to allow for the production of sufficient resin flow required for overcoming beetle attacks (Berg et al. 2006, Werner et al. 2006). I found that investment in constitutive defense, represented by the number of xylem resin ducts produced, was greater in attacked trees than unattacked trees (Figure 3.6), and in addition to diameter and growth rate, resin duct production was one of the strongest predictors of spruce beetle attack (Figure 3.6). Resin duct production has been positively linked to resin flow (Nagy et al. 2000, Rodríguez-García et al. 2014) and it has previously been suggested that trees that have more resin ducts should be able to respond to attacks with the production of more resin and a higher resin flow rate, due to their enhanced reservoir capacity (Hood et al. 2015). Given that constitutive resin ducts and an increased resin flow rate is associated with a defensive response, trees that have a higher density of resin ducts should be better equipped to defend against an incoming spruce beetle attack and therefore less likely to be attacked, contrary to what I observed. Successful host tree approach and colonization by the

spruce beetle is more complex, however, and relies on a number of different cues and stimuli (Raffa et al. 2008, Raffa et al. 2015). Because there was no correlation between the number of resin ducts a tree produced in the 5-year period prior to attack and the number of induced traumatic ducts produced in the year of attack, constitutive defense levels in spruce may not provide meaningful information on defensive capabilities to spruce beetles.

3.4.2 Multi-tiered role of carbon-based defenses in conifers

Aggregation and the initiation of mass attack often involve the interaction between host tree kairomones, usually monoterpenes, and attractant beetle pheromones (Borden 1989). Some of the major monoterpene constituents of resin can also serve as primary attractants for bark beetles, with certain components even acting as derivative precursors to the development of beetle pheromones (Seybold et al. 2000). The behaviour of bark beetles is directly linked to tree physiology (Raffa et al. 2008), given that the beetles are able to exploit trees' terpenes as elicitors, synergists and even precursors to their pheromones (Wood 1982, Raffa and Berryman 1983, Sandstrom et al. 2006, Raffa et al. 2008). The primary component of pine tree resin, α -pinene, is also largely responsible for mountain pine beetle pheromone production and attraction, despite the fact that when present in large quantities it can be quite toxic to the beetles themselves. In addition to frontalin, α -pinene is also a demonstrably important component of spruce beetle pheromone production, with most commercial lures produced using a combination of these two compounds (Ross et al. 2005). Used as either a cue from tree kairomones, or exploited as a pre-cursor for beetle pheromone, the monoterpenes present in resin may be serving to make better-defended trees easier to locate as potential hosts. This explanation could be used to explain the increased likelihood of attack for individuals that have a higher level of defense observed in the present study, as they would be most detectable by beetles searching for

appropriate host trees. Tree diameter may also be viewed in this context. If increasing tree diameter results in hosts that are more easily detectable to the spruce beetles, this could explain why larger trees were more likely to be attacked, with no significant effect of diameter on tree mortality.

Additionally, given that the current study examines only the relationships observed during an epidemic phase of spruce beetle activity, the sheer number of spruce beetles that are available to mass attack and overcome tree defenses may result in less of an importance placed on individual host tree defensive traits. At high population densities such as those encountered during an outbreak, the beetle likelihood of a successful attack is increased whether or not the host tree is well defended (Raffa et al. 2015). The behavioural strategies that are employed by bark beetles exhibit plasticity, with different behaviour observed at either endemic or outbreak population densities (Elkin and Reid 2010, Kausrud et al. 2011, Kausrud et al. 2012). During outbreaks, it could be that individual spruce beetles are more likely to attack trees with higher defenses due to the lowered risk of failure compared to when beetle populations are low, in addition to the ease of locating these hosts.

3.4.3 Likelihood of spruce tree mortality

Once an individual tree was attacked by spruce beetles, slower-growing individuals that produced fewer resin ducts in the year of attack had the highest likelihood of mortality (Figure 3.8, Table 3.1). This demonstrates that in conjunction with the observed spruce beetle preference for attacking slower growing trees, of the attacked trees, the slower growing individuals were also more likely to succumb to their injuries following attack, indicating beetle success. Indeed, growth rate was the most significant predictor of tree mortality status following attack, with a strong, negative relationship observed between the two (Figure 3.8). As described above, the

relationship between growth rate and spruce tree susceptibility and beetle-induced mortality has been examined in the past, and the results of the present study generally agree with those for spruce stands in other areas (Watson 1928, Hard et al. 1983, Hard 1985, Doak 2004). Although previous studies have investigated this relationship, these studies do not often distinguish between susceptibility to attack and the likelihood of mortality following attack. The current study examines these important stages separately, and provides insight into spruce beetle behaviour with respect to host choice and eventual host suitability.

Opposite to the trends observed for growth rate, diameter did not play a similar role for both attack likelihood and eventual beetle-induced mortality. Despite the spruce beetle preference of attacking large-diameter trees, diameter did not have a significant effect on tree mortality (Figure 3.8, Table 3.1). The number of resin ducts produced in response to beetle attack was a significant predictor of mortality, with trees that produced more resin ducts less likely to die following spruce beetle attack. This was anticipated given that the induced defensive response of spruce primarily involves the production of traumatic resin ducts in response to attackers. It is unique with respect to the comparisons between attack and tree mortality likelihoods however, because higher constitutive defenses were seen to lead to an increased probability of attack despite lowered beetle success in trees better defended by induced defenses.

Even at epidemic levels, individual trees in the current study were less likely to experience beetle-induced mortality when they were investing more heavily in induced defense following attack. This has important implications for our understanding of spruce-beetle-host-tree dynamics, and suggests that despite high population densities of beetles, individual tree defensive traits still play an active role in tree survival. These results further suggest that trees traditionally viewed as more vulnerable, those with fewer constitutive defenses, may in fact be

less likely to be targeted and attacked by spruce beetles. A recent study examining the effect of drought on the susceptibility of Norway spruce (*Picea abies*) to infestations by the Eurasian spruce bark beetle (*Ips typographus*) came to a similar conclusion (Netherer et al. 2015). A situation that was previously thought to be putting spruce at risk, drought stress, may possibly be allowing them to escape detection by spruce beetles. Despite their empirical evidence that spruce trees under increasingly severe stress are less able to mount defenses, they also observed reduced host acceptance under more extreme drought stress (Netherer et al. 2015). In conjunction with previous research, my study helps to provide a more complete understanding of bark-beetle host dynamics. The results can additionally serve to provide insights into how these dynamics may be expected to change in the future, especially with changing climates.

3.4.4 The role of reproduction: masting in plants and the role of storage

Cone count was included as a predictor variable in all models examining the likelihoods of a tree being attacked and of a tree surviving an attack, and in no model was it found to be significant. This suggests that contrary to the predicted importance of resource investment towards reproduction, what an individual tree does with respect to cone production in a given year does not contribute at all to that individual's likelihood of being attacked, or succumbing to their injuries following attack. There are several possible explanations for this result.

Reproduction might not rely only on current year resources at the expense of other functions. Although growth, defense, and reproduction are all major plant functions that require a high investment of resources, one additional area to which incoming photoassimilates can be diverted was not considered in the present study. Non-structural carbohydrates (NSC), those involved in both primary and secondary metabolism of tissues, can also be compartmentalized by an individual plant and formed into storage reserves (Chapin et al. 1990, Hartmann and

Trumbore 2016). The degree to which an individual plant is able to draw from those reserves will vary, and there is some evidence to suggest that stored carbohydrates are not always accessible to individuals (reviewed in Chapin et al. 1990). Some studies suggest that in mast-cropping conifers such as white spruce, marked declines in storage reserves are seen following reproduction, indicating a significant effect on subsequent reproductive effort with a period of replenishment being required (Koenig and Knops 2000). Other studies demonstrate that some trees do use the current year's photosynthesis (Hoch et al. 2013), which would predict an annual trade-off between growth and reproduction.

The mechanisms by which masting species synchronize their reproductive efforts have been examined, and the evidence for all proposed mechanisms show mixed support (Koenig and Knops 2005). One proposed hypothesis, resource matching, suggests that plants may be matching their reproductive output to the variable resources that are available to them in a given year, indicating no underlying selective pressures for large scale variations. If this was indeed occurring, one would expect individuals to invest more in everything (growth and reproduction) in years with high resource availability, and less in everything when years are poorer, resulting in a positive correlation between growth and reproduction (Monks and Kelly 2006). The opposite trend has been observed most frequently in Northern Hemisphere genera *Abies*, *Acer*, *Betula*, *Fagus*, *Picea*, *Pinus* and *Pseudotsuga*, with a negative correlation found between growth and reproduction (Kelly and Sork 2002). I found a weakly positive relationship between annual growth and cone count (Figure 3.4C), which could suggest a potential for resource matching in this species. It is important to note, however, that with the present dataset, only one year of cone count data was used for each individual for comparison to growth rate. More significant and meaningful trends may emerge when cone count and growth are compared over multiple years,

and so the conclusions based on the current study's analysis of reproduction must be tempered. In a larger, multi-year study of the Kluane area, large cone crops corresponded to years of reduced growth (Krebs et al. 2017).

Because of the potential shortcomings of using only one year of cone data, I ran separate models to more precisely examine the effect of cones that were produced either during the year of spruce beetle attack (Table 3.2) or in the year prior to spruce beetle attack (Tables 3.3, 3.4). Only individual trees that had data available matching those descriptions were included in these analyses, and as in previous models cone count had no significant effect on either attack or survival status. Given this lack of any significant effect, and the lack of a trade-off observed between growth and cones, these results suggest that white spruce in this system may be relying more heavily on resource reserves for yearly investment towards allocation, or that masting may occur primarily as a result of external variables, or some combination of both. Further studies would need to be conducted to more directly investigate the mechanisms responsible for masting in this system, along with the degree to which individual trees are utilizing stored resources for reproduction.

3.4.5 Alignment with the Growth-Differentiation-Balance Hypothesis

The growth-differentiation balance hypothesis (GDBH) presents the idea of a trade-off between allocating towards competing life history traits, growth and defense, as a dilemma for plants. An individual needs to grow fast enough to remain competitive while still remaining sufficiently defended to prevent the loss of already acquired resources through injury and to survive when faced with pathogens and herbivores (Herms and Mattson 1992). As such, a balance between resource allocation towards growth and defense is needed. It is likely, however, that a third axis is involved in the dilemma of allocation, with overall plant allocation patterns

dividing into more of a triangle with growth, defense, and reproduction competing for the same limited resources (Obeso 2002). The predicted trade-off between growth and defence was detectable in the white spruce trees that were sampled, with a slightly negative correlation between the two variables when compared over a 5-year period (Figure 3.4A). This trade-off would have been predicted by the GDBH in situations where resource availability was moderate or high, and net assimilation of resources was consistent (Herms and Mattson 1992). On the other hand, I did not detect the predicted trade-off between growth and reproduction, with a positive correlation observed between the two variables (Figure 3.4C). A positive relationship between two competing areas of allocation can only be explained by the GDBH in situations of low resource availability, where allocation towards growth is limited by overall low levels of photosynthesis and unfavourable conditions (Herms and Mattson 1992). Under these circumstances there would be a predicted positive relationship, as the inherent trade-off would not yet be observable.

A separate situation that would result in the observed positive correlation between growth and reproduction involves the opposite level of resources being available to an individual. Trees with more total resources (i.e. larger trees) could still have more defenses or cones in absolute terms, given their improved access to resources over smaller trees. As many species of plants require similar resources for growth, reproduction, and defense (Bazzaz et al. 1987, Chapin et al. 1990), conditions that are conducive for growth are also likely conducive for reproduction. Alternatively, it is also possible that while access to carbon may not be limited in an individual, other things such as nitrogen or phosphorus may limit reproduction (Ferrenberg et al. 2015). The predicted trade-off between growth and defense was observed, and white spruce tree defenses are primarily carbon-based. Previous studies have suggested that simple estimates of reproductive

effort based only on biomass allocation to flower and/or fruiting structures poorly reflect total carbon allocation to reproduction (Reekie and Bazzaz 1987b), and plant reproductive structures are usually more nutrient-enriched than are other biomass (Reekie and Bazzaz 1987b, a, Hemborg and Karlsson 1998, Sala et al. 2012). As such, future studies need to investigate allocation of key nutrients in addition to simply the allocation of carbon, when considering reproduction.

3.4.6 Conclusions

Differences in resource allocation to defensive resin ducts and growth of white spruce predicted the likelihood of an individual tree being attacked by spruce beetles during an outbreak. According to the growth-differentiation balance hypothesis, trees are faced with a dilemma when forced to allocate finite resources towards either growth or defense. As predicted by this hypothesis, a trade-off was observed between growth rate and the production of resin ducts over a 5-year period (Figure 3.4A). During the outbreak examined here, the likelihood of attack by the spruce beetle was highest for large diameter, slower-growing trees that produced a larger number of resin ducts in the 5-year period preceding attack. Beetles were more likely to attack trees that were better defended, possibly as a result of these trees being more easily located due to the presence of highly concentrated terpenes produced in the resin.

Differences in resource allocation between these life history functions also predicted the likelihood of an individual tree surviving beetle attack, even at the outbreak population densities encountered in the current study. Growth rate was the most significant predictor of tree mortality, with slower growing individuals most likely to die. Additionally, investment in induced defense played a significant role, with trees that produced fewer ducts in response to an attack being more likely to die. Beetles were more likely to attack trees that were better defended despite the

observed decrease in beetle success in better-defended trees. This could indicate that trees traditionally viewed as most vulnerable, those with fewer defenses, may in fact be capable of avoiding detection by the spruce beetle and at a lower risk of beetle attack. Although at high beetle population density it has been suggested that the role of individual host defenses may be less prominent in determining beetle success, induced defenses produced in the white spruce examined in the current study affected mortality rates of white spruce.

A tree's investment towards reproduction, represented by cone count data obtained for each individual, was not a significant predictor to either attack or survival likelihood. Cone production and the level of carbon allocated towards reproduction therefore do not appear to contribute to a tree's overall susceptibility to spruce beetle attack. Despite the predicted significant cost of reproduction, no trade-off was observed between cone output and growth, and a positive correlation was observed between the two. This could indicate that trees are not relying on the current year's photoassimilates for investment in reproduction, or that total resource availability is masking the trade-off that must inherently be present. Further studies examining the process of masting in this system and the relationship between growth and reproductive output over a longer time scale is needed.

Chapter Four: **General conclusions**

With this thesis, I set out to determine how carbon allocation in white spruce towards growth, reproduction, and defense affected the success of spruce beetles during a large-scale, unprecedented outbreak. At the population level, I examined how yearly variation in average growth rate and cone crop production affected spruce beetle population growth. At the individual tree level, I examined how these allocation patterns affected beetle-attack and spruce-tree mortality probabilities. Spruce beetle population growth was greater in years that had less average spruce growth, and at the individual tree level, trees that were slower growing relative to their diameter were more likely to be both attacked and killed. At both scales examined, this indicates a beetle preference for and advantage with relatively slow tree growth. Diameter was also a significant predictor of attack, with larger trees more likely to be attacked. With respect to mortality, however, diameter was no longer significant except when considering its interaction with resin-duct production. This could indicate that larger trees are easier for spruce beetles to locate, but that diameter is not inherently important to tree survival while defenses are. Because there was a negative relationship between growth rate and constitutive defense production, the increased probability of attack for slow growing trees does not indicate these trees were less able to mobilize resources for defense.

Individual trees with a higher level of constitutive defense were more likely to be attacked despite the fact that better-defended trees in the year of attack (with more induced defense) were less likely to die. This could indicate that spruce beetles rely on constitutive tree defenses as a means of locating suitable tree hosts. Because there was no relationship between the constitutive and induced defenses produced by a tree, the constitutive defenses that the beetles may be attracted to do not necessarily reflect the tree's defensive capability. The trends

observed with respect to defense may have other implications, in that trees traditionally viewed as most vulnerable (those with fewer defenses) actually have a lower likelihood of being attacked, and may therefore be able to escape beetle detection.

At the population level, years of higher spruce beetle population growth were associated with overall less cone production, but no effect was observed of individual cone production in a given year on the probabilities of spruce beetle attack or related mortality. To the best of my knowledge, cone production has not previously been examined with respect to its relationship to tree susceptibility and defense, making this result a novel one. These findings could indicate that trees are not relying on the current year's photoassimilates for investment in reproduction, or that total resource availability is masking the trade-off that must inherently be present. Further studies examining the process of masting in this system and the relationship between growth and reproductive output over a longer time scale are needed.

When examining the effect of climate on this system at the population scale, neither summer or winter temperature were found to have a significant effect on spruce beetle population growth. Despite the predicted importance of these factors on spruce beetle biology and population density, either climate was not an important process explaining population growth in this outbreak, or other climate variables I did not investigate are important and should be investigated.

The results of my study suggest several new lines of inquiry that will help elucidate the relationship between tree traits and susceptibility to spruce beetle attack. It would be useful to directly examine the source from which individual trees are obtaining the carbon required for both defense and reproduction; whether it be primarily from the current year's photosynthesis, or from stored carbohydrate reserves. An additional line of inquiry could therefore be to run a more

controlled experiment examining these questions directly, or to better quantify the amount of carbon being allocated to each of these functions. Taking storage reserve capacity and use into account would provide a more accurate depiction of white spruce allocation strategy, and would therefore aid in understanding the effect of allocation on spruce beetle success. Because these allocation processes are complex, more sensitive techniques may be required to address the underlying mechanisms.

The spruce beetle outbreak that was examined in the present thesis caused widespread and substantial spruce mortality across the southwest Yukon. Currently there is increasing concern over bark beetle disturbance frequency and severity, due to the effects of climate change on range expansion and increasing beetle population densities (Raffa et al. 2008). Coniferous forests provide essential ecosystem services, are home to a wide variety of plant and animal species, and are thought to be especially vulnerable to climatic shifts (McNulty and Aber 2001, Bentz et al. 2010). Understanding which tree characteristics make individuals more susceptible to spruce (and other bark) beetle species an essential component of understanding the spruce beetle-host dynamic, and can be useful when advising on forest management strategies or predicting future beetle outbreak progression. My thesis explored the relationships between carbon allocation at both the spruce population and individual tree level, and provides important insights into the relationships between spruce beetle attack, subsequent mortality and their host tree species.

References

- Alkan-Akinci, H., and F. Ersen-Bak. 2016. Assessment of tree vigor parameters in successful establishment of *Dendroctonus micans* on *Picea orientalis* in Turkey. *Journal of the Entomological Research Society* **18**:119-125.
- 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.
- Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* **262**:263-286.
- Balch, R. E. 1942. On the estimation of forest insect damage with particular reference to *Dendroctonus piceaperda* Hopk. *Journal of Forestry* **40**:621-629.
- Bannan, M. W. 1936. Vertical resin ducts in the secondary wood of the Abietineae. *New Phytologist* **35**:11-46.
- Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* **405**:668-673.
- Barringer, B. C., W. D. Koenig, and J. M. H. Knops. 2013. Interrelationships among life-history traits in three California oaks. *Oecologia* **171**:129-139.
- Bazzaz, F. A. 1997. Allocation of resources in plants: State of the science and critical questions. *in* F. A. Bazzaz and G. John, editors. *Physiological ecology: Plant resource allocation*. Academic Press, San Diego, US.
- Bazzaz, F. A., N. R. Chiariello, P. D. Coley, and L. F. Pitelka. 1987. Allocation of resources to reproduction and defense. *Bioscience* **37**:58-67.

- Bentz, B. J., J. Régnière, C. J. Fettig, 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. David 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.
- Berg, E. E., and J. D. Henry. 2003. The history of spruce bark beetle outbreak in the Kluane region as determined from the dendrochronology of selected forest stands. Parks Canada.
- Berryman, A. A. 1976. Theoretical explanation of mountain pine beetle dynamics in Lodgepole pine forests 1. *Environmental Entomology* **5**:1225-1233.
- Blanche, C. A., P. L. Lorio, R. A. Sommers, J. D. Hodges, and T. E. Nebeker. 1992. Seasonal cambial growth and development of loblolly pine: xylem formation, inner bark chemistry, resin ducts, and resin flow. *Forest Ecology and Management* **49**:151-165.
- Boone, C. K., B. H. Aukema, J. Bohlmann, A. L. Carroll, and K. F. Raffa. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Canadian Journal of Forest Research* **41**:1174-1188.
- Boonstra, R., L. Desantis, C. J. Krebs, and D. S. Hik. 2008. Climate and nutrient influences on the growth of white spruce trees in the boreal forests of the Yukon. *Climate Research* **36**:123-130.
- Borden, J. H. 1989. Semiochemicals and bark beetle populations: Exploitation of natural phenomena by pest management strategists. *Holarctic Ecology* **12**:501-510.

- Bright, D. E. 1976. The insects and arachnids of Canada, part 2: the bark beetles of Canada and Alaska (Coleoptera: Scolytidae). *Agriculture Canada* **1576**:11-19.
- Bryant, J. P., F. S. Chapin, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* **40**:357-368.
- Chapin, F. S., S. Ernst-Detleif, and H. A. Mooney. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* **21**:423-447.
- Chavardes, R. D., L. D. Daniels, P.O. Waeber, J. L. Innes, and C. R. Nitschke. 2013. Unstable climate-growth relations for white spruce in southwest Yukon, Canada. *Climatic Change* **116**:593-611.
- Christiansen, E., P. Krokene, A. A. Berryman, V. R. Franceschi, T. Krekling, F. Lieutier, A. Lonneborg, and H. Solheim. 1999. Mechanical injury and fungal infection induce acquired resistance in Norway spruce. *Tree Physiology* **19**:399-403.
- Christiansen, E., R. H. Waring, and A. A. Berryman. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *Forest Ecology and Management* **22**:89-106.
- Clark, E. L., A. L. Carroll, and D. P. W. Huber. 2012. Differences in the constitutive terpene profile of lodgepole pine across a geographical range in British Columbia, and correlation with historical attack by mountain pine beetle. *The Canadian Entomologist* **142**:557-573.
- Cody, M. L. 1966. A general theory of clutch size. *Evolution* **20**:174-184.
- Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. *Science* **230**:895-899.
- Crone, E. E., E. Miller, and A. Sala. 2009. How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecology Letters* **12**:1119-1126.

- Daubenmire, R. 1960. A seven-year study of cone production as related to xylem layers and temperature in *Pinus ponderosa*. *The American Midland Naturalist* **64**:187-193.
- Dawson, T. E., S. Mambelli, A. H. Plamboeck, P. H. Templer, and K. P. Tu. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* **33**:507-559.
- de Jong, M., and H. Saarenmaa. 1985. A mechanistic simulation model for the movement of bark beetle larvae (Coleoptera: Scolytidae). *Ecological Modeling* **27**:109-138.
- de Jong, T. J., and E. van der Meijden. 2000. On the correlation between allocation to defence and regrowth in plants. *Oikos* **88**:503-508.
- DeRose, R. J., and J. N. Long. 2012. Factors influencing the spatial and temporal dynamics of Engelmann spruce mortality during a spruce beetle outbreak on the Markagunt Plateau, Utah. *Forest Science* **58**:1-14.
- Dietze, M. C., A. Sala, M. S. Carbone, C. I. Czimczik, J. A. Mantooth, A. D. Richardson, and R. Vargas. 2014. Nonstructural carbon in woody plants. *Annual Review Plant Biology* **65**:667-687.
- Doak, P. 2004. The impact of tree and stand characteristics on spruce beetle (Coleoptera: Scolytidae) induced mortality of white spruce in the Copper River Basin, Alaska. *Canadian Journal of Forest Research* **34**:810-816.
- Dyer, E. D. A., and D. W. Taylor. 1971. Spruce beetle brood production in logging slash and wind-thrown trees in British Columbia. *Canadian Forest Service Information Report BC-X-62*, Vic., BC.
- Eis, S., E. H. Garman, and L. F. Ebell. 1965. Relation between cone production and diameter increment of douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis*

- (Dougl.)Lindl.), and western white pine (*Pinus monticola* Dougl.). Canadian Journal of Botany **43**:1553-1559.
- Elkin, C. M., and M. L. Reid. 2010. Shifts in breeding habitat selection behaviour in response to population density. *Oikos* **119**:1070-1080.
- Fatichi, S., S. Leuzinger, and C. Korner. 2014. Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *New Phytologist* **201**:1086-1095.
- Ferrenberg, S., J. M. Kane, and J. M. Langenhan. 2015. To grow or defend? Pine seedlings grow less but induce more defences when a key resource is limited. *Tree Physiology* **35**:107-111.
- Ferrenberg, S., J. M. Kane, and J. B. Mitton. 2014. Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. *Oecologia* **174**:1283-1292.
- Fettig, C. J., M. L. Reid, B. J. Bentz, S. Sevanto, D. L. Spittlehouse, and T. Wang. 2013. Changing climates, changing forests: a western North American perspective. *Journal of Forestry* **111**:214-228.
- Franceschi, V. R., P. Krokene, E. Christiansen, and T. Krekling. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* **167**:353-375.
- Frye, R. H., H. W. Flake, and C. J. Germain. 1974. Spruce beetle winter mortality resulting from record low temperatures in Arizona. *Environmental Entomology* **3**:752-754.
- Funk, K. A., W. D. Koenig, and J. M. H. Knops. 2016. Fire effects on acorn production are consistent with the stored resource hypothesis for masting behavior. *Canadian Journal of Forest Research* **46**:20-24.

- Garbutt, R., B. Hawkes, and E. Allen. 2006. Spruce beetle and the forests of the southwest Yukon. BC-X-406, Natural Resources Canada, Canada Forest Service, Pacific Forestry Center.
- Gaylord, M. L., T. E. Kolb, W. T. Pockman, J. A. Plaut, E. A. Yopez, A. K. Macalady, R. E. Pangle, and N. G. McDowell. 2013. Drought predisposes pinon-juniper woodlands to insect attacks and mortality. *New Phytologist* **198**:567-578.
- Glynn, C., D. A. Herms, M. Egawa, R. Hansen, and W. J. Mattson. 2003. Effects of nutrient availability on biomass allocation as well as constitutive and rapid induced herbivore resistance in poplar. *Oikos* **101**:385-397.
- Glynn, C., D. A. Herms, C. M. Orians, R. C. Hansen, and S. Larsson. 2007. Testing the growth-differentiation balance hypothesis: dynamic responses of willows to nutrient availability. *New Phytologist* **176**:623-634.
- Green, T. R., and C. A. Ryan. 1972. Wound-induced proteinase inhibitor in plant leaves: a possible defense mechanism against insects. *Science* **175**:776-777.
- Han, Q., D. Kabeya, A. Iio, and Y. Kakubari. 2008. Masting in *Fagus crenata* and its influence on the nitrogen content and dry mass of winter buds. *Tree Physiology* **28**:1269-1276.
- Hansen, E. M., B. J. Bentz, and D. L. Turner. 2001. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Canadian Entomologist* **133**:827-841.
- Hard, J. S. 1985. Spruce beetles attack slowly growing spruce. *Forest Science* **31**:839-850.
- Hard, J. S., R. A. Werner, and E. H. Holsten. 1983. Susceptibility of white spruce to attack by spruce beetles during the early years of an outbreak in Alaska. *Canadian Journal of Forest Research* **13**:676-684.

- Hart, S. J., T. T. Veblen, K. S. Eisenhart, D. Jarvis, and D. Kulakowski. 2014. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* **4**:930-939.
- Hartmann, H., and S. Trumbore. 2016. Understanding the roles of nonstructural carbohydrates in forest trees - from what we can measure to what we want to know. *New Phytologist* **211**:386-403.
- Haukioja, E., and T. Hakala. 1975. Herbivore cycles and periodic outbreaks. Formulation of a general hypothesis. Report of the Kevo Subarctic Research Station **12**:1-9.
- Hawksworth, F. G., C. K. Listern, and D. B. Cahill. 1983. Phloem thickness in lodgepole pine: its relationship to dwarf mistletoe and mountain pine beetle (Coleoptera: Scolytidae). *Environmental Entomology* **12**:1447-1448.
- Hebertson, E. G., and M. J. Jenkins. 2007. The influence of fallen tree timing on spruce beetle brood production. *Western North American Naturalist* **67**:452-460.
- Hemborg, A. M., and P. S. Karlsson. 1998. Somatic cost of reproduction in eight subarctic plant species. *Oikos* **82**:149-157.
- Hermes, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* **67**:283-335.
- Hoch, G., R. T. Siegwolf, S. G. Keel, C. Korner, and Q. Han. 2013. Fruit production in three masting tree species does not rely on stored carbon reserves. *Oecologia* **171**:653-662.
- Hogg, E. H. 1994. Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research* **24**:1835-1845.

- Hogg, E. H., and A. G. Schwarz. 1997. Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. *Journal of Biogeography* **24**:527-534.
- Hood, S., and A. Sala. 2015. Ponderosa pine resin defenses and growth: metrics matter. *Tree Physiology* **35**:1223-1235.
- Hood, S., A. Sala, E. K. Heyerdahl, and M. Boutin. 2015. Low-severity fire increases tree defense against bark beetle attacks. *Ecology* **96**:1846-1855.
- Ichie, T., and M. Nakagawa. 2013. Dynamics of mineral nutrient storage for mast reproduction in the tropical emergent tree *Dryobalanops aromatica*. *Ecological Research* **28**:151-158.
- Ives, W. G. H., and H. R. Wong. 1988. Tree and shrub insects of the prairie provinces. Canadian Forestry Service, Northern Forestry Centre, Edmonton, Alberta. Information Report NOR-X-292. 327 p.
- Jones, C. G., and S. E. Hartley. 1999. A protein competition model of phenolic allocation. *Oikos* **86**:27-44.
- Juday, G. P., V. Barber, S. Rupp, J. C. Zasada, and M. Wilmking. 2003. A 200-year perspective of climate variability and the response of white spruce in interior Alaska. Pages 226-250 *in* D. Greenland, D. G. Goodin, and R. C. Smith, editors. *Climate variability and ecosystem response at long-term ecological research sites*, Oxford University Press, Oxford.
- Kane, J. M., and T. E. Kolb. 2010. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia* **164**:601-609.
- Karban, R. 2011. The ecology and evolution of induced resistance against herbivores. *Functional Ecology* **25**:339-347.

- Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. The University of Chicago Press, Ltd.
- Kausrud, K., B. Okland, O. Skarpaas, J. C. Gregoire, N. Erbilgin, and N. C. Stenseth. 2012. Population dynamics in changing environments: the case of an eruptive forest pest species. *Biological Reviews* **87**:34-51.
- Kausrud, K. L., J. C. Gregoire, O. Skarpaas, N. Erbilgin, M. Gilbert, B. Okland, and N. C. Stenseth. 2011. Trees wanted--dead or alive! Host selection and population dynamics in tree-killing bark beetles. *PLoS One* **6**:e18274.
- Keeling, C. I., and J. Bohlmann. 2006. Genes, enzymes and chemicals of terpenoid diversity in the constitutive and induced defence of conifers against insects and pathogens. *New Phytol* **170**:657-675.
- Kelly, D., A. Geldenhuis, A. James, E. Penelope Holland, M. J. Plank, R. E. Brockie, P. E. Cowan, G. A. Harper, W. G. Lee, M. J. Maitland, A. F. Mark, J. A. Mills, P. R. Wilson, and A. E. Byrom. 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters* **16**:90-98.
- Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* **33**:427-447.
- Klapwijk, M. J., M. P. Ayres, A. Battisti, and S. Larsson. 2012. Assessing the impact of climate change on outbreak potential *in* P. Barbosa, J. C. Shultz, and D. Letourneau, editors. *Insect outbreaks revisited*, 2nd ed. Blackwell Publishing Ltd., Oxford.
- Knebel, L., D. J. Robison, T. R. Wentworth, and K. D. Klepzig. 2008. Resin flow responses to fertilization, wounding, and fungal inoculation in loblolly pine (*Pinus taeda*) in North Carolina. *Tree Physiology* **28**:847-853.

- Koenig, W. D., and J. M. H. Knops. 2000. Patterns of annual seed production by Northern Hemisphere trees: A global perspective. *The American Naturalist* **155**:59-69.
- Koenig, W. D., and J. M. H. Knops. 2005. The mystery of masting in trees. *American Scientist* **93**:340-347.
- Krebs, C. J., and R. Boonstra. 2001. The Kluane Region. Pages 9-24 *in* C. J. Krebs, S. Boutin, and R. Boonstra, editors. *Ecosystem dynamics of the boreal forest: the Kluane project*. Oxford University Press, New York.
- Krebs, C. J., J. M. LaMontagne, A. J. Kenney, and S. Boutin. 2012. Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. *Botany* **90**:113-119.
- Krebs, C. J., M. O'Donoghue, S. Taylor, A. J. Kenney, E. J. Hofer, and S. Boutin. 2017. Predicting white spruce cone crops in the boreal forests of southern and central Yukon. *Canadian Journal of Forest Research* **47**:47-52.
- Kyto, M., P. Niemela, E. Annala, and M. Varama. 1999. Effects of forest fertilization on the radial growth and resin exudation of insect-defoliated Scots pines. *Journal of Applied Ecology* **36**:763-769.
- LaMontagne, J. M. 2007. Spatial and temporal variation in white spruce (*Picea glauca*) cone production: individual and population responses of North American red squirrels (*Tamiasciurus hudsonicus*). PhD thesis. University of Alberta, Edmonton, AB.
- LaMontagne, J. M., and S. Boutin. 2007. Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. *Journal of Ecology* **95**:991-1000.
- Lerdau, M., M. Litvak, and R. Monson. 1994. Plant chemical defense monoterpenes and the growth-differentiation balance hypothesis. *Trends in Ecology and Evolution* **9**:58-61.

- Levins, R. 1968. Evolution in changing environments: Some theoretical explorations. Princeton, NJ, USA: Princeton University Press.
- Lewinsohn, E., M. Gijzen, and R. Croteau. 1991. Differences in constitutive and wound-induced monoterpene biosynthesis among species. *Plant Physiology* **96**:44-49.
- Lindgren, B. S., and K. F. Raffa. 2013. Evolution of tree killing in bark beetles (Coleoptera: Curculionidae): trade-offs between the maddening crowds and a sticky situation. *The Canadian Entomologist* **145**:471-495.
- Lloyd, D. G. 1988. A general principle for the allocation of limited resources. *Evolutionary Ecology* **2**:175-187.
- Logan, J. A., and J. A. Powell. 2009. Ecological consequences of climate change altered forest insect disturbance regimes. Pages 98-109 *in* F.H. Wagner, editor. Climate warming in western North America: Evidence and environmental effects. University of Utah Press, Salt Lake City, Utah, USA.
- Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* **1**:130-137.
- Marini, L., M. P. Ayres, A. Battisti, and M. Faccoli. 2012. Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. *Climatic Change* **115**:327-341.
- Marini, L., Å. Lindelöw, A. M. Jönsson, S. Wulff, and L. M. Schroeder. 2013. Population dynamics of the spruce bark beetle: a long-term study. *Oikos* **122**:1768-1776.
- Marquis, R. J., E. A. Newell, and A. C. Villegas. 1997. Non-structural carbohydrate accumulation and use in an understorey rain-forest shrub and relevance for the impact of leaf herbivory. *Functional Ecology* **11**:636-643.

- Massey, C., and N. Wygant. 1954. Biology and control of the Engelmann spruce beetle in Colorado. USDA Forest Service, Circular no. 944, Washington DC.
- Mattson, W. J., and R. A. Haack. 1987. Role of drought in outbreaks of plant-eating insects. *Bioscience* **37**:110-118.
- McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution* **26**:523-532.
- McKey, D. 1974. Adaptive patterns in alkaloid physiology. *The American Naturalist* **108**:305-320.
- McNulty, S. G., and J. D. Aber. 2001. US national climate change assessment on forest ecosystems: An introduction. *Bioscience* **51**:720-722.
- Mihaliak, C. A., and D. E. Lincoln. 1985. Growth pattern and carbon allocation to volatile leaf terpenes under nitrogen-limiting conditions in *Heterotheca subaxillaris* (Asteraceae). *Oecologia* **66**:423-426.
- Miller, L. K., and R. A. Werner. 1987. Cold-hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. *Canadian Journal of Zoology* **65**:2927-2930.
- Miyazaki, Y., T. Hiura, E. Kato, and R. Funada. 2002. Allocation of resources to reproduction in *Styrax obassia* in a masting year. *Annals of Botany* **89**:767-772.
- Monks, A., and D. Kelly. 2006. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). *Austral Ecology* **31**:366-375.

- Moreira, X., R. Zas, A. Solla, and L. Sampedro. 2015. Differentiation of persistent anatomical defensive structures is costly and determined by nutrient availability and genetic growth-defence constraints. *Tree Physiology* **35**:112-123.
- Nagy, N. E., V. R. Franceschi, H. Solheim, T. Krekling, and E. Christiansen. 2000. Wound-induced traumatic resin duct development in stems of Norway spruce (Pinaceae): anatomy and cytochemical traits. *American Journal of Botany* **87**:302-313.
- Netherer, S., B. Matthews, K. Katzensteiner, E. Blackwell, P. Henschke, P. Hietz, J. Pennerstorfer, S. Rosner, S. Kikuta, H. Schume, and A. Schopf. 2015. Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist* **205**:1128-1141.
- Nienstaedt, H., and J. C. Zasada. 1990. *Picea glauca*. in R. M. Burns and B. H. Honkala, editors. *Silvics of North America, Volume 1. Conifers*. . USDA Forest Service Agricultural Handbook 654, Washington, D.C.
- Novick, K. A., G. G. Katul, H. R. McCarthy, and R. Oren. 2012. Increased resin flow in mature pine trees growing under elevated CO₂ and moderate soil fertility. *Tree Physiol* **32**:752-763.
- Obeso, J. R. 2002. The costs of reproduction in plants. *New Phytologist* **155**:321-348.
- Okland, B., and A. A. Berryman. 2004. Resource dynamics plays a key role in regional fluctuations of the spruce beetle, *Ips typographus*. *Agricultural and Forest Entomology* **6**:141-146.
- Pearse, I. S., W. D. Koenig, and D. Kelly. 2016. Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist* **212**:546-562.

- Pearse, I. S., W. D. Koenig, and J. M. H. Knops. 2014. Cues versus proximate drivers: testing the mechanism behind masting behavior. *Oikos* **123**:179-184.
- Pesendorfer, M. B., W. D. Koenig, I. S. Pearse, J. M. H. Knops, K. A. Funk, and K. Whitney. 2016. Individual resource limitation combined with population-wide pollen availability drives masting in the valley oak (*Quercus lobata*). *Journal of Ecology* **104**:637-645.
- Powell, J. A., and B. J. Bentz. 2009. Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. *Landscape Ecology* **24**:657-672.
- Priesler, H. K., J. A. Hicke, A. A. Ager, and J. L. Hayes. 2012. Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. *Ecology* **93**:2421-2434.
- Prowse, T. D., C. Furgal, B. R. Bonsal, and T. W. D. Edwards. 2009. Climatic conditions in Northern Canada: Past and future. *AMBIO: A Journal of the Human Environment* **38**:257-265.
- Raffa, K., J. C. Gregoire, and B. S. Lindgren. 2015. Natural history and ecology of bark beetles. *in* F. E. Vega and R. W. Hofstetter, editors. *Bark beetles*. Academic Press, Elsevier Inc. London, UK.
- Raffa, K. F. 2014. Terpenes tell different tales at different scales: glimpses into the Chemical Ecology of conifer - bark beetle - microbial interactions. *Journal of Chemical Ecology* **40**:1-20.
- Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* **58**:501-517.

- Raffa, K. F., and A. A. Berryman. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* **53**:27-49.
- Rapp, J. M., E. J. B. McIntire, E. E. Crone, and P. Zuidema. 2013. Sex allocation, pollen limitation and masting in whitebark pine. *Journal of Ecology* **101**:1345-1352.
- Reekie, E. G., and F. A. Bazzaz. 1987a. Reproductive effort in plants I. Carbon allocation to reproduction. *The American Naturalist* **129**:876-896
- Reekie, E. G., and F. A. Bazzaz. 1987b. Reproductive effort in plants II. Does carbon reflect the allocation of other resources? *The American Naturalist* **129**:897-906
- Reeve, J. D. 1997. Predation and bark beetle dynamics. *Oecologia* **112**:48-54.
- Regniere, J., J. Powell, B. Bentz, and V. Nealis. 2012. Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *Journal of Insect Physiology* **58**:634-647.
- Reid, M. L., and T. Robb. 1999. Death of vigorous trees benefits bark beetles. *Oecologia* **120**:555-562.
- Reynolds, K. M., and E. H. Holsten. 1996. Classification of spruce beetle hazard in Lutz and Sitka spruce stands on the Kenai peninsula, Alaska. *Forest Ecology and Management* **84**:251-262.
- Reznick, D. 1985. Costs of reproduction: An evaluation of the empirical evidence. *Oikos* **44**:257-267.
- Rodríguez-García, A., R. López, J. A. Martín, F. Pinillos, and L. Gil. 2014. Resin yield in *Pinus pinaster* is related to tree dendrometry, stand density and tapping-induced systemic changes in xylem anatomy. *Forest Ecology and Management* **313**:47-54.

- Rosner, S., and B. Hannrup. 2004. Resin canal traits relevant for constitutive resistance of Norway spruce against bark beetles: environmental and genetic variability. *Forest Ecology and Management* **200**:77-87.
- Ross, D. W., G. E. Daterman, and A. S. Munson. 2005. Spruce beetle (Coleoptera: Scolytidae) response to traps baited with selected semiochemicals in Utah. *Western North American Naturalist* **65**:123-126.
- Rowe, J. S. 1972. Forest regions of Canada. Fisheries and Environment Canada, Canadian Forest Service, Ottawa, ON. 172 p.
- Rudinsky, J. A. 1962. Ecology of Scolytidae. *Annual Review of Entomology* **7**:327-348.
- Safranyik, L., and A. L. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *in* L. Safranyik and W. R. 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, B.C, Canda.
- Sala, A., W. Fouts, and G. Hoch. 2011. Carbon storage in trees: Does relative carbon supply decrease with tree size? Pages 287-306 *in* F. C. Meinzer, B. Lachenbruch, and T. E. Dawson, editors. *Size- and age-related changes in tree structure and function*. Springer, London, UK.
- Sala, A., K. Hopping, E. J. McIntire, S. Delzon, and E. E. Crone. 2012. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist* **196**:189-199.
- Sandstrom, P., W. H. Welch, G. J. Blomquist, and C. Tittiger. 2006. Functional expression of a bark beetle cytochrome P450 that hydroxylates myrcene to ipsdienol. *Insect Biochem Mol Biol* **36**:835-845.

- Schardl, C., and C. Feng. 2010. Plant defences against herbivore attack. Encyclopedia of life sciences. John Wiley & Sons Ltd., Chichester.
- Schmid, J. M. 1981. Spruce beetles in blowdown. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Note RM-411, 5 pp.
- Schmid, J. M., and R. H. Frye. 1977. Spruce beetle in the Rockies. General Technical Report RM-49. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Seybold, S. J., J. Bohlmann, and K. Raffa. 2000. Biosynthesis of coniferophagous bark beetle pheromones and conifer isoprenoids: Evolutionary perspective and synthesis. The Canadian Entomologist **132**:697-753.
- Seybold, S. J., D. P. W. Huber, J. C. Lee, A. D. Graves, and J. Bohlmann. 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. Phytochemistry Reviews **5**:143-178.
- Smith, R. J. 2009. Use and misuse of the reduced major axis for line-fitting. American Journal of Physical Anthropology **140**:476-486.
- Stamp, N. 2004. Can the growth-differentiation balance hypothesis be tested rigorously? Oikos **107**:439-448.
- Stamp, N., M. Bradfield, S. Li, and B. Alexander. 2004. Effect of competition on plant allometry and defense. The American Midland Naturalist **151**:50-64.
- Stokes, M. A., and T. L. Smiley. 1968. An introduction to tree-ring dating. Chicago: University of Chicago Press.
- Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on plants: Community patterns and mechanisms. Harvard University Press, Cambridge (MA).

- 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.
- van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist* **128**:137-142.
- Watson, E. B. 1928. The bionomics of the spruce bark beetle *Dendroctonus Piceaperda* Hopk: The result of observations carried out in the Algoma district of Ontario. *Scientific Agriculture* **8**:613-635.
- Werner, R. A., and E. H. Holsten. 1985. Factors influencing generation times of spruce beetles in Alaska. *Canadian Journal of Forest Research* **15**:438-443.
- Werner, R. A., E. H. Holsten, S. M. Matsuoka, and R. E. Burnside. 2006. Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research. *Forest Ecology and Management* **227**:195-206.
- Wesołowski, T., P. Rowiński, and M. Maziarz. 2015. Interannual variation in tree seed production in a primeval temperate forest: does masting prevail? *European Journal of Forest Research* **134**:99-112.
- Westbrook, J. W., A. R. Walker, L. G. Neves, P. Munoz, M. F. Resende, Jr., D. B. Neale, J. L. Wegrzyn, D. A. Huber, M. Kirst, J. M. Davis, and G. F. Peter. 2015. Discovering candidate genes that regulate resin canal number in *Pinus taeda* stems by integrating genetic analysis across environments, ages, and populations. *New Phytol* **205**:627-641.
- Wilkens, R. T., J. M. Spoerke, and N. Stamp. 1996. Differential responses of growth and two soluble phenolics of tomato to resource availability. *Ecology* **77**:247-258.

- Wood, S. L. 1982. The Bark and Ambrosia Beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs, No. 6, Brigham Young University.
- Wyka, T. P., P. Karolewski, R. Zytowski, P. Chmielarz, and J. Oleksyn. 2016. Whole-plant allocation to storage and defense in juveniles of related evergreen and deciduous shrub species. *Tree Physiology* **36**:536-547.
- YukonGovernment. 2010. Spruce bark beetle, Yukon forest health- forest insect and disease. Energy, Mines, and Resources, Forestry Management Department.
- YukonGovernment. 2013. Forest health report. Energy, Mines, and Resources, Forestry Management Department.